THESIS

GENETIC PARAMETER ESTIMATION AND DRY MATTER INTAKE CALCULATION AS IT APPLIES TO

FEED UTILIZATION IN BEEF CATTLE

Submitted by

Cory T. Pendley

Department of Animal Sciences

COLORADO STATE UNIVERSITY

July 8, 2010

WE HEREBY RECOMMEND THAT THE THESIS PREPARED UNDER OUR SUPERVISION BY CORY T. PENDLEY ENTITLED GENETIC PARAMETERS AND DRY MATTER CALCULATION AS IT APPLIES TO FEED UTILIZATION IN BEEF CATTLE BE ACCEPTED AS FULFILLING IN PART REQUIREMENTS FOR THE DEGREE OF MASTER OF SCIENCE.

Committee on Graduate Work

Gordon Carstens

Dustin Pendell

Advisor: Denny Crews, Jr.

Co-Advisor: R. Mark Enns

Department Head: William Wailes

ABSTRACT OF THESIS

GENETIC PARAMETER ESTIMATION AND DRY MATTER INTAKE CALCULATION AS IT APPLIES TO

FEED UTILIZATION IN BEEF CATTLE

The majority of mating systems in the U.S. beef industry have focused on increasing revenue by applying selection pressure to economically relevant traits (ERT) for outputs such as growth, calving ease, and carcass quality. There are other ERTs that affect profitability that can be improved through selection like feed intake, heifer pregnancy, and longevity. The purpose of this thesis was to expand the effective use of residual feed intake (RFI) in two distinct manners. Therefore, the objectives of the first study were to compile published estimates of heritability and genetic correlations of feed conversion ratio (FCR), RFI, average daily gain (ADG), metabolic body weight (MBW) and dry matter intake (DMI). These estimates were used to calculate weighted estimates of the respective genetic parameters. Twenty-five sets of estimates involving more than 40,000 cattle published between 1961 and 2010 were included in a meta-analysis of genetic parameters for feed intake and related traits. A generalized least squares approach was used to compute weighted mean heritability and genetic correlation estimates, as well as their SE, where weights were a function of inverse SE. Weighted heritability estimates for FCR, RFI, ADG, MBW and DMI were 0.28±0.06, 0.38±0.08, 0.32±0.08, 0.39±0.08, and 0.38±0.06, respectively. Weighted genetic correlations of FCR with RFI, ADG, MBW, and DMI were 0.60±0.07, -0.31±0.14, 0.03±0.14, and 0.35±0.11, respectively. Weighted genetic correlations of RFI with ADG, MBW were near zero, but were correlated 0.38±0.11 with DMI. The weighted genetic correlation of ADG with MBW was 0.45±0.13. These weighted heritability and genetic

correlation estimates may be more useful in the design of genetic improvement programs than relying on estimates from individual studies with low numbers of feed intake observations. For the second study, daily feed intakes were recorded on 3,702 bulls and 314 heifers across nine tests between 2007 and 2010 at Midland Bull Test in Columbus, Montana. Daily feed intake was recorded and from this DMI was calculated. Genetic variances were estimated using a multiple trait animal model and average information REML. The model was equivalent for DMI, ADG, MBW and RFI which included a fixed effect of contemporary group (breed x test x pen, n=112) and a linear covariate for age at start of test (=298.28d, SD=36.65). The heritability estimate for RFIp was 0.17 ± 0.05. Genetic correlations among growth traits (ADG, MBW and DMI) were moderate to high and positive, ranging from 0.33 to 0.70. The model including DMI and RFIp failed to converge. This resulted in the need for estimation of genetic residual feed intake (RFIg), defined as the difference between DMI EBV and expected DMI EBV. Genetic regression was used to predict expected DMI EBV from the EBVs of ADG and MBW. This approach to the genetic evaluation of RFIg allows for the estimation of breeding values that may truly reflect feed utilization differences among animals without simultaneously affecting growth or body size.

Cory Thomas Pendley
Department of Animal Science
Colorado State University
Fort Collins, CO 80523
Summer 2010

Table of Contents

LIST OF TABLES

Chapter I

Introduction and Objectives

1.1   Introduction

The majority of mating systems in the U.S. beef industry have focused on increasing

revenue by applying selection pressure to Economically Relevant Traits (**ERT**) for output such as

growth, calving ease, and carcass quality. This method has been effective in improving income

and production output of the U.S. beef industry. There are other ERTs that affect profitability

that can be improved through selection like feed intake, heifer pregnancy, and longevity. These

traits are difficult and expensive to measure, or they are expressed later in life, prohibiting early

selection decisions with any significant amount of accuracy. This is likely the primary reason for

their minimal contribution in genetic improvement schemes.

Feed efficiency has received significant attention for its potential to improve profitability

through the reduction of feed costs without affecting outputs. Average Daily Gain (**ADG**) and Dry

Matter Intake (**DMI**) are two of the most commonly used phenotypes when calculating various

traditional measures of feed efficiency. The most recent improvement has been made in the

area of Residual Feed Intake (**RFI**) as a measure of feed utilization in beef cattle. While the idea

was first introduced in by Koch et al. (1963), interest has been renewed in RFI as a measure of

beef cattle feed efficiency. The reduction of feed costs without affecting outputs

1.2   Objectives of Thesis

The objectives of this research were to:

1.2.1   Conduct a meta-analysis, or synthesize the results of many different but related

studies to obtain one quantitative result that summarizes current published parameter

estimates of feed intake and utilization traits. The limited number of animals with feed intake

data due to the difficulties associated with collected performance on large numbers of animals has caused the need for a summarization of published estimates for use in genetic evaluation. The meta analytic results may be more reliable and better suited for genetic evaluation than one set of published estimates.

1.2.2 Estimate genetic parameters for feed utilization traits as they apply to national cattle evaluation. The increasing availability of feed intake data has lead to the prospect of its incorporation in genetic evaluation. The genetic parameters are necessary for inclusion of feed utilization in these evaluations.

Chapter II

Review of Literature

2.1   Feed Efficiency and Utilization Traits

The term efficiency has traditionally implied a ratio of inputs to outputs (Carstens and

Tedeschi, 2006). Considering the umbrella trait of efficiency, gain and consumption are the only

traits that can be measured directly. Feed efficiency is then inferred from the manipulation of

gain and intake data (Koch et al. 1963). Crews (2006) pointed out that efficiency traits are

among the few measured that focus on reducing inputs; most traits included in breeding

objectives revolve around increasing outputs.

Feed inputs in beef cattle production typically occur in the feedlot sector and in the

breeding herd. Measuring cow herd forage intake on a large scale is rarely achieved; therefore,

most feed intake data is collected on growing and finishing cattle. Guidelines have been

developed for the collection of feed intake data and include age restrictions for weaned calves

specifying that cattle should be on test not before 240 days old, testing should be completed

before 390 days of age (Crews et al., 2010). Feed efficiency is most often considered an

economically relevant trait because selecting for it will directly reduce feed inputs (Golden et al.,

2000). Basarab et al. (2003) found under typical feed costs ($0.10/kg), decreasing daily feed

intake by 2.5 kg would decrease feed costs by $37.87 per head in a 150 day finishing period. In a

similar study, Herring and Bertrand (2002) found that a 2% decrease in intake with all other

traits held constant would save the U.S beef industry $111 million dollars. These are significant

savings that warrant the collection of individual feed intake data; even with the $100-200 cost

per animal. Schenkel et al. (2004) has shown statistical methods to force genetic variation in

feed intake independent of size, growth rate and back fat. We can select for lower feed intake

while accounting for and limiting correlated responses to other production traits.

2.2   Average Daily Gain and Dry Matter Intake

An animal's ADG can be computed by several different approaches. The choice of formula relies almost solely on the type of data being used. The first equation is used when only start and end weights are collected. The start and end weights can be either a single weight or more commonly, two weights for each point measured on consecutive days then averaged to get one value for each weight. With either single or dual weights, way the formula is then:

$$\underline{\hspace{4cm}}$$

The above equation will give the average body weight gained per day across the testing period. This is the more common formula; it's the simplest and requires the least amount of data collection. The above equation was dubbed the "usual" equation by Rattanaronchart et al. (1983).

There are many causes that affect the accuracy of the weights and thus the actual ADG computation. The time of measurement in relation to feeding, ambient temperature, and previous weight can all have an effect on the weight taken (Rattanaronchart et al., 1983). A variation to for calculating ADG uses two starting weights on consecutive days and averaging them to get the new start weight; the same procedure is also done with the end weights. This is essentially the same equation and has the same down fall of not accounting for body weight gain during the intermediate portion of the testing period (Rattanaronchart et al., 1983).

An alternative method used to calculate ADG is by the regression of serial weights on test day. Interval weights are taken, typically on a 2- and 3-week basis for standard feeding tests, per Beef Improvement Federation guidelines (Crews et al., 2010). A minimum of 5-6 weights need be recorded on evenly spaced time intervals across the testing period (Crews et

al., 2010). Using this approach of regression more closely estimates the true ADG for the individual. The regression equation for ADG is given as:

In this situation, β_0 is the intercept and β_1 would be the ADG estimate. If the ability to collect serial BW for the individuals is possible, this would be the more appropriate model. Fitting this model allows for the utilization of more data points while still incorporating all the information of the simple average model. It accounts for the error associated with the weight measurement process and as research has demonstrated is more appropriate when the correct data is available (Crews et al., 2010.

2.3   Feed Conversion Ratio

Feed Conversion Ratio (**FCR**) is the most common and widely used measure used to describe feed efficiency in beef cattle, even though more than two dozen other feed efficiency traits have been described in scientific literature (Archer et al., 1999). The calculation of FCR is the division of daily DMI by ADG.

The FCR estimate provides the average feed required for the animal to gain one unit of body mass. (Carstens and Tedeschi, 2006). The inverse of FCR or gross feed efficiency (**GFE**) can also be used, though it not as common in North America. The estimate of GFE would represent the amount of gain exhibited per unit of feed intake.

The use of FCR can be a useful tool when evaluating the effect differing variables on production such as diet quality, environment, and management practices (Carstens and Tedeschi, 2006). Estimates of FCR have many positive attributes that have added to its utility in the industry and have been found to be moderately heritable (Crews, 2005) and strongly

correlated to growth traits (Arthur 2001a; Koots et al., 1994b; Schenkel et al., 2004). As a result, of its moderate heritability and high correlation with growth traits, selecting for increased FCR would lead to increased performance in growth traits and increased mature size, a result of indirect selection (Herd and Bishop, 2000). The use of FCR as a selection tool is not without its inherent problems though. Crews (2006) outlines two properties of FCR suggesting that selection for increased FCR has an adverse effect on mature cow size: 1) cattle with larger mature size have higher intake requirements 2) decreasing selection for FCR (improved FCR) would result in larger mature size.

A change in FCR could be the due to either a change in numerator or denominator (ADG or DMI) and may not actually reflect a change in feed efficiency. Carstens and Tedeschi (2006) suggested the increase in feed inputs would be larger than the increase in outputs and thus the production system would be less efficient. Several publications illustrate that selection based on FCR is not the proper approach to improve feed utilization (Packard and Boardmaan, 1999; MacNeil, 2007). Gunsett (1984) agrees as this is the case for all ratio traits as selection results in divergent and unpredictable responses to the component traits if the genetic variances are different; which is the typical case. When selecting on ratio traits, the assumption is made that there is a linear relationship between the numerator and the denominator, that the regression of the numerator on the denominator is the origin and that the variance increases with increasing values (Betz, 2008). These assumptions are rarely tested so selection on ratios may result in unintended selection results (MacNeil, 2007). Due to these issues with FCR, perceived genetic gain may not indicate an actual change in the metabolic processes responsible for feed efficiency.

2.4   Partial Efficiency of Growth

When compared to FCR, partial efficiency of growth (**PEG**) is a more recent development in the area of feed efficiency. The calculation of PEG partitions intake into requirements for maintenance and requirements for growth, although it suffers from the same drawbacks as other ratio traits. The formula is given below to illustrate this:

Where, ADG is average daily gain, DMI is dry matter intake on a daily basis and DMIm is expected dry matter intake required for maintenance on a daily basis according to published population estimates for maintenance (Carstens and Tedeschi, 2006).

The DMI parameters required for maintenance are pulled directly from feeding standards such as those in NRC (1996). These estimates are population estimates for all beef cattle and thus have an inherent disadvantage; individual variations in maintenance and growth requirements are not captured. Regardless, there are advantages for PEG over FCR. The genetic (Arthur et al., 2001b) and phenotypic correlations (Nkrumah et al., 2004; Lancaster et al., 2005) between ADG and PEG are significantly lower than those of ADG and FCR. The PEG estimate has also been shown to be more favorably associated with intake than FCR. While these less severe genetic correlations are certainly more desirable from a genetic prediction standpoint, PEG does not fully capture individual variation in feed efficiency, limiting its use.

2.5   Residual Feed Intake

Residual Feed Intake (**RFI**) was first suggested as a measure to evaluate feed efficiency by Koch et al. (1963). The attempt was to evaluate the various measures of feed intake and utilization and more specifically the results of indirect selection associated with these traits. As RFI has gained in popularity and is the difference between actual and expected feed intake on the basis of production requirements and maintenance of body weight (Kennedy et al., 1993).

The RFI estimate is a linear combination of feed inputs and production traits and therefore is not subject to the problems that arise when selecting on ratios, such as FCR (Luiting et al., 1992). An example of the base model for calculating RFI is:

Where b_0 is the intercept of the regression model, b_1 is the partial regression coefficient for ADG, b_2 is the partial regression coefficient for MBW, and RFI is the residual portion of the model (Crews, 2005). Other effects can be included in the model such as a fixed effect of contemporary group, sex, year, test location, etc. Covariates for age have been found to be significant in this prediction equation, especially when large variation in age of animals during the test exists (C. Pendley, unpublished data). Due to the fact RFI is the residual of the above regression model, by definition it has the properties of being normally distributed with a mean of zero. RFI is also phenotypically independent of production, therefore it may reflect the variation in metabolic processes rather than variation due to production levels of the animal (Crews, 2005).

Two separate forms of RFI can be estimated, phenotypic and genetic, and they have different statistical properties because of the methodology used in estimation. Phenotypic RFI (**RFIp**) is the component of feed intake that is independent of production on a phenotypic level. It is a linear combination of feed intake and growth, so single trait selection on RFIp is equivalent to multiple trait selection on, or using a selection index on its components (Kennedy et al., 1993). This measure is not genetically independent of the partial regressors in the model and the genetic correlations between RFIp and production traits can vary depending on the genetic and phenotypic parameters of production and feed intake within the test population (Kennedy et al., 1993). To remove this relationship, genetic RFI (**RFIg**) can be estimated as feed intake

minus the genetic regression of feed intake on production, which makes it genetically

independent of production (Kennedy et al., 1993). The response variable in this regression is

feed intake EPD, and can be calculated as:

$$\mathbf{u}=\mathbf{U}\mathbf{G}^{-1}\mathbf{k}$$

where **u** is a vector of feed intake EPD, **U** is a matrix of body weight and daily gain EPD, **G^{-1}** is the

inverse matrix containing genetic (co)variances between the regressors, and **k** is a vector of

genetic covariance's of feed intake with the regressors (Crews, 2005). Selecting for RFIg is

equivalent to a restricted selection index holding production constant (Kennedy et al., 1993).

Literature estimates of correlations between RFIp and RFIg are high, some estimates of genetic

correlations are 0.92 and 0.97 (Nkrumah et al., 2007a; Hoque et al., 2006) and phenotypic

correlations are 0.97 and 0.98 (Nkrumah et al., 2007a; Hoque et al., 2006). Even though

selecting for RFIp is not genetically independent of production, correlated response to selection

in RFIg has been estimated to be very high. This is to say, RFIp forces phenotypic independence

with ADG and MBW but that does not translate to genetic independence.

One of the problems of using FCR as a feed efficiency measure from a genetic

improvement standpoint is that selection for it can increase mature cow size and therefore

increase feeding requirements for the cow herd. According to literature estimates of

correlations, selection for RFI will not have this problem. Estimates of genetic correlations

between postweaning RFI and mature cow size are (-0.09 to -0.22) (Herd et al., 2003). This

indicates that selection for RFI will not result in increased cow size. Supporting evidence for this

comes from Burrow and Bindon (2005) and Arhtur et al. (2005) who both reported that in

Australian beef cattle populations females that were more efficient at weaning (had lower RFI)

required less feed as non-lactating mature cows, with their performance otherwise not being

affected thus, selection for RFI may not have the adverse consequences on mature size and maintenance requirements that selection on FCR has.

There have been several studies investigating the effects of selecting for RFI on carcass traits with conflicting results. Nkrumah et al. (2004) found that RFI was weakly correlated with carcass leanness (r= -0.22) and fat depth (0.25), but that efficient animals had adequate carcass characteristics, indicating that RFI can be selected for without penalties to carcass merit. Nkrumah et al. (2007a) found that selection for RFI could lead to a small reduction in carcass fat depth in beef cattle with phenotypic correlations between carcass fat depth and RFIp of 0.23 and RFIg of 0.19; and genetic correlations with RFIp of 0.33 and RFIg of 0.27, respectively. They also found a slight improvement in carcass lean meat yield as RFI improved with phenotypic correlations with RFIp and RFIg of -0.21, and -0.16, respectively; genetic correlations were -0.54 with RFIp and -0.43 with RFIg. They found no differences between marbling scores in low, medium and high RFI groups. Robinson and Oddy (2004) reported a phenotypic correlation of 0.25 with percent intramuscular fat and RFIp. These studies were conducted using feedlot cattle, and the results suggest that selection for RFI may decrease carcass fat content. Similarly, Barendse et al. (2007) report positive genetic correlations between RFI and carcass fat, and negative genetic correlations with longisimus muscle area in a composite cattle population. Baker et al. (2006) found no differences between high and low RFI Angus steers in meat quality and palatability, and found no unfavorable relationships between RFI with carcass quality or palatability. This is in contrast to the findings of Burrow and Bindon (2005), where they report that favorable selection for RFI may negatively affect meat tenderness in Australian *Bos taurus* cattle. More research is needed to obtain valid and consistent answers as to the effect of selection for improved RFI on the beef quality atributes.

In an attempt to account for this addition variation in the utilization of feedstuffs by beef cattle, additional forms of RFIp have been approved by the Beef Improvement Federation (Crews et al., 2010); they are denoted as RFI_2 and RFI_3. If these are calculated and reported, RFIp is often referred to as RFI_1. RFI_2 is the same RFIp formula with the inclusion of subcutaneous fat depth at the 12th-13th rib interface (**FAT**), measured using ultrasound. RFI_3 is the calculation of RFI_2 with the addition of an ultrasound measure of logissimus muscle area (**REA**). The linear representations of the three RFI measures on the phenotypic level are given below; they are provided by Crews et al. (2010).

$$RFI_1=DMI-(\beta_0+\beta_1\times ADG+\beta_2\times MBW)=DMI-E(DMI)$$

$$RFI_2=DMI-(\beta_0+\beta_1\times ADG+\beta_2\times MBW+\beta_3\times FAT)$$

$$RFI_3=DMI-(\beta_0+\beta_1\times ADG+\beta_2\times MBW+\beta_3\times FAT+\beta_4\times REA)$$

When selecting for improved RFI, it is important to take into account correlations that might exist between RFI and other traits in order to be aware of consequences that could arise when selecting for RFI. This trait has a clear biological interpretation and heritability estimates suggest that genetic improvement in possible. Another benefit of selecting for RFI is that it will respond like a selection index on its component traits, and does not have the disadvantages inherent with the ratio traits such as FCR. The residualization of feed efficiency forces the correlation with the component traits (ADG and MBW) to zero by law or regression. This limits the unpredictable indirect selection that occurs with most measures of feed utilization. The extent to which RFI reflects true biological efficiency depends on the way production is measured and defined, and the magnitude of measurement errors, which is not trivial (van der Werf, 2004).

There are several challenges to the use of RFI as a selection criterion. The relationships between RFI and other traits involved in production are not yet well known. The publication and

exploration of RFI is still in relatively infantile stages. The consistency of parameter estimates has not yet been achieved. There needs to be standards for the collection and manipulation of these data. The Beef Improvement Federation has recently approved guidelines for feed intake data collection; these guidelines will enable a standard data collection and use strategy to be adhered to and the thus the estimates should become more stable and reliable.

Selection on RFI is no different than selection on all component traits (Luiting, 1992). This is to say there are no advantages to RFI selection if selection on all component traits already exists. The genetic parameters are a function of the genetic parameters of the component traits (Kennedy et al., 1993; van der Werf, 2004). Others persist that RFI is still essentially a ratio trait and thus has little to no value in a genetic evaluation setting. The basis for these arguments is, selecting on and prediction of inputs and outputs will provide more accurate estimations of producer profitability. Garrick (2006) states, selection to improve profit will be more effective when based on predicted outputs and predicted inputs than on ratios such as efficiency.

2.6   Heritability estimates and correlations between feed utilization traits

Heritability estimates for multiple measures of feed efficiency taken from literature are given below in Table 2.1. The estimates for FCR vary from 0.46 to 0.06. The majority of estimates fall in the moderately heritable range indicating the potential for genetic improvement.

Table 2.1 Literature reported heritability estimates (±SE) for various feed efficiency related traits

Source	Trait[1]				
	FCR	RFI	ADG	MBW	DMI
Arthur et al. (2001 b)	0.46±0.04	0.39±0.04	0.34±0.04	0.37±0.04	0.48±0.04
Arthur et al. (1997)	0.31±0.09	0.44±0.07	0.41±0.08	.	0.59±0.07
Fan et al. (1995)	0.16±0.14	.	0.26±0.20	.	0.24±0.11
Herd and Bishop (2000)	0.17±0.09	.	0.38±0.10	0.36±0.09	0.31±0.08
Nkrumah et al. (2007)	.	0.21±0.12	0.59±0.17	0.31±0.14	0.54±0.15
Hoque et al. (2009)	0.38±0.07	0.49±0.09	.	.	0.36±0.09
Lancaster et al. (2009)	0.29±0.12	0.47±0.13	0.21±0.12	.	0.48±0.14
Elzo et al. (2009)	0.24±0.11	0.19±0.11	.	.	0.42±0.13
Schenkel et al. (2004)	0.37±0.06	0.38±0.07	0.35±0.03	0.35±0.02	0.44±0.06
Herring and Bertrand (2002)	0.15±.	0.50±.	0.28±.	.	0.44±.
Arthur et al. (2001 a)	0.29±0.04	0.39±0.03	0.28±0.04	0.40±0.02	0.39±0.03
Robinson and Oddy (2004)	0.06±0.04	0.18±0.06	0.23±0.06	0.41±0.07	0.27±0.06
Crowley et al. (2010)	0.30±0.06	0.45±0.06	0.30±0.06	0.69±0.07	0.49±0.06
Brown and Gacula (1962)	0.41±0.25	.	.	.	0.43±0.18
Swinger et al. (1961)	.	.	.	.	0.38±0.36
Koch et al. (1963)	0.36±0.10	.	.	.	0.64±0.12
Brown et al. (1974)	0.36±0.17	.	.	.	0.44±0.20
Dickerson et al. (1978)	.	.	.	.	0.41±0.14
Marvogenis et al. (1978)	0.16±0.10	.	.	.	0.44±0.25
Sasaki et al. (1982)	0.24±0.08	.	.	.	0.32±0.08
Hanset et al. (1987)	0.39±0.14	.	.	.	0.28±0.13
Chewing et al. (1990)	0.38±0.13	.	.	.	0.58±0.15
Chewing et al. (1990)	0.30±0.11	.	.	.	0.48±0.13
Bishop (1992)	0.14±0.08	.	.	.	0.30±0.09
Mrode et al. (1990)	0.29±0.09	.	.	.	0.06±0.05
Swinger et al. (1965)	.	.	.	.	0.46±0.20

FCR= Feed Conversion Ratio, RFI= Residual Feed Intake, ADG= Average Daily Gain, MBW=Metabolic Body Weight, DMI= Dry Matter Intake

The phenotypic and genetic correlations between FCR and other traits related to beef cattle feed efficiency are provided below in tables 2.2 and 2.3 respectively.

Table 2.2: Phenotypic correlations between Feed Conversion Ratio (FCR) and other traits related to feed efficiency

Source	Measure related to feed efficiency[1]			
	RFI	ADG	MBW	DMI
Arthur et al. (2001b)	0.57	-0.54	-0.08	0.48
Arthur et al. (1997)	0.51	.	.	.
Fan et al. (1995)	.	-0.74	.	.
Fan et al. (1995)	.	-0.12	.	.
Herd and Bishop (2000)	0.61	.	.	.
Hoque et al. (2009)	0.60	.	.	0.21
Lancaster et al. (2009)	0.59	-0.71	0.10	0.15
Elzo et al. (2009)	0.55	.	.	0.37
Schenkel et al. (2004)	0.76	-0.58	0.05	0.47
Arthur et al. (2001a)	0.53	-0.74	0.16	0.23
Robinson and Oddy (2004)	0.45	-0.08	-0.14	-0.14
Crowley et al. (2010)	0.41	-0.71	0.12	0.34

[1]RFI= Residual Feed Intake, ADG= Average Daily Gain, MBW= Metabolic Body Weight, DMI= Dry Matter Intake

The estimates for phenotypic correlations vary from 0.76 to 0.41, -0.08 to -0.74, 0.16 to -0.14, and 0.48 to -0.14 between FCR and RFI, ADG, Metabolic Body Weight (**MBW**), and DMI, respectively. Strong correlations exist, both favorable and unfavorable, on a phenotypic level between FCR and other measures used to quantify feed utilization. This reaffirms what many studies have suggested; selection for FCR would affect multiple traits in unknown ways from a phenotypic standpoint. Due to the unknown magnitude of these components, predicting and controlling the extraneous effects when selecting for FCR becomes nearly impossible.

Table 2.3: Genetic correlations (±SE) between Feed Conversion Ratio (FCR) and other traits related to feed efficiency

	Trait[1]			
	RFI	ADG	MBW	DMI
Arthur et al. (2001b)	0.85±0.05	-0.46±0.08	0.24±0.09	0.64±0.07
Herd and Bishop (2000)	0.70±0.22	.	.	.
Nkrumah et al. (2007	0.62±0.09			
Hoque et al. (2009)	0.78±0.06	.	.	0.37±0.09
Lancaster et al. (2009)	0.93±0.09	-0.36±0.31	-0.29±0.32	0.60±0.26
Elzo et al. (2009)	0.09±0.38	.	.	.
Schenkel et al. (2004)	0.69±.	-0.52±.	-0.13±.	0.39±.
Herring and Bertrand (2002)	0.65±.	0.01±.	.	0.56±.
Arthur et al. (2001a)	0.66±0.05	-0.62±0.06	-0.01±0.07	0.31±0.07
Robinson and Oddy (2004)	0.41±0.32	-0.86±0.10	-0.62±0.18	-0.49±0.22
Crowley et al. (2010)	0.48±0.10	-0.53±0.10	0.35±0.11	0.38±0.11
Brown et al. (1974)	.	.	.	-0.11±0.42
Bishop (1992)	.	.	.	0.18±.
Koch et al. (1963)	.	.	.	0.04±.
Marvogenis et al. (1978)	.	.	.	0.72±0.25
Sasaki et al. (1982)	.	.	.	0.91±0.17
Hanset et al. (1987)	.	.	.	0.20±0.30
Mrode et al. (1990)	.	.	.	0.05±0.37

[1]RFI= Residual Feed Intake, ADG= Average Daily Gain, MBW= Metabolic Body Weight, DMI= Dry Matter Intake

The estimates for genetic correlations vary from 0.93 to 0.41, 0.86 to 0.01, 0.35 to -0.65, 0.83 to -0.49 between FCR and RFI, ADG, MBW, and DMI, respectively. There is substantial variation in estimates of these genetic correlations. Consistent and more stable estimates would be needed if FCR were to ever be incorporated into a selection index or to justify selection for its improvement. Although given the downsides of selection on ratio traits given in above in section 2.3, this would not be ideal.

The phenotypic and genetic correlations to other traits related to beef cattle feed efficiency are provided below in Tables 2.4 and 2.5 respectively.

Table 2.4: Phenotypic correlations between phenotypic Residual Feed Intake (RFI) and other traits related to feed efficiency

Source	Measure related to feed efficiency[1]			
	FCR	DMI	MBW	ADG
Arthur et al. (2001b)	0.57	0.6	0.01	0.03
Arthur et al. (1997)	0.51	0.52	.	0.01
Herd and Bishop (2000)	0.61	0.7	0.01	0.01
Nkrumah et al. (2007)	.	0.64	0.00	-0.007
Hoque et al. (2009)	0.60	0.83	.	.
Lancaster et al. (2009)	0.59	0.7	0.00	0.00
Elzo et al. (2009)	0.55	0.89	.	.
Schenkel et al. (2004)	0.76	0.81	-0.06	-0.11
Arthur et al. (2001a)	0.53	0.72	-0.06	0.02
Robinson and Oddy (2004)	0.45	0.57	-0.01	-0.01
Crowley et al. (2010)	0.41	0.58	0.00	0.00

[1]FCR=Feed Conversion Ratio, ADG= Average Daily Gain, MBW= Metabolic Body Weight, DMI= Dry Matter Intake

The phenotypic correlations vary from 0.76 to 0.41, 0.82 to 0.59, 0.01 to -0.06, and 0.01 to -0.11 between RFI and FCR, DMI, MBW, and ADG, respectively. RFI is strongly and positively correlated to DMI and FCR on a phenotypic level. The correlations with ADG and MBW are what are to be expected, near zero. This holds true to the statistical properties of regression, the residual is uncorrelated with the component traits.

Table 2.5: Genetic correlations between phenotypic Residual Feed Intake (RFI) and other traits related to feed efficiency

Source	Measure related to feed efficiency[1]			
	FCR	DMI	MBW	ADG
Arthur et al. (2001b)	0.85±0.05	0.79±0.04	0.32±0.10	-0.10±0.13
Herd and Bishop (2000)	0.70±0.22	0.64±0.16	0.22±0.29	0.09±0.29
Nkrumah et al. (2007)	.	0.73±0.18	0.27±0.33	0.46±0.45
Hoque et al. (2009)	0.78±0.06	0.70±0.05	.	.
Lancaster et al. (2009)	0.93±0.09	0.85±0.08	0.33±0.29	0.04±0.32
Elzo et al. (2009)	0.09±0.38	0.73±0.13	.	.
Schenkel et al. (2004)	0.69±.	0.81±.	-0.17±.	-0.01±.
Herring and Bertrand (2002)	0.65±.	0.92±.	.	.
Arthur et al. (2001a)	0.66±0.05	0.69±0.03	-0.06±0.06	-0.04±0.08
Robinson and Oddy (2004)	0.41±0.22	0.43±0.15	-0.20±0.16	0.09±0.20
Crowley et al. (2009)	0.48±0.10	0.59±0.13	-0.17±0.09	0.01±0.13

[1]FCR=Feed Conversion Ratio, ADG= Average Daily Gain, MBW= Metabolic Body Weight, DMI= Dry Matter Intake

Contrary to the phenotypic correlations between RFI and the component traits of ADG and MBW being zero, the genetic correlations are not. These genetic correlations vary from 0.93 to 0.09, 0.92 to 0.43, 0.46 to -0.1 and 0.33 to -0.17 between RFI and FCR, DMI, MBW, and ADG, respectively. This residualization process forces correlations of zero between the component trait and the residual. The calculation forces only a phenotypic correlation of RFI with ADG and MBW to zero, but this does not mean the genetic correlations will be zero.

2.7   Literature Cited

Archer, J. A., E. C. Richardson, R. M. Herd, P. F. Arthur. 1999. Potential for selection to improve efficiency of feed use in beef cattle: a review. Aust. J. Agric. Res. 50:147–61.

Arthur, P.F., J.A. Archer,R.M. Herd, E.C. Richardson, S.C. Exton, J.H. Wright, K.C.P. Dibley, D.A. Burton. 1997. Genetic and phenotypic variation in feed intake, feed efficiency and growth in beef cattle. Proceedings of the 12th Conf. of the Assoc. for the Advancement of Anim. Breeding and Genetics 12:234-237.

Arthur, P. F., J. A. Archer, D. J. Johnston, R. M. Herd, E. C. Richardson, P. F. Parnell. 2001a. Genetic and phenotypic variance and covariance components for feed intake, feed efficiency, and other postweaning traits in Angus cattle. J. Anim Sci. 79:2805–2811.

Arthur, P. F., G. Renandb, D. Krauss. 2001b. Genetic and phenotypic relationships among different measures of growth and feed efficiency in young charolais bulls. Livestock Prod Sci. 68:131–139.

Basarab, J.A., M.A. Price, J.L. Aalhus, E.K. Okine, W.M. Snelling, K.L. Lyle. 2003. Residual feed intake and body composition in young growing cattle. Can. J. Anim. Sci. 83:189-204.

Betz, G.C.M. 2008. QTL influencing feed efficiency in beef cattle. Thesis. Colorado State Univ., Fort Collins.

Burrow, H. M., and B. M. Bindon. 2005. Genetics research in the Cooperative Research Centre for Cattle and Beef Quality. Aust. J. of Expe. Ag. 45: 941-957.

Carstens, G.E. and L.O. Tedeschi. 2006. Defining feed efficiency in beef cattle. Proceedings of the 38th Beef Improvement Federation Annual Research Symposium and Meeting 38:12-21.

Crews Jr., D. H. 2005. Genetics of efficient feed utilization and national cattle evaluation: a review. Genet. Mol. Res. 4:152-65

Crews Jr., D.H. 2006. The genetics of feed efficiency in beef cattle. Proceedings of the 38th Beef Improvement Federation Annual Research Symposium and Meeting 38:22-31.

Crews Jr.,D.H., G.E. Carstens, J.A. Basarab, R.A. Hill, and M.K. Nielsen. 2010. Feed intake and efficiency in: guidelines for uniform beef improvement programs, 9th Ed. [In Pres]

Crowley, J. J., M. McGee, D. A. Kenny, D. H. Crews, Jr., R. D. Evans, D. P. Berry. 2009. Phenotypic and genetic parameters for different measures of feed efficiency in different breeds of Irish performance tested beef bulls J. Anim. Sci. 88:885-894

Elzo, M.A., D.G. Riley, G.R. Hansen, D.D. Johnson, R.O. Myer, S.W. Coleman, C.C. Chase, J.G.

Wasdin, J.D. Driver. 2009. Effect of breed composition on phenotypic residual feed intake and growth in Angus, Brahman, and Angus x Brahman crossbred cattle. J Anim. Sci. 2009. 87:3877-3886.

Fan, L.Q., D.R. Bailey, N.H. Shannon. 1995. Genetic parameter estimation of postweaning gain, feed intake, and feed efficiency for Hereford and Angus bulls feed two different diets. J Anim Sci 1995. 73:365-372.

Golden, B. L., Garrick, D.J., Newman, S., Enns, R. M. 2000. A framework for the next generation of EPDs. Proceedings of the 32nd Beef Improvement Federation Annual Research Symposium and Meeting 32:2-12.

Gunsett, F. C. 1984. Linear Index Selection to Improve Traits Defined as Ratios. J. Anim Sci. 59:1185–1193.

Herd, R.M and S.C. Bishop. 2000. Genetic variation in residual feed intake and its association with other production traits in British Hereford cattle. Livest. Prod. Sci. 63: 111-119.

Herring, W. O. and J. K. Bertrand. 2002. Multi-trait prediction of feed conversion. Proceedings of the 34th Beef Improvement Federation Annual Research Symposium and Meeting 34: 89-97

Hoque, M.A., M. Hosono, T. Oikawa, K. Suzuki. 2009. Genetic parameters for measures of energetic efficiency of bulls and their relationship with carcass traits of field progeny in Japanese Black cattle. J. Anim. Sci. 87:99-106

Koch, R. M., L. A. Swiger, D. Chambers, K. E. Gregory. 1963. Efficiency of feed use in beef cattle. J. Anim Sci., 22:486–494.

Koots, K., J. Gibson, C. Smith, J. Wilton, J. 1994a. Analyses of published genetic parameter estimates for beef production traits. 1. heritability. Anim. Breed. Abst., 62:309–338.

Koots, K., J. Gibson, J. Wilton. 1994b. Analyses of published genetic parameter estimates for beef production traits. 2. phenotypic and genetic correlations. Anim. Breed. Abst., 62:825–853.

Lancaster, P.A., G.E. Carstens, D.H. Crews, Jr., T.H. Welsh, Jr., T.D.A. Forbes, D.W. Forrest, L.O. Tedeschi, R.D. Randel, F.M. Rouquette. 2009. Phenotypic and genetic relationships of residual feed intake with performance and ultrasound carcass traits in Brangus heifers. J Anim. Sc. 2009. 87: 3887-3896.

Luiting, P., J.H.J. Van der Werf, T.H.E. Meuwissen. 1992. Proof of equivalence of selection indicies containing traits adjusted for each other. Proceedings of the 43rd annual meeting of the European Association of Animal Production. (Madrid, Spain)

Nkrumah, J.D., J.A. Basarab, Z. Wang, C. Li, M.A. Price, E.K. Okine, D. H. Crews, S. S. Moore. 2007. Genetic and phenotypic relationships of feed intake and different measures of feed efficiency with growth and carcass merit of beef cattle. J Anim. Sci. 85: 2711-2720.

Nutrient Requirements of Beef Cattle, 7th ed. Committee on Animal Nutrition, Booard of Agriculture, National Research Council. National Academy of Press. Washington, D.C. 1996.

Packard, G. C. and T. J. Boardman. 1999. The use of percentages and size-specific indices to normalize physiological data for variation in body size: wasted time, wasted effort? Comp. Biochem. Physiol, Part A 122:37–44.

Rattanaronchart, S., M. Grossman, R.L. Fernando, R.D. Shanks. 1983. A Monte-Carlo Comparison of Estimators of Average Daily Gain in Body Weight. J. Anim Sci. 57: 885-891

Renand, G. and Krauss, D. 2002. Genetic relationship between fattening and slaughter traits In purebred Charolais young bulls. Proc. 7th World Congr. Genet. Appl. Livest. Prod., Institut Nacional de la Recherche Agronomique, France. Montpellier, France. Communication No. 10-08. [CD-ROM].

Robinson, D.L. and V.H. Oddy. 2004. Genetic parameters for feed efficiency, fatness, muscle area and feeding behavior of feedlot finished beef cattle. Livestock Prod. Sci. 90:255-270

Schenkel, F.S., S.P. Miller, and J.W. Wilton. 2004. Genetic parameters and breed differences for feed efficiency, growth, and body composition traits of young beef bulls. Can. J. Anim. Sci. 84:177-184.

van der Werf, J. H. J. 2004. Is it useful to define residual feed intake as a trait in animal breeding programs? Aust. J. Exp. Agric. 44:405–409.

Chapter III

Analysis of published genetic parameter estimates for feed utilization traits in beef cattle

3.1 ABSTRACT

The potential for increasing profitability of beef production through the reduction of input costs has been documented with an increasing number of published genetic parameter estimates for feed intake and utilization traits. The inclusion of input traits in genetic improvement programs requires knowledge of parameters for those traits, but an understanding of these parameters, especially for feed intake, is limited due to the cost of recording individual feed intake on cattle and reports are scarce. Therefore, the objectives of this study was to compile published estimates of heritability and genetic correlations of feed conversion ratio (**FCR**), residual feed intake (**RFI**), ADG, metabolic body weight (**MBW**) and DMI. These estimates were used to calculate weighted estimates of the respective genetic parameters where SE was the weighting factor. Twenty-five sets of estimates involving more than 40,000 cattle published between 1961 and 2010 were included in a meta-analysis of genetic parameters for feed intake and related traits. Papers were required to include heritability estimates with computed SE and at least one or more genetic correlation estimates between feed utilization traits. A generalized least squares approach was used to compute weighted mean heritability and genetic correlation estimates, as well as their SE, where weights were a function of inverse SE. Weighted heritability estimates for FCR, RFI, ADG, MBW and DMI were 0.28±0.06, 0.38±0.08, 0.32±0.08, 0.39±0.08, and 0.38±0.06, respectively. Weighted genetic correlations of FCR with RFI, ADG, MBW, and DMI were 0.60±0.07, -0.31±0.14, 0.03±0.14, and 0.35±0.11, respectively. Weighted genetic correlations of RFI with ADG, MBW were near zero, but were 0.38±0.11 with DMI. The phenotypic correlation of RFI with ADG and MBW are forced to zero by definition. The weighted genetic correlation of ADG with MBW was 0.45±0.13. These weighted heritability and genetic correlation estimates may be more useful in the design of

genetic improvement programs compared to relying on estimates from individual studies with low numbers of feed intake observations.

3.2   Introduction

The potential to increase profitability of beef cattle production through the reduction of input costs is documented by an increasing number of published genetic parameter estimates for feed intake and related utilization traits (e.g., Herring and Bertrand, 2002; Basarab et al., 2003; Golden et al., 2000). The inclusion of input traits in genetic improvement protocols requires knowledge of genetic and residual parameters for those traits, but an understanding of these parameters, especially for feed intake, is limited primarily due to the cost of recording individual feed intake on cattle. Accordingly, reports including parameters are scarce. The lack of feed intake data collection has limited its incorporation in national cattle evaluation (**NCE**). Unlike most relevant output traits, which have ample records to complete a useful NCE, input traits such as feed utilization lack the data to conduct evaluations on a regular basis. Recent improvement in the technology used to collect individual daily feed intake on group fed cattle is becoming more common throughout the industry, thus the testing supply can more adequately meet the demand of producers wishing test their cattle. This should reduce the per head cost of collecting data. The purpose of this study was to provide weighted mean parameter estimates for feed conversion ratio (**FCR**), residual feed intake (**RFI**), ADG, metabolic body weight (**MBW**), and DMI based on the limited number of published studies with these estimates. The Beef Improvement Federation has accepted a draft for feed intake and efficiency guidelines by Crews et al. (2010) that outlines the protocols of feed intake data collection. These standards to follow should improve the availability and consistency of feed intake records for use in NCE.

3.3 Materials and Methods

Twenty five papers with parameter estimates published between 1961 and 2010 were included in this meta-analysis of genetic parameters for feed intake and related traits. Papers were required to include heritability estimates with computed SE and genetic correlation estimates of FCR, RFI, ADG, MBW, and DMI. A generalized least squares approach, as described by Koots et al. (1994a; 1994b), was used to compute weighted mean heritability and genetic correlation estimates, as well as their weighted SE, where weights were a function of inverse SE. The weighted heritability was calculated by pooling the published estimate and weighting it by the inverse of sampling variance (SE^2). The standard error of the pooled heritability is weighted by the relation of the heritability estimate to the mean heritability estimate. The equation for weighted heritability is:

$$h^2 \text{ pooled} = \frac{\sum_{i=1}^{n} h^2{}_i / (SE_{h^2{}_i})^2}{\sum_{i=1}^{n} 1 / (SE_{h^2{}_i})^2}$$

$$\overline{} \atop \overline{} \qquad .$$

Genetic correlations (*r*) and their SE were first transformed to an approximate normal scale by Fisher's Z transformation (Fisher,1921; Steele and Torrie, 1980) using:

$$Z = 0.5 \log \frac{(1+r)}{(1-r)}$$

with $\qquad SE_Z = \sqrt{1/(n-3)}$.

The Z values were pooled and weighted with the inverse of their SE_{Zi} :

$$Z_{pooled} = \frac{\sum_{i=1}^{n} Z_i / (SE_{Zi})^2}{\sum_{i=1}^{n} 1 / (SE_{Zi})^2}$$

The mean pooled Z was transformed back to the correlation using:

$$r = \frac{(e^{2z} - 1)}{(e^{2z} + 1)}.$$

The published heritability estimates for FCR, RFI, ADG, MBW, and DMI are given below in Table 3.1. The fixed effects used in the models to produce these estimates were not included in the weighted means due to the lack of similarity among publications. Koots et al. (1994a; 1994b) included effects like breed, location, year and sex of the cattle. Due to the limited number of parameter estimates and the wide variety of fixed effects represented in these studies; this weighted mean method was unable to account for these fixed effects. These literature parameters had accounted for the relevant fixed effects within their respective studies, without knowledge of these fixed effect solutions, readjusting for them could have skewed the results; thus SE was the only weighting factor in the pooled estimates.

Table 3.1 Literature reported heritability estimates (±SE) for various feed efficiency related traits

Source	Trait[1]				
	FCR	RFI	ADG	MBW	DMI
Arthur et al. (2001 b)	0.46±0.04	0.39±0.04	0.34±0.04	0.37±0.04	0.48±0.04
Arthur et al. (1997)	0.31±0.09	0.44±0.07	0.41±0.08	.	0.59±0.07
Fan et al. (1995)	0.16±0.14	.	0.26±0.20	.	0.24±0.11
Herd and Bishop (2000)	0.17±0.09	.	0.38±0.10	0.36±0.09	0.31±0.08
Nkrumah et al. (2007)	.	0.21±0.12	0.59±0.17	0.31±0.14	0.54±0.15
Hoque et al. (2009)	0.38±0.07	0.49±0.09	.	.	0.36±0.09
Lancaster et al. (2009)	0.29±0.12	0.47±0.13	0.21±0.12	.	0.48±0.14
Elzo et al. (2009)	0.24±0.11	0.19±0.11	.	.	0.42±0.13
Schenkel et al. (2004)	0.37±0.06	0.38±0.07	0.35±0.03	0.35±0.02	0.44±0.06
Herring and Bertrand (2002)	0.15±.	0.50±.	0.28±.	.	0.44±.
Arthur et al. (2001 a)	0.29±0.04	0.39±0.03	0.28±0.04	0.40±0.02	0.39±0.03
Robinson and Oddy (2004)	0.06±0.04	0.18±0.06	0.23±0.06	0.41±0.07	0.27±0.06
Crowley et al. (2010)	0.30±0.06	0.45±0.06	0.30±0.06	0.69±0.07	0.49±0.06
Brown and Gacula (1962)	0.41±0.25	.	.	.	0.43±0.18
Swinger et al. (1961)	.	.	.	.	0.38±0.36
Koch et al. (1963)	0.36±0.10	.	.	.	0.64±0.12
Brown et al. (1974)	0.36±0.17	.	.	.	0.44±0.20
Dickerson et al. (1978)	.	.	.	.	0.41±0.14
Marvogenis et al. (1978)	0.16±0.10	.	.	.	0.44±0.25
Sasaki et al. (1982)	0.24±0.08	.	.	.	0.32±0.08
Hanset et al. (1987)	0.39±0.14	.	.	.	0.28±0.13
Chewing et al. (1990)	0.38±0.13	.	.	.	0.58±0.15
Chewing et al. (1990)	0.30±0.11	.	.	.	0.48±0.13
Bishop (1992)	0.14±0.08	.	.	.	0.30±0.09
Mrode et al. (1990)	0.29±0.09	.	.	.	0.06±0.05
Swinger et al. (1965)	.	.	.	.	0.46±0.20

FCR= Feed Conversion Ratio, RFI= Residual Feed Intake, ADG= Average Daily Gain, MBW=Metabolic Body Weight, DMI= Dry Matter Intake

3.4   Results and Discussion

The heritability estimates for FCR range from 0.06 to 0.46 which is both lower and more variable than the heritability estimate range of 0.18 to 0.50 for RFI. The published estimates of heritability of the component traits (ADG, MBW and DMI) range from 0.16 to 0.69. The phenotypic and genetic correlations between FCR and other related traits are provided in Tables 3.2 and 3.3, respectively.

Table 3.2: Phenotypic correlations between FCR and RFI, ADG, MBW, and DMI

Source	Measure related to feed efficiency[1]			
	RFI	ADG	MBW	DMI
Arthur et al. (2001b)	0.57	-0.54	-0.08	0.48
Arthur et al. (1997)	0.51	.	.	.
Fan et al. (1995)	.	-0.74	.	.
Fan et al. (1995)	.	-0.12	.	.
Herd and Bishop (2000)	0.61	.	.	.
Hoque et al. (2009)	0.60	.	.	0.21
Lancaster et al. (2009)	0.59	-0.71	0.10	0.15
Elzo et al. (2009)	0.55	.	.	0.37
Schenkel et al. (2004)	0.76	-0.58	0.05	0.47
Arthur et al. (2001a)	0.53	-0.74	0.16	0.23
Robinson and Oddy (2004)	0.45	-0.08	-0.14	-0.14
Crowley et al. (2009)	0.41	-0.71	0.12	0.34

[1]RFI= Residual Feed Intake, ADG= Average Daily Gain, MBW= Metabolic Body Weight, DMI= Dry Matter Intake

Table 3.3: Genetic correlations (±SE) between Feed Conversion Ratio (FCR) and other traits related to feed efficiency

| | Trait[1] | | | |
	RFI	ADG	MBW	DMI
Arthur et al. (2001b)	0.85±0.05	-0.46±0.08	0.24±0.09	0.64±0.07
Herd and Bishop (2000)	0.70±0.22	.	.	.
Nkrumah et al. (2007	0.62±0.09			
Hoque et al. (2009)	0.78±0.06	.	.	0.37±0.09
Lancaster et al. (2009)	0.93±0.09	-0.36±0.31	-0.29±0.32	0.60±0.26
Elzo et al. (2009)	0.09±0.38	.	.	.
Schenkel et al. (2004)	0.69±.	-0.52±.	-0.13±.	0.39±.
Herring and Bertrand (2002)	0.65±.	0.01±.	.	0.56±.
Arthur et al. (2001a)	0.66±0.05	-0.62±0.06	-0.01±0.07	0.31±0.07
Robinson and Oddy (2004)	0.41±0.32	-0.86±0.10	-0.62±0.18	-0.49±0.22
Crowley et al. (2010)	0.48±0.10	-0.53±0.10	0.35±0.11	0.38±0.11
Brown et al. (1974)	.	.	.	-0.11±0.42
Bishop (1992)	.	.	.	0.18±.
Koch et al. (1963)	.	.	.	0.04±.
Marvogenis et al. (1978)	.	.	.	0.72±0.25
Sasaki et al. (1982)	.	.	.	0.91±0.17
Hanset et al. (1987)	.	.	.	0.20±0.30
Mrode et al. (1990)	.	.	.	0.05±0.37

[1]RFI= Residual Feed Intake, ADG= Average Daily Gain, MBW= Metabolic Body Weight, DMI= Dry Matter Intake

The genetic correlations were used in calculation of the weighted mean estimates between FCR and the other feed utilization traits. The phenotypic and genetic correlations between RFI and other related traits are given in Tables 3.4 and 3.5, respectively. Correlations of RFI with FCR, ADG, MBW and DMI are provided as examples of how the one of the newer measures of feed utilization (RFI) compares to one of the more traditional measures (FCR).

Table 3.4: Phenotypic correlations between RFI and FCR, DMI, MBW and ADG

Source	Measure related to feed efficiency[1]			
	FCR	DMI	MBW	ADG
Arthur et al. (2001b)	0.57	0.60	0.01	0.03
Arthur et al. (1997)	0.51	0.52	0.01	.
Herd and Bishop (2000)	0.61	0.70	0.01	0.01
Nkrumah et al. (2007)	.	0.64	0.00	-0.01
Hoque et al. (2009)	0.60	0.83	.	.
Lancaster et al. (2009)	0.59	0.70	0.00	0.00
Elzo et al. (2009)	0.55	0.89	.	.
Schenkel et al. (2004)	0.76	0.81	-0.06	-0.11
Arthur et al. (2001a)	0.53	0.72	-0.06	0.02
Robinson and Oddy (2004)	0.45	0.57	-0.01	-0.01
Crowley et al. (2009)	0.41	0.58	0.00	0.00

[1]RFI=Residual Feed Intake, FCR=Feed Conversion Ratio, ADG=Average Daily Gain, MBW= Metabolic Body Weight, DMI=Dry Matter Intake

Table 3.5: Genetic correlations between phenotypic Residual Feed Intake (RFI) and other traits related to feed efficiency

Source	Measure related to feed efficiency[1]			
	FCR	DMI	MBW	ADG
Arthur et al. (2001b)	0.85±0.05	0.79±0.04	0.32±0.10	-0.10±0.13
Herd and Bishop (2000)	0.70±0.22	0.64±0.16	0.22±0.29	0.09±0.29
Nkrumah et al. (2007)	.	0.73±0.18	0.27±0.33	0.46±0.45
Hoque et al. (2009)	0.78±0.06	0.70±0.05	.	.
Lancaster et al. (2009)	0.93±0.09	0.85±0.08	0.33±0.29	0.04±0.32
Elzo et al. (2009)	0.09±0.38	0.73±0.13	.	.
Schenkel et al. (2004)	0.69±.	0.81±.	-0.17±.	-0.01±.
Herring and Bertrand (2002)	0.65±.	0.92±.	.	.
Arthur et al. (2001a)	0.66±0.05	0.69±0.03	-0.06±0.06	-0.04±0.08
Robinson and Oddy (2004)	0.41±0.22	0.43±0.15	-0.20±0.16	0.09±0.20
Crowley et al. (2009)	0.48±0.10	0.59±0.13	-0.17±0.09	0.01±0.13

[1]FCR=Feed Conversion Ratio, ADG= Average Daily Gain, MBW= Metabolic Body Weight, DMI= Dry Matter Intake

Residual correlations and variance components are not provided although they are

necessary for NCE. These estimates are rarely published and without phenotypic variance the

back calculation of these parameters is not possible. The limited availability of published

residual variance components is the primary factor for the weighted means of these necessary

estimates not being provided. Approximation of the variances would be possible as the SD of

the phenotypic observations is most often available but they are not adjusted for the fixed

effects of the study. Calculation of the residual parameters would be plausible based on the

phenotypic variances of the prospective data set in which these weighted estimates would be

utilized for a NCE. The genetic correlations were used in calculation of the weighted mean

estimate. The weighted estimates of heritability and genetic correlations are given in Table 3.6.

Heritability mean estimates are on the diagonal while genetic correlations are on the off

diagonal. The weighted mean heritability and genetic correlations represent published estimates

regarding the four discussed feed utilization traits. The weighted means may be the best option

in cases where data sets including feed intake data, are too small for direct estimation of genetic

parameters or when the SE is too large to rely on the local estimate. Given the large variability

and the large SE for these published parameters, a weighted mean approach is often more

prudent.

Table 3.6: Weighted estimates of heritability (on-diagonal) and
genetic correlations (off-diagonal) for feed utilization measures

Trait [1]	FCR	RFI	ADG	MBW	DMI
FCR	0.28±0.06				
RFI	0.60±0.07	0.38±0.08			
ADG	-0.31±0.11	-0.01±0.09	0.32±0.08		
MBW	0.03±0.14	0.00±0.15	0.45±0.13	0.39±0.08	
DMI	0.35±0.11	0.38±0.12	0.38±0.11	0.40±0.09	0.38±0.06

[1]FCR= Feed Conversion Ratio, RFI= Residual Feed Intake, ADG=
Average Daily Gain, MBW= Metabolic Body Weight, DMI= Dry Matter
Intake

3.5   Literature Cited

Arthur, P.F., J.A. Archer,R.M. Herd, E.C. Richardson, S.C. Exton, J.H. Wright, K.C.P. Dibley, D.A. Burton. 1997. Genetic and phenotypic variation in feed intake, feed efficiency and growth in beef cattle. Proceedings of the 12th Conference of the Association for the Advancement of Animal Breeding and Genetics 12:234-237.

Arthur, P. F., J. A. Archer, D. J. Johnston, R. M. Herd, E. C. Richardson, P. F. Parnell. 2001a. Genetic and phenotypic variance and covariance components for feed intake, feed efficiency, and other postweaning traits in Angus cattle. J. Anim Sci. 79:2805–2811.

Arthur, P. F., G. Renandb, D. Krauss. 2001b. Genetic and phenotypic relationships among different measures of growth and feed efficiency in young charolais bulls. Livestock Prod Sci. 68:131–139.

Basarab, J.A., M.A. Price, J.L. Aalhus, E.K. Okine, W.M. Snelling, K.L. Lyle. 2003. Residual feed intake and body composition in young growing cattle. Can. J. Anim. Sci. 83:189-204.

Bishop, S.C. 1992. Phenotypic and genetic variation in body weight, food intake and energy utilization in Hereford cattle I. Performace test results. Liv. Prod. Sci. 30: 1-18.

Brown, C.J., J.E. Brown, and, W.T. Butts. 1974. Evaluating relationships among immature measures of size, shape and performance of beef bulls IV. Regression models for predicting post weaning performance of young Hereford and Angus bulls using preweaning measures of size and shape. J. Anim. Sci. 38: 12-19.

Brown, C.J., M. Gacula. 1962. Estimates of heritability of beef cattle performance traits by regression of offspring on sire. J. Anim. Sci. 23: 321-324.

Chewning, J.J., A.H. Brown, Jr, Z.B. Johnson, C.J. Brown. 1990. Breed means for average daily gain, feed conversion and intake of beef bulls during postweaning feedlot performance tests. J. Anim. Sci.68: 1500-1504.

Crowley, J. J., M. McGee, D. A. Kenny, D. H. Crews, Jr., R. D. Evans, D. P. Berry. 2009. Phenotypic and genetic parameters for different measures of feed efficiency in different breeds of Irish performance tested beef bulls J. Anim. Sci. 88:885-894.

Dickerson, G. E., Kunzi, Niklaus, L.V. Cundiff, R.M. Koch, V.H. Arthaud, K.E. Gregory. 1974. Selection Criteria for Efficient Beef Production. J. Anim Sci. 39: 659-673.

Elzo, M.A., D.G. Riley, G.R. Hansen, D.D. Johnson, R.O. Myer, S.W. Coleman, C.C. Chase, J.G. Wasdin, J.D. Driver. 2009. Effect of breed composition on phenotypic residual feed intake and growth in Angus, Brahman, and Angus x Brahman crossbred cattle. J Anim. Sci. 87:3877-3886.

Fan, L.Q., D.R. Bailey, N.H. Shannon. 1995. Genetic parameter estimation of postweaning gain, feed intake, and feed efficiency for Hereford and Angus bulls feed two different diets. J Anim Sci 1995. 73:365-372.

Fisher, R.A. 1921. "On the `probable error' of a coefficient of correlation deduced from a small sample". Metron 1: 3–32.

Golden, B.L., D.J. Garrick, S. Newman, and R.M. Enns. 2000. Economically relevant traits, a framework for the next generation of EPD's. Pages 2-13 in proc. Beef Improv. Fed., Wichita, KS.

Hanset, R., C. Michaux, and A. Stasse. 1987. Relationships between growth rate, carcass composition, feed intake, feed conversion ratio and income in four biological types of cattle. Genet. Sel. Evol. 19: 225-248.

Herd, R.M. and S.C. Bishop. 2000. Genetic variation in residual feed intake and its association with other production traits in British Hereford cattle. Livest. Prod. Sci. 63: 111-119.

Herring, W. O. and J. K. Bertrand. 2002. Multi-trait prediction of feed conversion. Pages 89-97 in Proc. Beef Improv. Fed., Omaha, NE.

Hoque, M.A., M. Hosono, T. Oikawa and K. Suzuki. 2009. Genetic parameters for measures of energetic efficiency of bulls and their relationship with carcass traits of field progeny in Japanese Black cattle. J. Anim. Sci. 2009. 87:99-106.

Koch, R. M., L. A. Swiger, D. Chambers and K. E. Gregory. 1963. Efficiency of Feed Use in Beef Cattle. J. Anim Sci., 22:486–494.

Koots, K., J. Gibson, C. Smith, J. Wilton 1994a. Analyses of published genetic parameter estimates for beef production traits. 1. heritability. Anim. Breed. Abst., 62:309–338.

Koots, K., J. Gibson and J. Wilton. 1994b. Analyses of published genetic parameter estimates for beef production traits. 2. phenotypic and genetic correlations. Anim. Breed. Abst., 62:825–853.

Lancaster, P.A., G.E. Carstens, D.H. Crews, Jr., T.H. Welsh, Jr., T.D.A. Forbes, D.W. Forrest, L.O. Tedeschi, R.D. Randel, F.M. Rouquette. 2009. Phenotypic and genetic relationships of residual feed intake with performance and ultrasound carcass traits in Brangus heifers. J Anim. Sci. 87: 3887-3896.

Mavrogenis, A. P., E.U. Dillard and O.W. Robison. 1978. Genetic Analysis of Postweaning Performance of Hereford Bulls. J. Anim Sci. 47: 1004-1013.

Mrode, R.A., C. Smith, R. Thompson. 1990. Selection for rate and efficiency of lean gain in Hereford cattle 2. Evaluation of of correlated responses. Animal Production 51: 35-46.

Nkrumah, J.D., J.A. Basarab, Z. Wang, C. Li, M.A. Price, E.K. Okine, D. H. Crews, S. S. Moore. 2007. Genetic and phenotypic relationships of feed intake and different measures of feed efficiency with growth and carcass merit of beef cattle. J Anim. Sci. 85: 2711-2720.

Robinson, D.L. and V.H. Oddy. 2004. Genetic parameters for feed efficiency, fatness, muscle area and feeding behavior of feedlot finished beef cattle. Livestock Prod. Sci. 90: 255-270.

Sasaki, Y., H. Iwaisaki, T. Masuno, S. Asoh. 1982. Interaction of sire x length of testing period and estimation of genetic parameters for performance testing traits of Japanese black bulls. J. Anim Sci. 55: 771-779.

Schenkel, F.S., S.P. Miller, and J.W. Wilton. 2004. Genetic parameters and breed differences for feed efficiency, growth, and body composition traits of young beef bulls. Can. J. Anim. Sci. 84:177-184.

Steele, R.D. and J.H. Torrie. 1980. Principles and procedures of statistics: a biometrical approach, 2nd edn. Auckland: McGraw-Hill.

Swiger, L.A., Koch, R.M., Gregory, K.E., Arthaud, V.H. 1961. Effect of length of feeding period on accuracy of selection for gain and feed consumption in beef cattle. J. Anim. Sci. 20: 802-808.

Swinger, L.A., K.E. Gregory, L.J. Sumption, C.C. Breidenstein, V.H. Arthaud. 1965. Selection indexes for efficiency of beef production. J. Anim. Sci. 24 : 418-424.

Chapter IV

Genetic parameter estimation of feed intake and utilization traits in growing beef cattle

4.1   Abstract

The increasing use of feed efficiency traits as selection criterion in recent years has improved the availability of literature regarding feed utilization traits. The number of studies which includes genetic parameters for feed utilization traits is quite limited. Selection for cost traits has the potential to improve profitability through increasing the efficiency of feed utilization and to reduce input costs. Daily feed intakes were recorded on 3,702 bulls and 314 heifers across nine tests between 2007 and 2010 at Midland Bull Test in Columbus, Montana. Daily feed intake was recorded and from this dry matter intake (**DMI**) was calculatedbased on moisture analysis of diet samples during the respective tests. The feed tests averaged 70d in length; serial weights were recorded at 14d intervals throughout each test. The average daily gain (**ADG**) estimate was calculated as the slope of from the within animal regression of weight on test day. Weight at mid-test is calculated as β_0+ADG*(length of test/2), metabolic body weight (**MBW**) was calculated by exponentiation of mid-test weight to 0.75. Phenotypic residual feed intake (**RFIp**) is the residual portion of the regression of DMI on ADG and MBW.

Genetic variances were estimated using a multiple trait animal model and average information REML. The model was equivalent for DMI, ADG, MBW and RFIp which included a fixed effect of contemporary group (breed x test x pen, n=112) and a linear covariate for age at start of test (=298.28d, SD=36.65). The heritability estimate for RFIp was 0.17 ± 0.05. Genetic correlations among growth traits (ADG, MBW and DMI) were moderate to high and positive, ranging from 0.33 to 0.70 as shown in Table 4.2. The model including DMI and RFIp failed to converge. This resulted in the need for estimation of genetic residual feed intake (**RFIg**), defined as the difference between DMI EBV and expected DMI EBV. Genetic regression was used to predict expected DMI EBV from the EBVs of ADG and MBW. This approach to the genetic

35

evaluation of RFIg allows for the estimation of breeding values that may truly reflect feed utilization differences among animals without simultaneously affecting growth or body size.

4.2   Introduction

In North American beef production systems, as much as 70% of non-fixed production costs can be attributed to feed costs, mainly in the feedlot sector and through supplementation of the cow herd (Taylor and Field, 2001). However, genetic evaluation of input traits such as feed intake is generally not performed. Selection for such traits has the potential to improve profitability through increasing the efficiency of beef cattle feed use and reducing input costs. Unlike most output traits, which have ample individual animal production records, input traits such as feed utilization lack the quantity of observations required for regular genetic evaluation. The adoption of recent improvements in the technology used to collect individual daily feed intake on group fed cattle is becoming more common throughout the industry and, thus the testing facilities can more adequately meet the demand of producers wishing to collect feed intake data on their cattle. Additionally, the Beef Improvement Federation has accepted a draft for feed intake and efficiency guidelines by Crews et al., (2010) that outlines the protocols of feed intake data collection. These standards should improve the repeatability and consistency of feed intake records for eventual use in NCE.

Genetic evaluation of feed intake and related traits requires appropriate parameter estimates to predict breeding values which can then be used to make genetic improvement in feed utilization of beef cattle. The objective of this study was to estimate genetic parameters among feed intake and growth traits measured on growing beef cattle. These results can then be used as preliminary estimates in genetic evaluation programs.

4.3   Materials and Methods

Daily feed intakes were recorded on 3,702 bulls and 314 heifers across nine tests between 2007 and 2010 at Midland Bull Test (**MBT**) in Columbus, Montana. There were 15 breeds represented in these tests although 68% of the test animals were Angus. Daily feed intake was recorded and daily dry matter intake (**DMI**) was calculated by multiplying the daily feed intake by the percent dry matter of the feed ration. The feed tests averaged 70d in length; serial weights were recorded at 14d intervals throughout and used to calculate average daily gain (**ADG**). The estimate of ADG was calculated as the slope of from the within animal regression of live weight on test day. Weight at mid-test is calculated as β_0+ADG*(length of test/2), metabolic body weight (**MBW**) was calculated by exponentiation of mid-test weight to 0.75. Phenotypic residual feed intake (**RFIp**) was computed as the residual remaining after the regression of DMI on ADG and MBW within test. The data was filtered for age outliers with animals were required to have a known age between 240 and 400d at the start of the test. All animals were required to have valid observations for DMI, ADG and MBW to be included in the dataset. A valid record was considered to be within 4 SD of the contemporary group mean for each of the traits. After these filters, 2,445 bulls and 117 heifers remained and phenotypes were used in the analysis of 11,229 animals resulting from formation of a three generation pedigree. Summary statistics are given in Table 4.1 for the input phenotypes of DMI, ADG, MBW and age at the start of test. Genetic variances were estimated using a multiple trait animal model and average information REML (Gilmour et al., 2001). The model was equivalent for DMI, ADG, MBW and RFIp which included a fixed effect of contemporary group (breed x test x pen, n= 112) and a linear covariate for age at start of test (= 298.28d, SD= 36.65).

Table 4.1: Summary statistics for phenotypic observations

Trait[1]	Mean	SD	Min	Max
DMI, kg/d	9.72	1.52	4.90	13.00
ADG, kg/d	1.42	0.30	0.51	2.38
MBW, kg	121.29	11.01	61.70	119.50
AGE	298.28	36.65	241	399

[1] DMI= daily dry matter intake; ADG=average daily gain; MBW=metabolic body weight; AGE= age at start of test

4.4   Results and Discussion

The multiple trait analysis was attempted with a four trait multivariate model among DMI, ADG, MBW and RFIp to solve for the genetic (co)variances directly, but failed to converge with all runs including both DMI and RFIp. The genetic covariance between RFIp and DMI in this dataset was nearing the boundary of 1.0, most likely causing the convergence issues. Other researchers have not reported convergence failure with multiple trait models including both RFIp and DMI simultaneously (e.g., Arthur et al., 2001a; Schenkel et al., 2004; Hoque et al., 2009). Reported genetic correlation estimates in 25 studies published since 1961 for DMI with RFIp were highly positive, with a weighted average of 0.60 (Pendley et al., 2010).

The convergence failure of the model including DMI and RFIp resulted in the need to estimate genetic residual feed intake (**RFIg**), defined as the difference between DMI EBV and expected DMI EBV. Genetic regression was used to predict expected DMI EBV from the EBVs for ADG and MBW (Crews et al., 2010b). The genetic regression approach requires estimates of genetic (co)variances between ADG and MBW, as well as genetic (co)variances of these with DMI. Similar to the phenotypic independence of RFIp from ADG and MBW, RFIg is genetically independent of ADG and MBW. In Table 4.2 the heritability, genetic correlation and genetic co variances are given among DMI, ADG, MBW and RFIp.

Table 4.2: Heritability estimates and genetic correlation/covariances[1]

Trait[2]	DMI	ADG	MBW	RFIp
DMI	0.20±0.05	0.39	0.63	.
ADG	0.33±0.16	0.21±0.05	0.11	0.012
MBW	0.70±0.09	0.16±0.15	0.25±0.05	-0.15
RFIp	.	0.27±0.18	-0.08±0.16	0.17±0.05

[1] Heritability on diagonal, genetic correlation below and genetic covariance above

[2] DMI= daily dry matter intake; ADG=average daily gain; MBW=metabolic body weight; RFIp= phenotypic residual feed intake

Heritability estimates for DMI, ADG, and MBW are lower than the average estimates but within the range included in Pendley et al., (2010). The heritability estimate for RFIp (0.17 ± 0.05) is within the range of those recently reported, although significantly lower than the weighted average of 0.38 (Pendley et al., 2010). Genetic correlations among growth traits (ADG, MBW and DMI) were moderate to high and positive, ranging from 0.33 to 0.70. These estimates are similar to those reported by Arthur et al., (2001a), but higher than Schenkel et al., (2004). Most recent studies have reported genetic parameters for RFIp, specifically estimating near-zero genetic correlations of RFIp with ADG and MBW. The estimate in these data of 0.27 ± 0.18 for the genetic correlation between ADG and RFIp illustrates that although RFIp has phenotypic independence from its components (including ADG and MBW), RFIp is not necessarily genetically independent from its components (Kennedy et al., 1993). Selection on RFIp breeding values, therefore, may result in an unfavorable correlated response in ADG (Crews et al., 2010). In Table 4.3 the summary statistics of EPDs are given for DMI, ADG, MBW and RFIg.

Table 4.3: Summary statistics of EPDs

Trait[1]	Mean	SD	Min	Max
DMI	0.02	0.10	-0.57	0.86
ADG	0.00	0.02	-0.10	0.10
MBW	0.17	0.82	-4.61	9.12
RFIg	0.00	0.05	-0.27	0.33

[1] DMI= daily dry matter intake; ADG=average daily gain; MBW=metabolic body weight; RFIg=genetic residual feed intake

This approach to the genetic evaluation of RFIg allows for the estimation of breeding values that may truly reflect feed utilization differences among animals without simultaneously affecting growth or body size. This allows for selection towards improved efficiency without indirectly selecting for ADG and MBW. This approach may limit indirect selection and thus, be more effective and appropriate than selection on RFIp. The use of EPDs for RFIg in selection is equivalent to selection on EPDs for all component traits. The use of one figure instead of multiple trait selection on several may be more appealing for the producers use in genetic improvement protocols. The RFIg EPDs should be used if genetic improvement in feed utilization is a part of the producer breeding objectives.

4.5   Implications

The results of this study provide genetic parameters necessary for the eventual genetic evaluation of residual feed intake from daily feed intake records. Genetic parameters were similar to or slightly lower than others recently published. These are some of the first parameters published since the acceptance of the guidelines for feed intake data collection by the Beef Improvement Federation. The recommendation of these guidelines regarding age at time of data collection appear to have an effect on the parameter estimates, though additional research is required to find the true repercussions of data collection on cattle outside the

growing phase of production. These results should serve as a starting point for the genetic evaluation of residual feed intake.

4.6   Literature Cited

Arthur, P. F., J. A. Archer, D. J. Johnston, R. M. Herd, E. C. Richardson, P. F. Parnell. 2001a. Genetic and phenotypic variance and covariance components for feed intake, feed efficiency, and other postweaning traits in Angus cattle. J. Anim Sci. 79:2805–2811.

Arthur, P. F., G. Renandb, D. Krauss. 2001b. Genetic and phenotypic relationships among different measures of growth and feed efficiency in young charolais bulls. Livestock Prod Sci. 68:131–139.

Basarab, J.A., M.A. Price, J.L. Aalhus, E.K. Okine, W.M. Snelling, K.L. Lyle. 2003. Residual feed intake and body composition in young growing cattle. Can. J. Anim. Sci. 83:189-204.

Crews,D.H., Jr., G.E. Carstens, J.A. Basarab, R.A. Hill, and M.K. Nielsen. 2010. Feed Intake and Efficiency: Guidelines for Uniform Beef Improvement Programs, 9th Ed. [IN PRES]

Crews, D.H., Jr., C.T. Pendley, G.E. Carstens, E.D.M. Mendes. Genetic Evaluation of Feed Intake and Utilization Traits of Beef Bulls. 2010b. 9th World Congress on Genetics Applied to Livestock Production: Leipzig, Germany.

Gilmour, A. R., R. Thompson, B. R. Cullis, and S. Welham. 2001. ASREML User's Manual. NSW Department of Primary Industries, Orange, Australia

Golden, B.L., D.J. Garrick, S. Newman, and R.M. Enns. 2000. Economically relevant traits, a framework for the next generation of EPD's. Beef Improv. Fed., Wichita, KS, Proc., 2-13.

Herring, W. O. and J. K. Bertrand. 2002. Multi-trait prediction of feed conversion. Beef Improv. Fed., Omaha, NE, Proc., 89-97.

Hoque, M.A., M. Hosono, T. Oikawa, K. Suzuki. 2009. Genetic parameters for measures of energetic efficiency of bulls and their relationship with carcass traits of field progeny in Japanese Black cattle. J. Anim. Sci. 2009. 87:99-106

Kennedy, B. W., J.H.J. van der Werf, T.H.E. Meuwissen. 1993. Genetic and statistical properties of residual feed intake. J. Anim. Sci., 71:3239-3250

Pendley, C. T., R.M. Enns, D.H. Crews,Jr. 2010. Analysis of published genetic parameter estimates for feed utilization traits in beef cattle. J. Anim. Sci. (Suppl.) (Abstr).

Schenkel, F.S., S.P. Miller, and J.W. Wilton. 2004. Genetic parameters and breed differences for feed efficiency, growth, and body composition traits of young beef bulls. Can. J. Anim. Sci. 84:177-184.

Taylor, R.E., T. G. Field. 2001. Scientific Farm Animal Production, an Introduction to Animal Science. 7th rev. ed. Prentice Hall, Upper Saddle River, NJ.

4.7 Appendix: Linux Code

4.7.1 Midland Bull Test Data preparation

```
sed 's/ //g' < mbtsum.1.csv | awk 'BEGIN{FS=","} {for(k=1;k<=NF;k++) if ($k=="") {$k="."}} NR>1
{print $1,$2,$3,$4,$5,$6,$7,$8,$9,$10,$11,$12,$13,$14,$15,$16,$17,$18,$36,$29,$35}' > work1

rm mbt.fin

rm mbt.rfi

# age filter and change sex code on complete file

awk '$19<=240 || $19>=400 {$19="."}{print}' work1 > work2

#sex  code

awk '$6=="Bull" || $6=="Bulls" {$6=2}; $6=="Heifer" {$6=1} {print}' work1 > work2

#Drop unknown ages

awk '$19!="." {print}' work2 > work3

#Change breed code to BIF

awk '$5=="GE" {$5="GV"}; $5=="LI" {$5="LM"}; $5=="RA" {$5="AR"}; $5=="SD" {$5="DS"};
$5=="SI" {$5="SM"}{print}' work3 > work4

awk '$20=="." || $20=="Commercial" || $20=="Pending" || $20=="WillNotGet" ||
$20=="XXXXX" || $20=="XXXXXX" || $20=="dnaTESTING" || $20=="xxxxxx" {$20=$2"_"$3}
{print $5"_"$20,$3,$13,$12,$16,$5,$6,$7,$19,$21}' work4 > work5

dos2unix 907.fin.csv

sed 's/ //g' < 907fin1 | awk 'BEGIN{FS=","} {for(k=1;k<=NF;k++) if ($k=="") {$k="."}} NR>1 {print
$1,$2,$3,$4,$5,$6,$7,$8,$9,$10,$11,$12,$13,$14,$15,$16,$17,$18,$19,$20,$21,$22}' >
907.temp

awk '$7=="." {$7=$5"_"$1}; $5!="." && $9!="." {print $3"_"$7,$5,$14,$13,$12,$3,$4,$6,$9,$8}'
907.temp >> work5

for i in `awk '{print $2}' work5 | sort -u`

do

    echo $i

    awk '$2==i && $9!="." {print}' i=$i work5 > $i.d.1

    awk '$3=="." || $4=="." || $5=="." {print}' $i.d.1 > $i.d.3

    # Filters for adg, mbw, dmi , set to pull any outside of 4 sd from test mean

    madg=$(awk '$2==i {print $4}' i=$i $i.d.1 | sst | grep mu | awk '{print $3}')
```

```
sdadg=$(awk '$2==i {print $4}' i=$i $i.d.1 | sst | grep SD | awk '{print $3*4}')

mdmi=$(awk '$2==i {print $3}' i=$i $i.d.1 | sst | grep mu | awk '{print $3}')

sddmi=$(awk '$2==i {print $3}' i=$i $i.d.1 | sst | grep SD | awk '{print $3*4}')

mmbw=$(awk '$2==i {print $5}' i=$i $i.d.1 | sst | grep mu | awk '{print $3}')

sdmbw=$(awk '$2==i {print $5}' i=$i $i.d.1 | sst | grep SD | awk '{print $3*4}')
```

```
awk '$4>=madg+sdadg || $4<=.5 { $4="."}; $3>=mdmi+sddmi || $3<=mdmi-sddmi { $3="."};
$5>=mmbw+sdmbw || $5<=mmbw-sdmbw { $5="."}; {print}' madg=$madg sdadg=$sdadg
mdmi=$mdmi sddmi=$sddmi mmbw=$mmbw sdmbw=$sdmbw $i.d.1 | awk '$3!="." && $4!="."
&& $5!="." {print $0}' > $i.d.2

awk '$4>=madg+sdadg || $4<=.5 { $4="."}; $3>=mdmi+sddmi || $3<=mdmi-sddmi { $3="."};
$5>=mmbw+sdmbw || $5<=mmbw-sdmbw { $5="."}; {print}' madg=$madg sdadg=$sdadg
mdmi=$mdmi sddmi=$sddmi mmbw=$mmbw sdmbw=$sdmbw work5 > d.4
```

```
# matrix formation

awk '{print $3}' $i.d.2 > $i.y

awk '{print "1", $4, $5}' $i.d.2 > $i.x

awk '{print $1,NR}' $i.d.2 | sort -k2 > $i.id.row

d2s $i.y $i.Y

d2s $i.x $i.X

mult -t$i.X $i.X $i.xtx

mult -t$i.X $i.Y $i.xty

invert -i $i.xtx -o $i.xtxinv

mult $i.xtxinv $i.xty $i.beta

mult $i.X $i.beta $i.xb
```

```
 awk 'NR>1 {print $0}' $i.xb | paste $i.d.2 - | awk '{print $1,$2,$3,$4,$5,$6,$7,$8,$9,$12,$3-$12}'
>> mbt.fin

 awk 'NR>1 {print $0}' $i.xb | sort | join  -1 2 -2 1 -e "." -o 1.1 2.3 $i.id.row - | sort > $i.id.xb

sort $i.d.2 | join -a1 -e "." -o 1.1 1.2 1.3 1.4 1.5 1.6 1.7 1.8 1.9 2.2 - $i.id.xb | awk '{print
$1,$2,$3,$4,$5,$6,$7,$8,$9,$10,$3-$10}' >> mbt.rfi
```

done

rm 701.*

rm 802.*

rm 803.*

rm 804.*

rm 805.*

rm 906.*

rm 907.*

```
     sort  mbt.rfi > mbt.rfi.s

     sort  d.4 | join -a1 -e "." -1 1 -2 1 -o  1.1 1.2 1.3 1.4 1.5 1.6 1.7 1.8 1.9 1.10 2.10 2.11 -
mbt.rfi.s > mbt.fin1

 awk '$3=="." {$3=$4}; $5=="." {$5=$6}; $7=="." {$7=$8} {print
$1,$2,$3,$5,$7,$9,$10,$11,$12,$13,$14,$15}' mbt.fin > mbt.fin1

awk 'substr($10,2,1)=="/" {$10=0$10}{print}' mbt.fin1 > mbt.fin2

awk 'substr($10,0,2)>"06" {$13="F"} {print}' mbt.fin2 | awk 'substr($10,0,2)<="06" {$13="S"}
{print}' > mbt.fin3

awk '$2!=803 && $2!=804 {print}' mbt.fin > mbt.fin1

echo id test dmi adg mbw breed sex pen  aged0  DOB pdmi rfi bs

##   1 2   3 4 5 6    7 8   9    10  11  12 13
```


with contemporary groups defined

```
awk '$3!="." && $4!="." && $5!="."{print $1,$3,$4,$5,$6"_"$2"_"$7"_"$8"_"$13,$9,$11,$12}'
mbt.fin3 > mbt.fin.cg
```

4.7.2 Midland Bull Test Pedigree Formation

```
## put pedigree into id, sire, dam

dos2unix 805906ped.csv

sed 's/ //g' < 805906ped.csv | awk 'BEGIN{FS=","} {for(k=1;k<=NF;k++) if ($k=="") {$k="."}} NR>1
{print $0}' | sed 's/,/ /g'

> p.1

rm an.pedfin

rm ar.pedfin

rm sa.pedfin

rm gv.pedfin

rm lm.pedfin

rm ch.pedfin

rm ma.pedfin

rm sm.pedfin

rm mg.pedfin

rm ds.pedfin

dos2unix 907ped.csv

awk 'BEGIN{FS=","}; NR>1 {print $1,$2,$3,$4,$5,$6,$7,$8,$9,$10,$11,$12,$13,$14,$15,$16}'
907ped.csv > 907.t


##angus ped

awk '$1=="AN" {print $1,
$1"_"$2,$1"_"$4,$1"_"$5,$1"_"$6,$1"_"$7,$1"_"$8,$1"_"$9,$1"_"$10,$1"_"$11,$1"_"$12,$1"_
"$13,$1"_"$14,$1"_"$15,$1"_"$16,$1"_"$17}' p.1 > an.ped

##1st generation

awk '{print $2,$3,$10}' an.ped >> an.pedfin

##2nd generation
```

```
awk '{print $3,$4,$5}' an.ped >> an.pedfin

awk '{print $10,$11,$12}' an.ped >> an.pedfin

##3rd generation

awk '{print $4,$6,$7}' an.ped >> an.pedfin

awk '{print $5,$8,$9}' an.ped >> an.pedfin

awk '{print $11,$13,$14}' an.ped >> an.pedfin

awk '{print $12,$15,$16}' an.ped >> an.pedfin

#Add in 907 pedigree

cat ped907.s >> an.ped


##Saler ped

awk '$1=="SA" {print $1, $1"_"$2,$1"_"$4,$1"_"$5,$1"_"$6,$1"_"$11,$1"_"$12,$1"_"$13}' p.1 >
sa.ped

## 1st generation

awk '{print $2,$3,$6}' sa.ped >> sa.pedfin

##2nd generation

awk '{print $3,$4,$5}' sa.ped >> sa.pedfin

awk '{print $6,$7,$8}' sa.ped >> sa.pedfin


##Gelbvieh ped

awk '$1=="GV" {print $1, $1"_"$2,$4,$5,$6,$7,$8,$9,$10,$11,$12,$13,$14,$15,$16,$17}' p.1 >
gv.ped

##1st generation

awk '{print $2,$3,$10}' gv.ped >> gv.pedfin

##2nd generation

awk '{print $3,$4,$5}' gv.ped >> gv.pedfin
```

awk '{print $10,$11,$12}' gv.ped >> gv.pedfin

##3rd generation

awk '{print $4,$6,$7}' gv.ped >> gv.pedfin

awk '{print $5,$8,$9}' gv.ped >> gv.pedfin

awk '{print $11,$13,$14}' gv.ped >> gv.pedfin

awk '{print $12,$15,$16}' gv.ped >> gv.pedfin

Red Angus ped

awk '$1=="AR" {print $1,$2,$4,$5,$6,$7,$8,$9,$10,$11,$12,$13,$14,$15,$16,$17}' p.1 > ar.ped

##1st generation

awk 'substr($3,3,1)!="_"{$3=$1"_"$3}; substr($10,3,1)!="_"{$10=$1"_"$10}{print $1"_"$2,$3,$10}' ar.ped >> ar.pedfin

##2nd generation

awk 'substr($3,3,1)!="_"{$3=$1"_"$3};substr($4,3,1)!="_"{$4=$1"_"$4};substr($5,3,1)!="_"{$5=$1"_"$5} {print $3,$4,$5}' ar.ped >> ar.pedfin

awk 'substr($10,3,1)!="_"{$10=$1"_"$10}; substr($11,3,1)!="_"{$11=$1"_"$11}; substr($12,3,1)!="_"{$12=$1"_"$12} {print $10,$11,$12}' ar.ped >> ar.pedfin

##3rd generation

awk 'substr($4,3,1)!="_"{$4=$1"_"$4}; substr($6,3,1)!="_"{$6=$1"_"$6}; substr($7,3,1)!="_"{$7=$1"_"$7} {print $4,$6,$7}' ar.ped >> ar.pedfin

awk 'substr($5,3,1)!="_"{$5=$1"_"$5}; substr($8,3,1)!="_"{$8=$1"_"$8}; substr($9,3,1)!="_"{$9=$1"_"$9} {print $5,$8,$9}' ar.ped >> ar.pedfin

awk 'substr($11,3,1)!="_"{$11=$1"_"$11}; substr($13,3,1)!="_"{$13=$1"_"$13}; substr($14,3,1)!="_"{$14=$1"_"$14} {print $11,$13,$14}' ar.ped >> ar.pedfin

awk 'substr($12,3,1)!="_"{$12=$1"_"$12}; substr($15,3,1)!="_"{$15=$1"_"$15}; substr($16,3,1)!="_"{$16=$1"_"$16} {print $12,$15,$16}' ar.ped >> ar.pedfin

##Simmental ped

awk '$1=="SM" {print $1,
$1"_"$2,$1"_"$4,$1"_"$5,$1"_"$6,$1"_"$7,$1"_"$8,$1"_"$9,$1"_"$10,$1"_"$11,$1"_"$12,$1"_
"$13,$1"_"$14,$1"_"$15,$1"_"$16,$1"_"$17}' p.1 > sm.ped

##1st generation

awk '{print $2,$3,$10}' sm.ped >> sm.pedfin

##2nd generation

awk '{print $3,$4,$5}' sm.ped >> sm.pedfin

awk '{print $10,$11,$12}' sm.ped >> sm.pedfin

##3rd generation

awk '{print $4,$6,$7}' sm.ped >> sm.pedfin

awk '{print $5,$8,$9}' sm.ped >> sm.pedfin

awk '{print $11,$13,$14}' sm.ped >> sm.pedfin

awk '{print $12,$15,$16}' sm.ped >> sm.pedfin

##Charolais ped

awk '$1=="CH" {print $1,
$1"_"$2,$1"_"$4,$1"_"$5,$1"_"$6,$1"_"$7,$1"_"$8,$1"_"$9,$1"_"$10,$1"_"$11,$1"_"$12,$1"_
"$13,$1"_"$14,$1"_"$15,$1"_"$16,$1"_"$17}' p.1 > ch.ped

##1st generation

awk '{print $2,$3,$10}' ch.ped >> ch.pedfin

##2nd generation

awk '{print $3,$4,$5}' ch.ped >> ch.pedfin

awk '{print $10,$11,$12}' ch.ped >> ch.pedfin

##3rd generation

awk '{print $4,$6,$7}' ch.ped >> ch.pedfin

awk '{print $5,$8,$9}' ch.ped >> ch.pedfin

```
awk '{print $11,$13,$14}' ch.ped >> ch.pedfin

awk '{print $12,$15,$16}' ch.ped >> ch.pedfin
```

Limousin ped

```
awk '$1=="LM" {print $1, $1"_"$2,$1"_"$4,$1"_"$5,$1"_"$6,$1"_"$11,$1"_"$12,$1"_"$13}' p.1
> lm.ped
```

1st generation

```
awk '{print $2,$3,$6}' lm.ped >> lm.pedfin
```

2nd generation

```
awk '{print $3,$4,$5}' lm.ped >> lm.pedfin

awk '{print $6,$7,$8}' lm.ped >> lm.pedfin
```

Maine ped

```
awk '$1=="MA" {print $1,$1"_"$2,$1"_"$4,$1"_"$5,$1"_"$6,$1"_"$7,$1"_"$8,
$1"_"$9,$1"_"$10,$1"_"$11, $1"_"$12,$1"_"$13,$1"_"$14,$1"_"$15,$1"_"$16,$1"_"$17}' p.1 >
ma.ped
```

1st generation

```
awk '{print $2,$3,$10}' ma.ped >> ma.pedfin
```

2nd generation

```
awk '{print $3,$4,$5}' ma.ped >> ma.pedfin

awk '{print $10,$11,$12}' ma.ped >> ma.pedfin
```

3rd generation

```
awk '{print $4,$6,$7}' ma.ped >> ma.pedfin

awk '{print $5,$8,$9}' ma.ped >> ma.pedfin

awk '{print $11,$13,$14}' ma.ped >> ma.pedfin

awk '{print $12,$15,$16}' ma.ped >> ma.pedfin
```

##Murrey Grey ped

awk '$1=="MG" {print $1, $1"_"$2,$1"_"$4,$1"_"$5,$1"_"$6,$1"_"$11,$1"_"$12,$1"_"$13}' p.1
> mg.ped

1st generation

awk '{print $2,$3,$6}' mg.ped >> mg.pedfin

##2nd generation

awk '{print $3,$4,$5}' mg.ped >> mg.pedfin

awk '{print $6,$7,$8}' mg.ped >> mg.pedfin

##South Devon ped

awk '$1=="DS" {print $1, $1"_"$2,$1"_"$4,$1"_"$5,$1"_"$6,$1"_"$11,$1"_"$12,$1"_"$13}' p.1
> ds.ped

1st generation

awk '{print $2,$3,$6}' ds.ped >> ds.pedfin

##2nd generation

awk '{print $3,$4,$5}' ds.ped >> ds.pedfin

awk '{print $6,$7,$8}' ds.ped >> ds.pedfin

South Devon ped from 907

##1st gen

awk '$1=="DS" {print $1"_"$2,$1"_"$3,$1"_"$4}' 907.t >> ds.pedfin

##2nd gen

awk '$1=="DS" {print $1"_"$3,$1"_"$5,$1"_"$6}' 907.t >> ds.pedfin

awk '$1=="DS" {print $1"_"$4,$1"_"$7,$1"_"$8}' 907.t >> ds.pedfin

##3rd gen

```
awk '$1=="DS" {print $1"_"$5,$1"_"$9,$1"_"$10}' 907.t >> ds.pedfin

awk '$1=="DS" {print $1"_"$6,$1"_"$11,$1"_"$12}' 907.t >> ds.pedfin

awk '$1=="DS" {print $1"_"$7,$1"_"$13,$1"_"$14}' 907.t >> ds.pedfin

awk '$1=="DS" {print $1"_"$8,$1"_"$15,$1"_"$16}' 907.t >> ds.pedfin
```

##Cat all ped files

```
cat an.pedfin ar.pedfin sa.pedfin gv.pedfin sm.pedfin ch.pedfin lm.pedfin ma.pedfin mg.pedfin
ds.pedfin > 805906ped.fin
```

##pre-formated ped

```
dos2unix 701802ped.csv

awk 'BEGIN{FS=","} {for(k=1;k<=NF;k++) if ($k=="") {$k="."}}{print $0}' 701802ped.csv |sed 's/,/
/g' > p.2

awk '$1=="RA" {$1="AR"}; substr($2,3,1)!="_"{$2=$1"_"$2}; substr($3,3,1)!="_"{$3=$1"_"$3};
substr($4,3,1)!="_"{$4=$1"_"$4}{pr

int $2,$3,$4}' p.2 > 701.pedfin

cat 805906ped.fin 701.pedfin > mbt.pedfin
```

##fix missings

```
awk 'substr($1,4,1)=="."{$1="."}; substr($2,4,1)=="."{$2="."}; substr($3,4,1)=="."{$3="."}{print}'
mbt.pedfin > mbt.pedfin.1

sort -uk1,1 mbt.pedfin.1 > p.3

join -a1 -a2 -e"." -o 1.1 1.2 1.3 2.1 p.3 mbt.fin.cg | awk '$1=="." {$1=$4}{print $1,$2,$3}'| awk
'$1!="." {print}' > p.4

awk '$1!="." {print $1}; $2!="." {print $2}; $3!="." {print $3}' p.4 | sort -u > p.5

join -a1 -e"." -1 1 -2 1 -o 1.1 2.2 2.3 p.5 p.4 | sort -uk1,1  > pedfin.1

stack_ped -r ped.r -s ped.s -d ped.d -p ped.p -n ped.n pedfin.1 mbt.pedstk

ped_recode mbt.pedstk > ped.rc

paste mbt.pedstk ped.rc | sort | awk '$5==0 {$5="."}; $6==0 {$6="."} {print}' > ped.rcs

awk '$1==AR; substr($13,1,3)!="AN_"{$13=$1"_"$13}; substr($16,1,3)!="AN_"{$16=$1"_"$16};
substr($17,1,3)!="AN_"{$17=$1"_"$17} {print $13,$16,$17}' p.1 >> ar.ped
```

4.7.3 Multivariate analysis of Midland Bull Test Data using ASREML

```
    id        !P

    reg    13402   !A

    dmi

    adg

    mbw

    cg     112    !A

    age

    expin

    rfi

    miss

ped.rc          !MAKE

d.8        !MVINCLUDE    !BLUP 3

miss adg mbw ~ Trait Tr.age !r Tr.id !f Tr.cg

1 2 1

0

Tr 0 US

0.8249

0.09439 0.04201

2.767   0.3160  27.68

Tr.id 2

3 0  US

0.2122

0.01568 0.01087

0.995   0.05067  9.427

id

!end
```

4.7.4 Multivariate analysis of Midland Bull Test Data (Three trait) using ASREML

```
    id        !P

    reg    13402   !A

    dmi

    adg

    mbw

    cg     112    !A

    age

    expin

    rfi

    miss

ped.rc         !MAKE

d.8        !MVINCLUDE

dmi adg mbw ~ Trait Tr.age !r Tr.id !f Tr.cg

1 2 1

0

Tr 0 US

0.5837

0.05137 0.03355

1.922   0.1311  15.43

Tr.id 2

3 0  US

0.4696

0.05922 0.01781

1.606   0.2684  17.90

reg

!end
```