Abstract

GRAY, KENT ANDREW. Relationships Among Measures of Feed Utilization, ADG, Behavior and Ultrasonic Measures. (Under the direction of Joe Cassady.)

The objective was to estimate phenotypic relationships among measures of feed utilization and economically important traits in beef cattle. Data were from 183 registered Angus bulls from the NCSU Historic Angus Herd which is maintained at the Upper Piedmont Research Station in Reidsville, NC. Means for BW and age were 271 ± 3.2 kg and 275 ± 1.5 d, respectively. Bulls were blocked based on BW and sire into groups of 12, adapted to a corn silage-based diet (140g CP, 1.73 Mcal NEm and 1.22 Mcal NEg per kg DM), and trained to use Calen gates. Feed offered was recorded daily and used to calculate DMI. Bulls were weighed every 14 d during the 84 d test, and ADG was determined by linear regression of weight on time. Means for ADG and DMI were 1.5 ± 0.02 kg/d and 7.5 ± 0.08 kg/d, respectively. Feed conversion ratio (FCR) was calculated by taking average DMI of each bull divided by ADG with mean 5.0 ± 0.05. Residual feed intake (RFI) was calculated based on NRC equations (RFI\(_{(NRC)}\)) with mean -0.42 ± 0.065. Alternatively, RFI was also calculated with a model including the dependent variable DMI, fixed effects of year, and regression covariates 42-d mid weight and ADG (RFI\(_{(reg)}\)) with mean 0.0 ± 0.05. Partial correlations were calculated using a model including fixed effects of year, pen, and sire nested within year. Fixed effects of year and covariates 42-d mid weight and ADG effected RFI\(_{(reg)}\) (P < 0.05). Phenotypic correlations between RFI\(_{(NRC)}\) with RFI\(_{(reg)}\), FCR, BW, and ADG were 0.77, 0.72, -0.54, and -0.54 (P < 0.01), respectively. The phenotypic correlation between RFI\(_{(reg)}\) and FCR was 0.65 (P < 0.01). Relationships between RFI\(_{(reg)}\) and ultrasonic measurements of intramuscular fat, LM area, rump fat, and rib fat were not statistically different from zero. As expected, RFI\(_{(NRC)}\) and RFI\(_{(reg)}\) were highly correlated. Both RFI\(_{(NRC)}\) and RFI\(_{(reg)}\) were highly correlated with FCR. It was concluded that alternative methods of calculating RFI
were found to be highly correlated, \( \text{RFI}_{\text{reg}} \) was, by design, phenotypically independent of ADG and BW, and \( \text{RFI}_{\text{NRC}} \) was phenotypically correlated with ADG and BW.
Relationships among Measures of Feed Utilization, ADG, Behavior and Ultrasonic Measures

by
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DEDICATION

To my loving wife Kim
and baby girl Brooke,
with love!
BIOGRAPHY

Kent A. Gray was born on May 18, 1981. He was raised on a large asparagus and alfalfa farm in Eastern Washington and participated in 4-H and FFA. When Kent graduated high school he lived in Cambodia for two years among farmers as a missionary for the Church of Jesus Christ of Latter-day Saints. Kent helped them tend to their rice fields, thin bananas, harvest sesame seeds and haul fish to the market.

As an undergraduate in college Kent worked in a molecular genetics lab working on Alpaca coat color determination and rat-tail disease in cattle. Kent developed an interest in genetics, which resulted in attending graduate school at North Carolina State University. After completion of his Masters Degree, he plans to continue his education by pursuing a Doctorate of Philosophy Degree in Animal Science at North Carolina State University under the Direction of Dr. Joe Cassady.
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CHAPTER 1

LITERATURE REVIEW
Introduction

The main goal for livestock producers should be to maximize profitability which is a function of both inputs and outputs. Selection programs within the livestock industry have mainly focused on production traits (outputs) and production costs (inputs) but relatively little attention has been focused on the difference between inputs and outputs. Reducing inputs in the swine and poultry industries has been accomplished, since feed intake is easier to measure in non grazing livestock species, selection programs for improved feed conversion rate have been implemented.

It is much more difficult to quantify feed that is consumed by a grazing species. In addition to feed, other costs associated with grazing animals can include land, pasture improvement, fertilizer, irrigation, operating costs, labor, machinery, etc (Archer et al., 1999). It is estimated that these costs are approximately 60-65% of total production costs within an average beef production business. Improving whole herd feed efficiency, while maintaining the same level of output will increase profitability. Feed efficiency can therefore be defined as the amount of beef output gained for each unit of feed consumed over the whole production system. This is called whole herd feed efficiency.

This review will explain different methods for estimating production system feed efficiency. It will include a description of genetic variation that exists in feed efficiency and how it can be estimated. The basis of this variation will then be described, and an evaluation of selection strategies that has been used for improving whole herd feed efficiency will be discussed.
Measures of Energy

All feeds have some amount of energy that contributes to the maintenance requirement for energy. In order to determine actual value of a ration, energy lost due to excretion of feces, urine, heat, and gases should be subtracted from the total energy available. (Maynard and Loosli, 1969). Digestible energy (DE) is a measure of energy in which fecal energy is subtracted from the net energy. Ruminants that are fed a high forage diet will lose most of their energy through defecation (Maynard and Loosli, 1969). This makes DE highly useful when comparing feeds due to its ease to measure. Digestibility is available for most feed commonly fed to cattle and sheep. Total Digestible Nutrients (TDN) is calculated by multiplying a constant to DE and is used in a similar manner as DE (Maynard and Loosli, 1969). The drawback in using this measure of energy is that it ignores some other important energy losses that occur during digestion and metabolism of food (Maynard and Loosli, 1969).

Metabolizable energy (ME) is defined as energy provided by a feedstuff after fecal energy (FE), urinary energy (UE), and gaseous energy (GE) is subtracted from gross energy available (Maynard and Loosli, 1969). This measurement of energy provides more accurate information on the amount of energy that is available for the animal use but is hard to measure (NRC, 1996). It is difficult and expensive to collect gaseous energy that is lost (Maynard and Loosli, 1969).

Net energy (NE) represents the fraction of gross energy that is actually utilized. This energy is defined as the sum of FE, UE, GE, and heat loss subtracted from gross energy. Net energy can be broken up into two portions, NE for gain (NEg) and NE for maintenance (NEm) (NRC, 1996). Some processes comprised in NEm include body temperature
regulation, essential metabolic processes and physical activity (Maynard and Loosli, 1969). Mathematical models have been developed to estimate these energy components so experiments can be accomplished in a more industry-like environment (NRC, 1996).

Variations in energy requirements for maintenance exist among sex, age, season, temperature, physiological state, previous nutrition and genotype (NRC, 1996). Recognizing which sires produce progeny with a superior genotype, requiring less NEm, per unit of mature body weight will decrease production costs through increased efficiency.

**Whole herd feed efficiency**

When feed efficiency is the main focus for improvement an index which includes feed intake and production traits can be used to pinpoint the most efficient animals within the herd (Gibson, 1986). Although this may sound like a simple way to determine feed efficiency for certain groups, one must keep in mind that whole herd efficiency is based on a summation of production traits from all groups within the herd. Production traits that are used in an index for growing cattle are different from production traits that are used in an index for the breeding herd; therefore making direct conclusions about whole herd efficiency somewhat difficult to determine. Whole herd feed efficiency is a very complex biological trait that cannot possibly be determined through a simple index. It is possible that an index using production traits could be genetically correlated with whole herd feed efficiency.

*Methods used to measure feed intake*

Before feed efficiency can be estimated feed intake must be carefully recorded. There are many methods used to measure feed intake which include modern computer collection methods and other more labor intensive methods. Common methods of collecting feed intake
that will be reviewed within this document include hand feeding and electronic feeding systems.

An early method to collect daily feed intake was to tie cattle to a stationary area with a known amount of feed in a bucket. Animals were allowed to eat for a certain amount of time at specific times during the day (Koch et al., 1963). Hand feeding cattle in this method is time consuming and labor intensive. It does not simulate standard industry practices which take away any type of behavioral eating patterns. This could bias results of an efficiency study making it difficult to interpret the significance of any findings.

As technology advanced other methods requiring electronic systems were developed. In 1973 the first electronic feeding method was called the Calan Broadbent door system (Karn, 1974). It is now more commonly referred to as Calan gates. This system takes advantage of a special door built in a fence which allows cattle access to their individual ration while blocking the other animals’ access to that ration. Access is controlled by an oscillator in the electrical circuit of each door. Each oscillator is controlled by a specific frequency that can only be opened by its matching “key coil”. When an animal is carrying the correct “key coil” around its neck it only needs to be within 2.5 – 5 cm from a specific gate and the locking bolt will be retracted allowing the animal to push the gate open (Karn, 1974). Early studies indicate that a training period of at least two weeks for a group of 24 animals is needed before individual intake can be collected accurately (Karn, 1974). The advantage to this system is that animals that are grouped together still can have individual feed intake collected. Orts can be measured and actual composition of feed consumed can be determined. Animals can stand shoulder to shoulder while feeding allowing for group eating behaviors to still take place. Some disadvantages include lack of ability to feed ad libitum
very easily. It takes away competition for feed that would usually occur in a natural production setting. It is also very labor intensive and requires a skilled technician to measure the feed on a daily basis so animals are offered as close to ad libitum access to feed as possible.

Recently a new system called Growsafe® has been developed which takes advantage of radio frequency technology for measuring feed intake (Schwartzkopf-Genswein et al., 1999). An antenna that emits an electromagnetic signal is embedded in a rubber mat that lines the outer wall of the bunk. Transponders encased in special eartags are detected by the antenna when they are at most 50 cm away and information is sent to a computer where duration and frequency of a feeding experience can be derived (Schwartzkopf-Genswein et al., 1999). Individual feed intake can be recorded as well when electronic scales transmit weights of a limited access bunk so only one animal can feed at any given time. The obvious advantage to this system is that it is less labor intensive than alternative methods and increases feeding behavior information that can be collected such as eating rate and meal time duration. One of the issues that can occur with such a system is that animals who sort their feed are not easily identified. This makes it difficult to determine what animals are consuming. Since a limited amount of space is available at the bunk, animals must take turns occupying the bunk which does not simulate standard industry practices. This controlled behavior may influence the animal’s efficiency making interpretation of data difficult.

The methods of measuring feed that have been discussed all assume that animals are in some type of penned off area. This is highly unrealistic when determining feed intake on cows within the breeding herd. These cows are most likely on a high forage grazing diet. Other methods have been developed for this type of feeding regimen. Some common
methods for measuring feed intake in grazing animals include the pulse-dose marker method, the animal performance method, and the herbage disappearance method (Macoon et al., 2003).

Feed intake can be estimated by calculating total organic matter intake based on fecal output and diet digestibility. Fecal output is estimated by using a pulse-dose marker such as chromium-mordanted fiber. By collecting fecal grabs at different times after the initial dose, marker concentrations can be analyzed and fit onto a recommended model (Macoon et al., 2003). An issue with using this technique for measuring feed intake is that it is a measurement that explains intake for a short period of time that must be extrapolated over a longer grazing period. It is unlikely that an animal will consistently eat in the same manner over the whole grazing period. Thus, this method of calculating feed intake may have substantial error (Macoon et al., 2003).

Herbage disappearance method of calculating feed intake is found by determining the difference in pre-grazing and post-grazing herbage mass (Macoon et al., 2003). This method seems to be the most logical but can be very labor intensive. One must measure the height of the grass and estimate how much grass was consumed. By determining nutritional content of the forage consumed net energy of the forage the animal has access to can be established. One advantage this method has is that it can, account for different pastures and pasture conditions. It is labor intensive, however and chance for measurement error increases significantly. Cattle are also herd animals and this method requires that animals be singled off, which may cause undo stress affecting feeding behavior. It is difficult to be confident that the animal would consume the same amount as normal.
The final method for determining feed intake is by estimating the energy requirements of the animal, called the animal performance method. By using prediction equations found in the NRC (2000) requirements, maintenance can be calculated for lactation, body weight changes, walking and grazing activity (Macaoon et al., 2003). Parity is also taken into account (Macaoon et al., 2003). The main drawback of using this method is the assumption that all animals are similar in physiology and use the same amount of energy for the same activities. This is highly unlikely, it is probable that there are significant physiological differences among animals and this is the very issue that is in question.

When comparing the three methods used to predict feed intake in grazing animals we find that animal performance and herbage disappearance methods are correlated insinuating that they are measuring the same trait (Macaoon et al., 2003). The pulse-marker method is not correlated with the other two methods, and thus, that method may be measuring something else (Macaoon et al., 2003).

Each method of measuring feed intake, whether it is on growing animals or mature grazing animals, has its advantages and disadvantages which should be considered when using each system. The method used in a project is mostly influenced by resources available. By knowing the method used, results collected can more accurately be interpreted.

_Test duration for post weaning animals_

Methods to measure and calculate feed efficiency take time. The amount of time needed when measuring feed efficiency in post weaning animals using the Growsafe® system for ADG, DMI, FCR, and RFI are 63, 35, 42 and 63 days respectfully (Wang et al., 2006) when weight is measured weekly. Recommended test durations given in other sources for ADG are 112d (Brown et al., 1991), 84d (Liu and Makarechian, 1993a, b; Swiger and
Hazel, 1961), and 70d (Archer et al., 1997). These recommended test durations are probably longer because weight was not measured weekly and the mode of collecting feed intake data was different. One must also remember that this time period does not take into account the time it takes for the animals to acclimate to the equipment used. A period of 84d should be sufficient for the acclimation and test period combined.

**Feed Efficiency as a Trait**

*Feed Conversion Ratio or Gross Efficiency*

The most common method described in the literature when calculating feed efficiency is gross efficiency or its inverse feed conversion ratio (FCR). This efficiency measurement can be measured either in a certain time interval, weight interval, maturity interval, or subcutaneous fat interval. It is then calculated by either dividing the interval of interest by amount of feed consumed (gross efficiency) or by inverting the ratio (FCR).

Feed conversion ratio is found to be highly correlated with growth rate estimated values range from -.61 to -.95 (Arthur et al., 2001a; Klosterman, 1972; Nkrumah et al., 2004). Improving herd efficiency through decreasing FCR of growing cattle can actually be detrimental to whole herd productivity. It has been shown that FCR is a function of rate of maturation (Salmon et al., 1990). This type of selection will increase mature size of the breeding animals which in turn increases maintenance feed costs. This does not mean that realized economic efficiencies of the slaughter generation cannot supersede those costs therefore making the herd as a whole more economically efficient; however, it is unlikely that this would be the case. It has been shown that when mature size is increased that reproductive rates decrease and age of puberty occurs at a later date. This all makes an increase in mature body size which contributes little to the feed efficiency of a herd. One
must keep in mind that feed efficiency of the herd encompasses all aspects of a beef production system (Dickerson, 1978; Fitzhugh, 1978).

Feed conversion ratio (FCR) as a measurement of efficiency is beneficial for operations that are centered on growing cattle such as feedlot production systems, or breeds that are used primarily for producing terminal sires. These types of cattle operations mainly acquire revenue through increased weight at slaughter. Improvement of FCR when used as an efficiency measurement increases size while intake remains constant (Nkrumah et al., 2004) which will increase profits.

**Maintenance Efficiency**

Maintenance efficiency is another method in which feed efficiency can be calculated. This method is defined as the feed required for an animal to gain no weight yet have enough energy to allow for all body components to receive the nourishment it needs to function properly (Ferrell and Jenkins, 1985). An alternative definition that is sometimes used is ratio of body weight to feed intake when there is no change in body weight (Ferrell and Jenkins, 1985).

It is estimated that 70 - 75% of the total energy that is required in beef production is allocated to maintaining the herd (Ferrell and Jenkins, 1984). Of that maintenance energy the cow herd uses approximately 65 – 75% of it (Ferrell and Jenkins, 1985; Gregory, 1972; Klosterman, 1972; Montano-Bermudez et al., 1990). That translates into about 50% of the total energy used in an average beef operation as being used by the cow for maintenance alone.

Although this measurement may seem like the obvious method to determine maintenance costs it cannot be measured on growing cattle very easily. Proxy measurements
for maintenance can be calculated in growing animals by measuring fasting heat production. The problem with this measurement is that it can be affected by growth that occurred before the measurement is collected therefore measuring more than just maintenance (Koong and Ferrell, 1990).

To accurately measure maintenance requirements for a particular animal can be very expensive and lengthy. In cattle it can take up to two years of maintaining a cow at a constant weight to reach any substantial conclusions on her maintenance energy requirements (Taylor et al., 1981).

*Partial Efficiency of growth*

Partial efficiency of growth is the ratio of weight gain to feed after expected maintenance requirements have been subtracted. Predicted maintenance requirements are calculated, in this method of determining feed efficiency, by using feeding tables based on average body weight or metabolic studies of the energy balance of the animal. The assumption is made that there is no variation in maintenance requirements for individual animals. This is highly unlikely (Veerkamp and Emmans, 1995).

*Residual Feed Intake – Regression method (RFI\textsubscript{(reg)})*

Using residual feed intake (RFI) as a method of calculating feed efficiency was first proposed by Koch et al. (1963). It is calculated by finding the difference between actual and predicted feed consumption. The prediction for feed intake should include some body weight measurement and a production trait of choice. Body weight should be adjusted to account for maintenance energy costs and the production trait should be adjusted so production energy costs are accounted for as well (Koch et al., 1963). This partitions feed intake into two portions. The first portion consisting of both maintenance and production energy costs and
the remaining portion commonly referred to as residual. By estimating how much the animal deviates from its predicted intake one can estimate its efficiency (RFI).

Koch et al. (1963) calculated efficiency using three different regression methods. He first calculated a FCR where gain was adjusted for weight. This method was the most common method used among producers at the time. A second method calculated feed intake (F) adjusting for gain (G) and weight (BW). The third method calculated gain adjusting for feed intake (F) and weight (BW). It was concluded that the best method to calculate efficiency was to calculate feed intake adjusting for weight and gain and was later given the name of “RFI”.

\[
\hat{F} = \beta_0 + \beta_1 (G - \bar{G}) + \beta_2 (BW - \bar{BW}) + e
\]

\[
e = \hat{F} - \beta_0 + \beta_1 (G - \bar{G}) + \beta_2 (BW - \bar{BW})
\]

\[
e = \text{RFI}
\]

(Koch et al., 1963)

It was correlated with the adjusted FCR by over .9 and was considered to be more representative of the efficiency of the animal (Koch et al., 1963).

Residual feed intake is calculated such that it is phenotypically independent of the trait used as the response variable and the animal body weight. It is believed by some (Korver, 1988) that it can quantify and represent the variation that can be found in basic metabolic processes which determine an animal’s efficiency.

Kennedy et al. (1993) showed that although RFI may be phenotypically independent of the traits that are adjusted it isn’t necessarily genetically independent. He proposes that one must adjust on a genotypic level for RFI to truly be independent.
Residual Feed Intake – Nutrition prediction of energy requirements method (RFI(NRC))

Fan et al. (1995) developed another method to calculate RFI. It was proposed that by using a three step procedure that partitioned energy intake into energy for maintenance and various production functions based on requirements that residual feed consumption and feed efficiency can be calculated.

The first step in this procedure used prediction equations from the NRC (1984). Fan et al. (1995) was able to calculate net energy required for maintenance (NERm) in Mcal of NE/day by using the live weight (W, kg) of the animal.

\[
\text{NER}_m = 0.077W^{0.75}
\]

Net energy required for medium sized bulls for live weight gain (NERg) in Mcal of NE/day was calculated using both live weight (W, kg) and live weight gain (LWG, kg/day).

\[
\text{NER}_g = 0.0493(W^{0.75})(\text{LWG}^{1.097}/\text{days on test})
\]

(Fan et al., 1995)

The second step simply calculated net energy values for maintenance (NEm) and growth (NEg) using average metabolizable energy values (AME) for each diet. Daily ME requirements for maintenance (MERm) and growth (MERg) in Mcal of ME/day were then calculated.

\[
\text{MER}_m = \text{NER}_m/(\text{NE}_m/\text{AME})
\]
\[
\text{MER}_g = \text{NER}_g/(\text{NE}_g/\text{AME})
\]

By summing daily ME requirements for both maintenance and growth the total ME requirements (MER) were calculated.

\[
\text{MER} = \text{MER}_m + \text{MER}_g
\]
In the third step feed efficiency measurements were calculated. Gross feed efficiency (FE) was measured as a ratio of ADG to metabolizable energy intake (MEI, Mcal of ME/day).

\[
FE = \frac{ADG}{MEI}
\]

Net feed efficiency (NFE) was measured as a ratio of ADG:MEI\textsubscript{g} where MEI\textsubscript{g} was metabolizable energy intake for growth per day, and calculated as the proportion of ME requirements for growth in MER.

\[
MEI_g = MEI \left( \frac{MER_g}{MER} \right)
\]

Residual feed consumption (RFC) for bulls per day in Mcal of ME/day was calculated as MER subtracted from MEI.

\[
RFC = MEI - MER
\]

This three-step approach takes into account breed, sex, weight gain, milk yield, and days pregnant. This method of calculating feed efficiency has two advantages. Net energy can be calculated independent of the diet fed and feed requirements can be estimated separately for maintenance and the production trait of interest (Fan et al., 1995). One main disadvantage is that it is not necessarily independent of production traits.

*Cow/calf Efficiency*

Cow/calf efficiency measures the total feed intake of the cow and her progeny over an entire production cycle. The cycle generally starts after the weaning of one calf to weaning of the next. Total amount of feed consumed is then compared to calf weight weaned and is given as a ratio of total weight of weaned calf over total weight of feed consumed (Jenkins and Ferrell, 1994; Shuey et al., 1993).
This is a reasonable method of calculating whole herd efficiency when accounting for both biological and economic efficiency of the cow herd. Some of its drawbacks include its exclusion of the terminal generation, herd replacements, and cull sales. Gregory (1972) on the other hand argues that these groups of animals only account for a very small portion of the total amount of feed used in production therefore making this method of calculating feed efficiency a viable option.

**Genetic Variation in feed efficiency**

There is plenty of evidence showing that when feed efficiency is provided as gross efficiency or residual feed intake that variation exists. Analysis of variance can be used to determine the components of variation. Residual maximum likelihood (REML) is the most popular method used to find these variance components (Mrode, 2005). This requires the mixed model commonly known as the animal model be converted to log-likelihood model (Mrode, 2005). This method is computationally extensive because estimation requires the derivatives of the model be set to zero finding the maximum using an iterative process first suggested by Patterson and Thompson (1971). Using this method additive variance components can be estimated along with maternal and epistatic variance components. After these components have been estimated an estimated heritability can be found.

Heritabilities have been calculated for feed efficiency measurements in growing cattle (Table 1). Heritabilities for gross efficiency range from 0.16 - 0.46 (Bishop et al., 1991; Bishop et al., 1992; Fan et al., 1995; Gengler et al., 1995; Jensen et al., 1991; Mrode et al., 1990b) while heritabilities for RFI range from .14 - .44 (Fan et al., 1995; Jensen et al., 1991; Koch et al., 1963; Korver et al., 1991).
As mentioned above feed conversion ratio (FCR) is highly correlated with growth rate and maturity patterns. Therefore, it is possible that the variation that can be estimated in FCR could be largely attributed to growth and maturity.

Residual feed intake heritabilities mentioned above have all been calculated using phenotypic regression and not genetic regression which Kennedy et al. (1993) suggests is more accurate. On the other hand genetic correlations between phenotypic RFI and production traits are reported to be quite low (Korver et al., 1991). If this truly is the case then phenotypic and genetic RFI is practically the same providing sufficient evidence that heritability estimates using RFI calculated from phenotypic regression is accurate.

There is evidence, however, that RFI and gain have a genetic correlation (Jensen et al., 1991). This allows for some doubt on whether there is true variation in RFI or if that variation can be attributed to gain instead. Fan et al. (1995) has displayed that both phenotypic and genetic correlations of RFI with production traits are influenced by the way RFI is calculated which depends on how the predicted feed intake is calculated.

Overall, the majority of researchers concluded that there is some type of phenotypic and genetic variation for feed efficiency in growing cattle. Variation within beef populations related to feed efficiency allows for the opportunity for selection for feed efficiency within growing cattle.

Determining variation among adult cattle pertaining to feed efficiency can be somewhat challenging. Adult cattle can be categorized into two groups: lactating and non-lactating. Some studies have shown that breeds with higher milk production potential are less efficient than those breeds that produce less (Montano-Bermudez et al., 1990; Solis et al., 1988). However, other researchers claim that there are no differences in breeds (Klosterman
et al., 1968; Russel and Wright, 1983). Archer et al. (1999) suggests that this conflict may have something to do with how adjustments were made when calculating the amount of metabolizable energy required.

Genetic variation has been calculated for feed efficiency in a few specific breeds including Ayershire (Taylor et al., 1981), Charolais (Arthur et al., 2001b), Angus (Arthur et al., 2001a), Wagyu (Hoque et al., 2006), Angus x Hereford and Barzona x Hereford (Hotovy et al., 1991). For all studies it was concluded that there is within breed variation, in non-lactating cattle, for selection with sufficient response. Little information is available for within breed variation of feed efficiency while cows are lactating.

Unlike chickens and pigs that have specialized genotypes for different parts within the production system estimating the amount of variation found in a cattle herd production system is very difficult. Small amount of progeny and large generation intervals in cattle contribute to the source of this particular issue. Many traits are considered when determining efficiency in the whole herd and it is difficult to compare between one part (slaughter generation) with another (breeding herd).

Cow/calf efficiency was used as a model for whole herd or production efficiency (Shuey et al., 1993). Although variation was observed the source of the variation was found not to be associated with weaned calf weight per unit of energy consumed unless the heifer was fed a limited diet. Jenkins and Ferrell (1994) on the other hand were able to verify that there was variation with weaned calf weight per unit energy consumed and concluded that estimating variation using cow/calf efficiency is possible.
Physiological basis for variation in feed efficiency

When variation in feed efficiency is understood on a physiological basis, correlated response to selection can be predicted much more accurately. Traits that are highly correlated with feed efficiency may be identified allowing for an easier method in identifying efficient animals within a herd. This could lead to physiological markers to be utilized in a strategic manner for the benefit of increasing the profitability of the herd.

When determining feed efficiency energy requirements are usually separated into two parts. The first partition set aside as energy for maintenance and the second as energy for production. Feed energy for maintenance contributes to many physiological processes which include the following: maintaining basal metabolism, voluntary body movement, thermoregulation, protein and fat synthesis, ion transport mechanisms and vital organ/nervous functions (Herd et al., 2004).

Separating these fundamental biological mechanisms into two distinct parts is not realistic, because there is no distinct separation between maintenance and production energy. It does show that some energy must be used for simply allowing the animal to live before production processes can take place such as growth. Variation found in efficiency may come from these partitions.

Heat production from metabolic processes can be attributed to variation in feed intake itself. As an animal consumes more feed, more energy is needed to digest the food, partly due to increase in the size of the gut itself (Herd et al., 2004). The increase in energy of digestive tissue proportional to animal weight also plays a role in the amount of heat produced (Herd et al., 2004).
Digestibility of dry matter could also play a role in variation within feed efficiency. Heifers and bulls during the growing stage separated by low and high RFI had a difference in the amount of dry matter they were able to digest at approximately 1% (Herd et al., 2004).

Body composition has an association with maintenance requirements of livestock. Fatter animals tend to have lower maintenance requirements than lean animals at the same weight (Afonso and Thompson, 1996a, b; Cleveland et al., 1983). Although protein synthesis takes less energy than fat synthesis, protein is continually degrading and resynthesizing requiring more energy to maintain than fat (Dicostanzo et al., 1990; Owens et al., 1995). Protein turnover can occur at different rates in individual animals which may be a large reason for the amount of variation we see in maintenance energy (Oddy, 1998). However, this explanation does not account for all the variation in maintenance energy (Taylor et al., 1986).

The most metabolically active tissues in the body are the heart, liver, mammary tissue, and gastrointestinal tissue. Relative sizes of these tissues directly influence the amount of energy required to maintain them (Smith and Baldwin, 1974). These organs also have larger protein turnover than in skeletal tissue requiring more energy (Early et al., 1990). Therefore animals that have larger organs require more energy making them less efficient.

Other sources of variation in feed efficiency could include disease susceptibility, environmental stress and energy used to find more feed (Luiting et al., 1994). Plasma insulin, milk protein, milk fat, and total plasma protein all have relationships with RFI but no definite relationship has been determined yet (Archer et al., 1999).

Testosterone and thyroid hormones thyroxine (T₄) and triiodothyronine (T₃) are important to growth. Testosterone stimulates muscle and skeletal growth by binding to
receptors on muscles cells stimulating them to grow (Lawrence and Fowler, 1998). Thyroid hormone receptors found in the nuclei of cells stimulate oxidative metabolism and anabolic function of cells in all tissues by regulating oxygen consumption, mineral balance and synthesis and metabolism of proteins, carbohydrates and lipids (Lawrence and Fowler, 1998). If these hormones are deficient severe retardation of growth will occur (Lawrence and Fowler, 1998). Concentrations of these hormones are variable and may effect feed efficiency (Archer et al., 1999).

Biological processes found to be most important explaining 73% of the total variation include heat production from metabolic processes, body composition, and activity (Richardson and Herd, 2004). Over a quarter of the variation can still not be completely explained.

Selection Strategies

Increasing breeding cows’ efficiency is the best method to increase whole herd efficiency. Although the breeding herd consumes the cheapest feed available, they remain in the herd the longest. The slaughter generation’s feed costs are important and must be considered when evaluating whole herd efficiency too.

The best way to determine efficiency of the herd is to measure daily feed intake of each individual animal over the full course of its existence within the herd. This would obviously be an economic challenge therefore requiring some alternative method. One method of selection that does not include collecting individual feed intake is using physiological markers. Using physiological markers alongside direct measurements is considered the best method because of its potential of increased accuracy (Woolliams and Smith, 1988). One marker that has been given considerable attention for indicating feed
efficiency is Insulin-like growth factor I (IGF-I). Some of the benefits of using IGF-I as a marker is that it is relatively inexpensive to assay and it is moderately heritable in cattle (Davis and Simmen, 2000). Low IGF-I concentrations are correlated with low RFI according to Moore et al. (2005).

Measuring feed intake at strategic periods within the animals’ life seems to be the best option for now. Once individual feed intake has been collected the next step is to determine which method should be used in calculating feed efficiency.

Feed conversion ratio or its inverse gross efficiency is the most common method in describing feed efficiency. Using a ratio will cause major problems when used in a linear selection index, especially when gain or feed intake are in the index as well (van der Werf, 2004). It is difficult to tell whether the herd is decreasing its feed intake or whether it is increasing in size. Yet, when one selects their herd for growth rate a positive correlated response to FCR occurs and feed intake is unnecessary to measure (Mrode et al., 1990a). In fact it is proposed that a better response of selection occurs when FCR is indirectly selected for through growth than when selected for directly when measured on growing cattle (Mrode et al., 1990a).

Selection on maintenance efficiency, decreasing feed intake without a change in mature weight, is considered to have detrimental effects on a whole herd basis. There is a high unfavorable correlation between this measurement of efficiency and appetite. A decrease in appetite reduces growth rate which limits the herds productivity (Taylor et al., 1981).

Residual feed intake is the most common measurement for feed efficiency used for selection and breeding programs in the recent literature. Some of its attractive components
include its phenotypic independence of production traits and weight. Most selection experiments are based on RFI measurements taken during the post-weaning period. Using mice as a model, selecting animals after determining RFI during a post-weaning period is sufficient evidence that they will remain efficient as mature animals (Archer et al., 1998). This selection method has increased efficiency in the feedlot by almost 4% (Richardson et al., 2001).

Ranking bulls on RFI and comparing the bulls with low values versus the bulls with high values shows that there is no significant differences in ultrasound measurements between groups (Basarab et al., 2004; Schenkel et al., 2004). There also is no difference in scrotal circumference or hip height (Schenkel et al., 2004). Genetic correlations with RFI and most ultrasonic measurements are not different from zero. The exception being ultrasonic backfat (Basarab et al., 2004) which can be adjusted for if need be (Schenkel et al., 2004). This indicates that selecting for RFI should have no detrimental effects on the quality of the end beef product that is being produced.

Five years of divergent selection based on residual feed intake in post-weaning bulls and heifers has not influenced maternal productivity in cows (Arthur et al., 2005). There is no difference whether the cows were bred artificially or naturally when compared to randomly bred cattle (Arthur et al., 2005). Residual feed intake has a genetic correlation of 0.98 between post-weaning and mature cows suggesting that even though feed intake was not recorded in these mature cows that they should have significant differences in feed intake (Archer, 2002).

Kennedy et al. (1993) on the other hand disagrees with the use of residual feed intake as selection criterion. A selection index which includes feed intake, production traits of
interest and weight was suggested to provide the same amount of information that RFI can provide. Furthermore, Kennedy et al. (1993) provides evidence that RFI in fact is a selection index manipulated into a different form. The most correct procedure for optimal selection may be to consider production traits and feed intake alone rather than RFI values (van der Werf, 2004). To increase accuracy of genetic improvement other efficiency traits can be included in the index such as body composition (van der Werf, 2004).

Although RFI provides no additional information for selection that a selection index can’t provide it can shed some light on genetic variation of feed efficiency (van der Werf, 2004). Residual feed intake clearly has a heritability, variance, and covariance with production traits. By understanding the covariance of RFI with other efficiency traits, such as heat production, activity, and body composition, production efficiency can be defined better (van der Werf, 2004). Essentially selecting on RFI is another method of multivariate selection.

Summary

As feed costs continue to increase feed efficiency will continue to be a trait of interest for cattle producers. It has been shown that there definitely is variation in feed efficiency among beef cattle within a production system. The source of this variation in feed efficiency has become somewhat clearer but is not totally understood. Although the source of this variation is still incomplete selection programs have been successful at increasing the efficiency of the growing animal within the slaughter generation.

An understanding of biological relationships between growing and mature animals pertaining to feed efficiency has yet to be established. Furthermore, most studies included data from bos taurus breeds and only a little attention has been given to the bos indicus...
breeds. A critical examination of feed efficiency between bos indicus and bos taurus with an emphasis on biological relationships between growing and mature animals can positively impact methods to improve breeding programs.

Relationships between groups of cattle within the same production system should be analyzed further. A lot of information is available on traits measured on growing animals. These same traits need to be collected on the same animals when they have matured and determine how related these traits are with each other. In addition a comparison of these traits with growing and mature relatives would help increase the amount of knowledge that is available in feed efficiency of beef cattle. Understanding this aspect of feed efficiency may be the key to developing not only more efficient individuals within a herd, but more importantly, it will help develop the whole herd efficiency, which is the ultimate goal.
Literature Cited


CHAPTER 2

RELATIONSHIPS AMONG MEASURES OF FEED UTILIZATION, ADG, BEHAVIOR AND ULTRASONIC MEASURES
Relationships among measures of feed utilization, ADG, behavior and ultrasonic measures

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ABSTRACT:

The objective was to estimate phenotypic relationships among measures of feed utilization and economically important traits in beef cattle. Data were from 183 registered Angus bulls from the NCSU Historic Angus Herd which is maintained at the Upper Piedmont Research Station in Reidsville, NC. Means for BW and age were 271 ± 3.2 kg and 275 ± 1.5 d, respectively. Bulls were blocked based on BW and sire into groups of 12, adapted to a corn silage-based diet (140g CP, 1.73 Mcal NEm and 1.22 Mcal NEg per kg DM), and trained to use Calen gates. Feed offered was recorded daily and used to calculate DMI. Bulls were weighed every 14 d during the 84 d test, and ADG was determined by linear regression of weight on time. Means for ADG and DMI were 1.5 ± 0.02 kg/d and 7.5 ± 0.08 kg/d, respectively. Feed conversion ratio (FCR) was calculated by taking average DMI of each bull divided by ADG with mean 5.0 ± 0.05. Residual feed intake (RFI) was calculated based on NRC equations (RFI\textsubscript{(NRC)}) with mean -0.42 ± 0.065. Alternatively, RFI was also calculated with a model including the dependent variable DMI, fixed effects of year, and regression covariates 42-d mid weight and ADG (RFI\textsubscript{(reg)}) with mean 0.0 ± 0.05. Partial correlations were calculated using a model including fixed effects of year, pen, and sire nested within year. Fixed effects of year and covariates 42-d mid weight and ADG affected RFI\textsubscript{(reg)} (P <
0.05). Phenotypic correlations between RFI_{(NRC)} with RFI_{(reg)}, FCR, BW, and ADG were 0.77, 0.72, -0.54, and -0.54 (P < 0.01), respectively. The phenotypic correlation between RFI_{(reg)} and FCR was 0.65 (P < 0.01). Relationships between RFI_{(reg)} and ultrasonic measurements of intramuscular fat, LM area, rump fat, and rib fat were not statistically different from zero. As expected, RFI_{(NRC)} and RFI_{(reg)} were highly correlated. Both RFI_{(NRC)} and RFI_{(reg)} were highly correlated with FCR. It was concluded that alternative methods of calculating RFI were found to be highly correlated, RFI_{(reg)} was, by design, phenotypically independent of ADG and BW, and RFI_{(NRC)} was phenotypically correlated with ADG and BW.

**Key words:** beef cattle, residual feed intake, feed efficiency
Introduction

Beef production is a business and like all businesses it is the relationship between the cost of inputs and value of outputs which determine profitability. Decreasing the cost of inputs while maintaining the value of outputs can increase profitability. Approximately 60 – 65% of overall production costs can be attributed to maintaining the cow herd, and about 80% of genetic change within a beef herd can be attributed to bull selection. Therefore, if one could identify bulls which will produce daughters that optimize efficiency of feed utilization then profitability would be expected to increase. Recent studies performed by Arthur et al. (2001a) showed that genetic variation exists in feed efficiency of beef cattle signifying that selection for feed efficiency can be successful.

Different methods have been proposed to measure feed efficiency among livestock species. The two most common methods to measure feed utilization include gross efficiency or its inverse FCR and residual feed intake (RFI). Residual feed intake (RFI) was first proposed by Koch et al (1963) which is defined as the difference between predicted DMI and observed DMI. Predicting DMI can be accomplished by using NRC prediction equations based on predicted energy requirements given body weight, gain and energy available in the diet (Fan et al., 1995). Another method of predicting DMI uses a multivariable regression approach adjusting for factors associated with energy for maintenance and energy for growth. The most common adjustment factors are ADG, weight and body composition in growing cattle.

All measures of efficiency currently require collection of individual DMI. This is labor intensive and expensive. Our objective is to identify both genetic and phenotypic relationships that may exist among the three main measures of feed utilization and
phenotypic correlations of feed utilization that may exist among other economic traits. This can provide evidence for an indirect method for selection of feed efficiency or identify how selection may affect other traits.

**Materials and Methods**

*Description of Animals*

Registered Angus bulls (n=183) were used over a three yr period in this study (Table 3). All bulls were part of the North Carolina State University historic Angus herd which is maintained at the Upper Piedmont research station near Reidsville, NC. Bulls were transported to the Butner Beef Cattle Center approximately 45 days after weaning in August. Before transport bulls were preconditioned using common protocol including training to eat from bunks, drink from waterers, and vaccination for respiratory and clostridiol diseases. Bulls were representative of 27 distinct sires and 131 dams. One sire was used between years one and two of the study with six and nine progeny being represented in each year respectively. Two sires were used between years two and three with both sires having two progeny each in year two. In year three one of these sires was represented with 5 progeny and the other with two. There were also a total of 47 dams that had at least two calves over three year interval.

*Description of Test*

Upon arrival bulls were blocked based on BW minimizing sire nested within pens of 10-12 and adapted to a growing ration (Table 2) estimated to allow for 1.5 kg gain per day. A two week acclimation period allowed for adjustment to the ration and training to use CALAN gates. Bulls (n = 3) which failed to adapt to CALAN gates were removed from the study. Beginning the third week fresh feed offered was recorded daily for a total of 84 days and orts
were weighed and recorded on a weekly basis. Average age of bulls at the beginning of test was 275 ± 1.5 d with an average weight of 271 ± 3.2 kg (Table 3). At the beginning and end of test all bulls were weighed for two consecutive days and shrunk weight was recorded.

During the 84 day test, bulls were weighed every 14 d. Within the first week of the test (beg-test) ultrasound measurements, hip height (HH), scrotal circumference (SC) and blood samples were collected. Behavioral measurements including temperament scores (TS) and exit velocity (EV) were collected as well. All of these measurements were again collected on d 42 ± 7 (mid-test) and d 84 ± 5 (end-test) of the test.

Ultrasound images were taken by a certified ultrasound technician and submitted to the CUP Lab, and estimates of rib fat, rump fat, intramuscular fat % (IMF), and rib eye area (REA) were provided.

Behavior data were collected in the scale box. A trained technician evaluated temperament of each bull and assigned TS that ranged from 1 – 5. A score of 1 signified a bull that was relaxed and calm on the scale while a bull that scored a 5 was considered to be a very agitated and exhibited an extreme desire to escape. When the bull was released from the squeeze chute EV (m/s) was calculated by measuring time it took to break two light beams at a distance of two meters from each other using a light beam generator-reflector system. The first beam was placed approximately .5 m from the chute and subject was allowed a straight exit from chute.

Plasma testosterone concentrations were measured using a previously validated radioimmunoassay (RIA) based on a commercially available assay kit (Coat-A-Count, Siemens Medical Diagnostics, Los Angeles, CA). Assays were conducted according to the manufacturer’s instructions. One hundred µl of sample or standard was pipetted into the
coated tubes and then 1 ml of $^{125}$I labeled testosterone was added to all tubes. The standard curve ranged from 0 to 1600 ng/dl and sensitivity of the assay was 4 ng/dl. After a three hour incubation in a 37°C waterbath tubes (except for the total count tubes) were decanted and left to dry and the tubes were counted for one minute using a gamma counter (Packard Cobra 5000B, Perkin Elmer, Waltham, MA). For validation increasing amounts of bovine plasma were added to the standard curve and the plotted curves were parallel. The assays were validated for bovine serum by testing serial dilutions of bovine serum from 25 to 250 µl for parallelism. Interassay coefficient of variation was 8.2% and intra-assay coefficients of variation ranged averaged 6.3%.

Plasma free tri-iodo-thyronine (T₃) and free thyroxine (T₄) were measured using previously validated RIA’s based on commercially available assay kits (Coat-A-Count, Siemens Medical Diagnostics, Los Angeles, CA). Assays were conducted according to instructions supplied by the manufacturer. The kits provide either $^{125}$I labeled T₃ or T₄, known amounts of T₃ or T₄ for standards and tubes coated with antibodies to either T₃ or T₄. Briefly, the procedure for both assays is as follows. One hundred µl of either standard or serum from experimental animals was added to antibody-coated tubes. The standards ranged from 0 to 60 ng/ml. Then 1 ml of $^{125}$I labeled T₃ or T₄ was added to these tubes as well as to four polypropylene tubes. Two of these tubes were counted in the gamma counter with the $^{125}$I labeled T₃ or T₄ still in the tubes to determine total counts. In the other two tubes the liquid was decanted and the empty tubes were counted to determine non-specific binding. After a two hour incubation in a 37°C waterbath the tubes were decanted to remove the liquid, left upside down for approximately 15 minutes to dry and then counted for one minute in a gamma counter and results compared to the standard curve by use of log-logit
transformation (Rodbard and Lewald, 1970) to determine serum concentrations. The assays were validated for bovine serum by testing serial dilutions of bovine serum from 25 to 250 µl for parallelism. Interassay coefficients of variation for T3 and T4 were 10.7 and 11.6%, respectively. Intraassay coefficients of variation for T3 and T4 averaged 6.2 and 4.9%, respectively.

RFI Calculations and statistics

Data were analyzed using the SAS system (Version 9.1, SAS Inst., Inc. Cary, NC). Linear regression of bi-weekly weights over an 84 day period was calculated to determine ADG. Feed conversion ratios (FCR) were calculated for each bull by calculating the ratio of average daily DMI over ADG. Residual feed intake (RFI) was calculated by subtracting predicted DMI from actual intake measured.

Predicted DMI was calculated using two different methods. One method takes advantage of NRC (2000) prediction equations using the three-step procedure introduced by Fan et al. (1995). Net energy required for maintenance (NERm) and for gain (NERg) as well as average metabolizable energy for maintenance (AMEm) and gain (AMEg) of diet were calculated using NRC (2000) values and constants. These values can in turn estimate daily metabolizable requirements for both maintenance and gain. Predicted DMI was then estimated by summing these two values and difference between predicted estimates of DMI from observed DMI and was called RFI(NRC).

The other method used to predict DMI was calculated by regressing DMI on gain (ADG) and mid-test BW (MidBW) (Koch et al., 1963). Dam age and year as fixed effects were not significant and were not included in model.

\[
RFI_{\text{reg}} = DMI - \left( \beta_1(\text{ADG}) + \beta_2(\text{MidBW}) \right)
\]
Differences between predicted DMI given from the regression model and observed DMI was called RFI\(_{\text{reg}}\).

All ultrasonic measurements, HH and SC were adjusted to 365d of age. Partial phenotypic correlations of all trait measurements collected were calculated using the MANOVA option in General Linear Model (GLM) procedure with an adjustment for year as a fixed effect. Differences among sires were estimated using Least Squares Means option in GLM procedure of SAS. Covariance of half sibs (Cov\(_{\text{HS}}\)) were estimated using Mixed Procedure in SAS with sire as a random effect. Heritabilities were then estimated by multiplying Cov\(_{\text{HS}}\) by four and dividing the product by phenotypic variance.

The American Angus association provided EPDs. Genetic parameters were estimated using a full animal model in MTDFREML (Boldman, 1995). The model included all known relationships for 5 generations. Each trait measured was analyzed separately to obtain direct (\(h^2_d\)) and maternal (\(h^2_m\)) heritabilities when applicable. An animal model was fitted which included a random individual direct animal effect with fixed effects of year (3-levels) when significant (P < 0.05). Iterations were assumed to have converged when variance of -2 times the log likelihood used in simplex search algorithm was less than 10\(^{-9}\). To ensure that log likelihood was estimated for global and not local maximum cold restarts of the MTDFREML program using previous converged values. Restarts were performed until -2 log likelihoods using the simplex search algorithm did not change from one restart to the next.

Two trait analyses were not estimated for traits that included maternal effects in model due to insufficient amounts of observations. Single trait analysis was successful for all traits.
Results and Discussion

Performance data LS means for all traits that were collected and calculated are reported in Table 3.

Bulls had an ADG of 1.5 kg/day which was consistent with the ration formulation. All traits had a significant difference between years (P < 0.10) except for RFI_{(reg)}, RFI_{(NRC)}, and DMI. Means were calculated over all three collection periods within year except for EV and TS in which only first score was used to calculate means. After bulls were weighed many times and were familiar with the process of entering and leaving the chute most bulls became acclimated and information collected on behavior traits had little variation among bulls at the end of the test.

Residual Feed Intake

A depiction of predicted DMI versus observed DMI predicted using two different methods are shown in Figures 1a and 1b. Figure 1a depicts feed intake predictions using energy maintenance and growing energy requirements. Figure 1b uses a regression method with observed feed intake as response variable and ADG and MidBW as covariates to predict feed intake. The same line that overlays Figures 1a and 1b represents a linear relationship of 1:1 with predicted feed intake and observed feed intake. Differences from this line and each individual point represent the values of RFI that were calculated. Differences in predicted feed intake and observed feed intake are reported as RFI_{(NRC)} and RFI_{(reg)} for Figures 1a and 1b respectively.

When comparing Figure 1a with Figure 1b we see that the range of values for predicted feed intake used to calculate RFI_{(NRC)} are much larger than for predicted feed intake used to calculate RFI_{(reg)}. Regression method clusters observations around the center of the
Figure 1a shows some animals were predicted to consume over 10 kg of feed a day while Figure 1b predicts no animals would consume over 10 kg of feed. Upon further analysis all animals that were expected to consume over 10 kg of feed had the largest MidBW on test. This is further evidence that low RFI\(_{(NRC)}\) values tend to bias towards animals that were larger. The NRC prediction equations overestimate maintenance requirements for bulls that had a MidBW of over 400 kg (figure 1a). Some reasons that may contribute to the lack of fit of this model for heavy bulls may be due to the prediction equation used to estimate energy for maintenance was developed from heifer and steer data. Heavy bulls in this study may differ in body composition from the data used to develop the model (Lofgreen and Garrett, 1968). This model could potentially be improved by further investigating other adjustment factors.

**Phenotypic correlations**

Partial phenotypic correlations shown in Table 4 are adjusted by year. Only one trait, TS, was not phenotypically correlated with any of the other traits that were collected during this study. This is most likely due to the fact that bulls were very even tempered and many did not ever score above a 2. There was not enough variation in this trait to find any relationships with any of the other traits measured.

Two traits with the highest correlation coefficient of 0.77 (P < 0.01) were feed utilization measures of RFI\(_{(NRC)}\) and RFI\(_{(reg)}\). This was a little higher than was reported on young Charolais bulls in the study performed by Arthur et al.(2001c). These two estimations of feed utilization use similar information of weight and gain to arrive at a value that could be considered to be measuring the same trait. There is some measurement error in estimation of RFI\(_{(NRC)}\) because it assumes that the cattle are biologically similar with fat composition of
28% (NRC, 2000), whereas RFI\textsubscript{(reg)} includes differences among animals in the residual. Feed efficiency measure of FCR had a significant correlation (P < 0.01) with other RFI measures similar to other studies (Arthur et al., 2001a; Fan et al., 1995).

Weight and ADG were negatively correlated to RFI\textsubscript{(NRC)} with correlation coefficients of \(-0.54\) (P<0.01) for both measures, these measures were similar to estimates found by Fan et al (1995) for Angus cattle. As RFI\textsubscript{(NRC)} increased (less efficient) on average MidBW and ADG would decrease signifying that animals who are small with low rates of gain are considered to be least efficient. Other traits associated to RFI\textsubscript{(NRC)} were HH, SC, and all ultrasound traits excluding IMF. Animals with low RFI\textsubscript{(NRC)} had more rump fat, rib fat, and greater SC and HH. In some cases this would be considered a favorable correlation although one must take into consideration that this measurement of feed utilization favors larger animals. Large animals require more maintenance energy which may increase feed consumption which would indirectly affect profitability. Exit velocity was found to be correlated with RFI\textsubscript{(NRC)} (r = -0.14, P < 0.05) as well which is different than previous studies performed by Nkrumah et al. (2007). This measurement is an indicator of a favorable association that efficient animals are also less excitable.

It was also determined that EV was associated with MidBW (r = .28, P < .01), ADG (r = 0.16, P > 0.01), DMI (r = 0.20, P < 0.01), REA (r = 0.15, P < 0.10), and IMF (r = -0.19, P < 0.01). Larger, faster growing bulls do not move as fast out of chutes as smaller, slower growing bulls which explains why EV was shown to be associated with RFI\textsubscript{(NRC)} since less efficient bulls share the same characteristics as bulls growing slower and weighing less.

Phenotypic correlations associated with RFI\textsubscript{(reg)} include DMI (r = 0.65, P < 0.01) similar to results discussed by Arthur et al.(2001a). Bulls with low values of RFI\textsubscript{(reg)} ate less
than bulls who were less efficient. This relationship is as expected. No other traits were found to be significantly correlated to this measure of feed utilization that have not already been mentioned. Calculating $\text{RFI}_{\text{reg}}$ adjusts for ADG and MidBW. This adjustment seems adequate enough to account for variation that may occur outside of feed utilization that $\text{RFI}_{\text{NRC}}$ is not able to accomplish.

Feed efficiency measures did not have overwhelming evidence of being phenotypically correlated with testosterone, T₃ or T₄. All three hormones were significantly correlated to MidBW ($P < 0.01$). Hormones T₃ and T₄ were also significantly correlated to ADG ($P < 0.01$). It is interesting to note that the highest phenotypic correlation that exists among the hormones with the feed efficiency related traits was T₄ T₃ with DMI ($P < 0.01$). The only hormone that was consistently found to be significant to DMI over all three measurement periods was T₄.

Partial Spearman rank correlations are adjusted by year in Table 5. Two methods used to calculate correlations between traits collected were slightly different. One main difference is using Spearman correlation coefficient TS is correlated with EV ($r = -0.14$, $P < 0.06$) and weight is correlated with FCR ($r = 0.13$, $P = 0.09$). Ranking bulls based on all three measures of feed utilization we found that the top and bottom five bulls are largely the same across each measure of feed utilization with $\text{RFI}_{\text{NRC}}$ and $\text{RFI}_{\text{reg}}$ agreed best at ranking least efficient animals while $\text{RFI}_{\text{reg}}$ and FCR agreed best at ranking most efficient animals. This phenomenon can be attributed to the favorability that $\text{RFI}_{\text{NRC}}$ has with increased MidBW whereas $\text{RFI}_{\text{reg}}$ is independent of weight and does not favor larger animals.

**Heritabilities**

Heritabilities using half sib analysis and MTDFREML are reported in Table 6.
Heritabilities were found to be different depending on method used to estimate them. Standard errors were found to be quite large due to small amount of data available; therefore, we would expect some difference between the two methods used strictly due to sample size. When comparing different feed efficiency measures RFI\textsubscript{(NRC)} was found to be slightly more heritable than RFI\textsubscript{(reg)} using both methods of estimation. Estimates of heritability are similar to those reported in other studies (Bishop et al., 1991; Fan et al., 1995).

Behavior traits EV ($h^2 = .39$) and TS ($h^2 = .20$) were both found to be moderately heritable. Previous research by Nkrumah et al. (2007) found slightly higher heritability for EV. Half sib analysis decreased the estimate by approximately 0.20 in both behavior traits. This trend was seen on other traits within the analysis as well. This is not surprising since half sib analysis, unlike MTDFREML, does not take into account all relationships that occur within this data set adjusting for covariance of relatives. High to moderate heritability of these traits signifies that response to selection for excitability can occur at a moderate rate.

**Genetic correlations**

Two trait analysis was performed to estimate genetic correlations between three methods used to calculate feed efficiency, RFI\textsubscript{(NRC)}, RFI\textsubscript{(reg)}, and FCR and behavior measurements TS and EV (Table 7). Due to the high phenotypic correlation between T\textsubscript{4} and DMI genetic correlations estimates were also analyzed for these two traits. Other correlations were not estimated because maternal effects were necessary in the model and there were not enough observations for convergence.

The largest genetic correlation between the feed efficiency measures and the other traits were seen between EV and RFI\textsubscript{(NRC)} ($r_g = -0.77$). This large correlation is largely due to shared variation these traits have with MidBW. Both RFI measurements had a genetic
correlation with each other ($r_g = 0.49$). Genetic correlations between RFI\(_{(\text{reg})}\) and FCR were not very large ($r_g = 0.16$) while genetic correlation between RFI\(_{(\text{NRC})}\) and FCR was similar to correlation coefficients of other efficiency measures ($r_g = 0.41$). Arthur et al. (2001b) found that genetic correlations between RFI\(_{(\text{reg})}\) and RFI\(_{(\text{NRC})}\) ($r_g = 0.89$) were much larger than what we found within our study ($r = 0.49$). Genetic correlations with TS were very small with all measures of efficiency ($r_g < .07$).

Genetic correlations between the three measures of T\(_4\) concentration over the three time points of the test and overall average DMI ranged from 0.50 – 0.80. This large genetic correlation provides evidence that a selection index that includes ADG, weight and some prediction equation that incorporates plasma T\(_4\) concentrations as a predictor of DMI could be developed.

While alternative methods of calculating RFI were found to be nearly identical, RFI\(_{(\text{reg})}\) was, by design, phenotypically independent of ADG and BW, and gross efficiency and its inverse FCR is correlated with ADG (Klosterman, 1972), in fact selection based on this measure could increase mature size (Salmon et al., 1990). Feed efficiency can be related to other economically important traits depending on method of estimation.

Although RFI\(_{(\text{NRC})}\) tends to bias larger faster growing animals to be more efficient there are some benefits to using this estimate of feed utilization. This method uses uniform prediction equations developed from animals outside our sample. Therefore, estimates of RFI\(_{(\text{NRC})}\) can be directly compared across herds with similar breeds and environment. As mentioned above the drawback of making such comparisons assumes that all animals across herds do not vary in body composition.
The method that was most independent of all other traits measured was RFI\textsubscript{(reg)}. This method of estimating efficiency of feed utilization would have the least effect on other economic traits. It is important to remember that phenotypic independence of other traits does not necessarily indicate that the other traits should be ignored. On the contrary RFI\textsubscript{(reg)} is a tool to be as only part of the selection criteria used within a breeding program. In fact RFI\textsubscript{(reg)} can be viewed as an index including DMI, ADG, and MidBW (Kennedy et al., 1993), this attempts to capture both maintenance and growth in efficiency calculation. It would be preferable to use an economic selection index to improve efficiency. If one were to measure DMI over a certain period of time it would seem to be much more advantageous to develop an index that would give appropriate economic weights to the traits of interest according to goals of an independent production program (Kennedy et al., 1993).

None of the traits measured were found to be an indicator of feed utilization. Due to the extreme cost and labor intensity of measuring individual DMI it is highly unlikely that this will become a practice that will be used on an average beef cattle herd. Alternative methods of estimating DMI would be of great worth to the beef industry. Further research on the genetic and phenotypic relationship between T\textsubscript{4} and DMI needs to be done. The beef industry needs an efficiency EPD. This EPD is likely to be based on a linear equation including DMI, ADG, and mature weight with appropriate economic weights on each component.

Other factors of feed efficiency must be researched as well, such as the correlation of efficiency as a growing animal compared to a mature animal. Input costs are mostly associated with the female population and estimating feed utilization among lactating and pregnant animals must be the focus of further research.
Literature Cited


Table 1  Heritabilities of feed utilization

<table>
<thead>
<tr>
<th>Breed</th>
<th>Type</th>
<th>Sex</th>
<th>Heritability</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Swedish R &amp;W</td>
<td>Beef</td>
<td>Bull and Female</td>
<td>0.35 ± 0.24</td>
<td>(Brelin and Brannang, 1982)</td>
</tr>
<tr>
<td>Herford</td>
<td>Beef</td>
<td>Bull</td>
<td>0.33 ± 0.10</td>
<td>(Mrode et al., 1990b)</td>
</tr>
<tr>
<td>Angus</td>
<td>Beef</td>
<td>Bull and Female</td>
<td>0.26</td>
<td>(Bishop et al., 1991)</td>
</tr>
<tr>
<td>British</td>
<td>Beef</td>
<td>Bull</td>
<td>0.16 ± 0.14</td>
<td>(Fan et al., 1995)</td>
</tr>
<tr>
<td>Belgian Blue</td>
<td>Beef</td>
<td>Bull</td>
<td>0.16</td>
<td>(Gengler et al., 1995)</td>
</tr>
<tr>
<td>Holstein</td>
<td>Dual purpose</td>
<td>Bull</td>
<td></td>
<td>(Jensen et al., 1991)</td>
</tr>
<tr>
<td>Fresian/Brown</td>
<td></td>
<td></td>
<td>0.20 and 0.27</td>
<td></td>
</tr>
<tr>
<td>Swiss</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Herford x Fresian</td>
<td>Beef-Dairy Cross</td>
<td>Steer and Female</td>
<td>0.46 ± 0.20</td>
<td>(Bishop et al., 1992)</td>
</tr>
<tr>
<td>Angus</td>
<td>Beef</td>
<td>Bulls and Female</td>
<td>0.29 ± 0.04</td>
<td>(Arthur et al., 2001a)</td>
</tr>
<tr>
<td>Bonsmara</td>
<td>Beef</td>
<td>Bulls</td>
<td>0.34</td>
<td>(van der Westhuizen et al., 2004)</td>
</tr>
<tr>
<td>Wagyu</td>
<td>Beef</td>
<td>Bulls</td>
<td>0.15 ± 0.04</td>
<td>(Hoque et al., 2006)</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Breed</th>
<th>Type</th>
<th>Sex</th>
<th>Heritability</th>
<th>Source</th>
</tr>
</thead>
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<tr>
<td>British</td>
<td>Beef</td>
<td>Bulls and Female</td>
<td>0.28 ± 0.11</td>
<td>(Koch et al., 1963)</td>
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<tr>
<td>British</td>
<td>Beef</td>
<td>Bulls</td>
<td>0.14 ± 0.12</td>
<td>(Fan et al., 1995)</td>
</tr>
<tr>
<td>British</td>
<td>Beef</td>
<td>Bulls and Female</td>
<td>0.44 ± 0.07</td>
<td>(Archer et al., 1999)</td>
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<tr>
<td>Swedish R &amp;W</td>
<td>Beef</td>
<td>Bulls and Female</td>
<td>0.27 ± 0.23</td>
<td>(Brelin and Brannang, 1982)</td>
</tr>
<tr>
<td>Swedish R &amp;W</td>
<td>Dairy</td>
<td>Female</td>
<td>0.22 ± 0.11</td>
<td>(Korver, 1988)</td>
</tr>
<tr>
<td>Holstein</td>
<td></td>
<td></td>
<td>0.08 ± 0.06</td>
<td>(Jensen et al., 1992)</td>
</tr>
<tr>
<td>Frisian/Brown</td>
<td>Dual Purpose</td>
<td>Bulls</td>
<td>0.36 ± 0.17</td>
<td>(Arthur et al., 2001a)</td>
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<td>Swiss</td>
<td></td>
<td></td>
<td></td>
<td>(van der Westhuizen et al., 2004)</td>
</tr>
<tr>
<td>Angus</td>
<td>Beef</td>
<td>Bulls and Female</td>
<td>0.39 ± 0.03</td>
<td>(van der Westhuizen et al., 2004)</td>
</tr>
<tr>
<td>Bonsmara</td>
<td>Beef</td>
<td>Bulls</td>
<td>0.31</td>
<td></td>
</tr>
<tr>
<td>Wagyu</td>
<td>Beef</td>
<td>Bulls</td>
<td>0.24 ± 0.11</td>
<td>(Hoque et al., 2006)</td>
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</tbody>
</table>
Table 2 Ration formulation of diet

<table>
<thead>
<tr>
<th>Ingredient</th>
<th>kg/h/d</th>
<th>DM</th>
<th>AS fed kg/h/d</th>
<th>% formulation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Gr. Corn(^1)</td>
<td>0.5</td>
<td>0.89</td>
<td>0.562</td>
<td>39.0</td>
</tr>
<tr>
<td>SBM(^2), 50%</td>
<td>0.6</td>
<td>0.89</td>
<td>0.674</td>
<td>46.8</td>
</tr>
<tr>
<td>Urea</td>
<td>0.05</td>
<td>1</td>
<td>0.050</td>
<td>3.5</td>
</tr>
<tr>
<td>CaCO3</td>
<td>0.105</td>
<td>1</td>
<td>0.105</td>
<td>7.3</td>
</tr>
<tr>
<td>TMS</td>
<td>0.05</td>
<td>1</td>
<td>0.050</td>
<td>3.5</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>1.441</td>
<td>100</td>
</tr>
</tbody>
</table>

\(^1\)Gr. Corn = Ground Corn

\(^2\)SBM = Soy bean meal
### Table 3. Number of bulls, sires, and dams and LS Means of traits measured or calculated during each year of the test

<table>
<thead>
<tr>
<th>Variable</th>
<th>2005 Mean</th>
<th>SEM</th>
<th>2006 Mean</th>
<th>SEM</th>
<th>2007 Mean</th>
<th>SEM</th>
<th>Total Mean</th>
<th>SEM</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bulls on Test</td>
<td>53</td>
<td></td>
<td>70</td>
<td></td>
<td>60</td>
<td></td>
<td>183</td>
<td></td>
</tr>
<tr>
<td>Sires</td>
<td>10</td>
<td></td>
<td>10</td>
<td></td>
<td>10</td>
<td></td>
<td>30</td>
<td></td>
</tr>
<tr>
<td>Age on test (d)</td>
<td>267</td>
<td>2.8</td>
<td>282</td>
<td>2.3</td>
<td>274</td>
<td>2.7</td>
<td>275</td>
<td>1.5</td>
</tr>
<tr>
<td>Weight on test (kg)</td>
<td>284</td>
<td>4.7</td>
<td>245</td>
<td>3.8</td>
<td>289</td>
<td>6.2</td>
<td>271</td>
<td>3.2</td>
</tr>
<tr>
<td>FCR</td>
<td>5.34</td>
<td>0.078</td>
<td>4.61</td>
<td>0.066</td>
<td>5.18</td>
<td>0.084</td>
<td>5.01</td>
<td>0.050</td>
</tr>
<tr>
<td>RFI (regression)&lt;sup&gt;1&lt;/sup&gt; (kg)</td>
<td>0.11</td>
<td>0.084</td>
<td>-0.07</td>
<td>0.100</td>
<td>-0.02</td>
<td>0.067</td>
<td>0.00</td>
<td>0.050</td>
</tr>
<tr>
<td>RFI (NRC)&lt;sup&gt;2&lt;/sup&gt; (kg)</td>
<td>-0.23</td>
<td>0.097</td>
<td>-0.49</td>
<td>0.118</td>
<td>-0.52</td>
<td>0.114</td>
<td>-0.42</td>
<td>0.065</td>
</tr>
<tr>
<td>ADG (kg/d)</td>
<td>1.42</td>
<td>0.029</td>
<td>1.60</td>
<td>0.025</td>
<td>1.49</td>
<td>0.030</td>
<td>1.51</td>
<td>0.017</td>
</tr>
<tr>
<td>Mid-weight (kg)</td>
<td>343</td>
<td>5.4</td>
<td>313</td>
<td>4.5</td>
<td>352</td>
<td>6.8</td>
<td>334</td>
<td>3.4</td>
</tr>
<tr>
<td>DMI (kg/d)</td>
<td>7.55</td>
<td>0.152</td>
<td>7.35</td>
<td>0.136</td>
<td>7.65</td>
<td>0.125</td>
<td>7.51</td>
<td>0.080</td>
</tr>
<tr>
<td>Scrotal Circumference&lt;sup&gt;4&lt;/sup&gt; (cm)</td>
<td>37</td>
<td>0.5</td>
<td>32</td>
<td>0.3</td>
<td>33</td>
<td>0.3</td>
<td>34</td>
<td>0.3</td>
</tr>
<tr>
<td>Hip height&lt;sup&gt;4&lt;/sup&gt; (in)</td>
<td>48</td>
<td>0.2</td>
<td>48</td>
<td>0.2</td>
<td>49</td>
<td>0.3</td>
<td>48</td>
<td>0.1</td>
</tr>
<tr>
<td>Rump Fat&lt;sup&gt;4&lt;/sup&gt; (in)</td>
<td>0.25</td>
<td>0.005</td>
<td>0.26</td>
<td>0.007</td>
<td>0.27</td>
<td>0.008</td>
<td>0.26</td>
<td>0.004</td>
</tr>
<tr>
<td>Rib Fat&lt;sup&gt;4&lt;/sup&gt; (in)</td>
<td>0.19</td>
<td>0.005</td>
<td>0.18</td>
<td>0.005</td>
<td>0.21</td>
<td>0.005</td>
<td>0.19</td>
<td>0.003</td>
</tr>
<tr>
<td>Rib eye area&lt;sup&gt;4&lt;/sup&gt; (in&lt;sup&gt;2&lt;/sup&gt;)</td>
<td>10.36</td>
<td>0.166</td>
<td>9.83</td>
<td>0.154</td>
<td>10.84</td>
<td>0.141</td>
<td>10.31</td>
<td>0.094</td>
</tr>
<tr>
<td>IMF&lt;sup&gt;3,4&lt;/sup&gt; (%)</td>
<td>3.66</td>
<td>0.114</td>
<td>4.29</td>
<td>0.071</td>
<td>5.38</td>
<td>0.114</td>
<td>4.46</td>
<td>0.076</td>
</tr>
<tr>
<td>Exit velocity (m/s)</td>
<td>1.19</td>
<td>0.066</td>
<td>1.21</td>
<td>0.064</td>
<td>1.51</td>
<td>0.125</td>
<td>1.30</td>
<td>0.052</td>
</tr>
<tr>
<td>Temperament Score</td>
<td>1.3</td>
<td>0.07</td>
<td>1.7</td>
<td>0.09</td>
<td>1.2</td>
<td>0.05</td>
<td>1.4</td>
<td>0.05</td>
</tr>
</tbody>
</table>

<sup>1</sup>RFI (regression) = Residual feed intake in which predicted feed intake was calculated by using a multivariate linear model adjusting for ADG and mid-weight

<sup>2</sup>RFI (NRC) = Residual feed intake in which predicted feed intake was calculated using prediction equations from the NRC (2000).

<sup>3</sup>IMF = intramuscular fat %

<sup>4</sup>Adjusted 365 d measurement
### Table 4: Partial Phenotypic Correlation Coefficients Adjusted for year

<table>
<thead>
<tr>
<th></th>
<th>RFI(^1)</th>
<th>FCR</th>
<th>MidBW(^1)</th>
<th>ADG</th>
<th>DMI</th>
<th>Adjusted 365d of age</th>
<th>TS(^8)</th>
<th>EV(^9)</th>
<th>Testosterone</th>
<th>T(_3)</th>
<th>T(_4)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>SC(^4)</td>
<td>HH(^5)</td>
<td>Rump fat</td>
<td>Rib fat</td>
<td>REA(^6)</td>
<td>IMF(^7)</td>
</tr>
<tr>
<td>RFI(_{reg})(^1)</td>
<td>0.77**</td>
<td>0.72**</td>
<td>0.05</td>
<td>0.65**</td>
<td>-0.08</td>
<td>-0.12</td>
<td>-0.06</td>
<td>0.05</td>
<td>0</td>
<td>-0.08</td>
<td>0</td>
</tr>
<tr>
<td>RFI(_{NRC})(^2)</td>
<td>0.72**</td>
<td>-0.54**</td>
<td>-0.54**</td>
<td>0.04</td>
<td>-0.23**</td>
<td>-0.42**</td>
<td>-0.15*</td>
<td>-0.17*</td>
<td>-0.33**</td>
<td>0.09</td>
<td>0</td>
</tr>
<tr>
<td>FCR</td>
<td>0.1</td>
<td>-0.42**</td>
<td>0.34**</td>
<td>-0.12</td>
<td>-0.09</td>
<td>-0.22**</td>
<td>-0.01</td>
<td>-0.13*</td>
<td>-0.09</td>
<td>-0.03</td>
<td>0.04</td>
</tr>
<tr>
<td>MidBW(^1)</td>
<td>0.60**</td>
<td>0.69**</td>
<td>0.23**</td>
<td>0.56**</td>
<td>0</td>
<td>0.31**</td>
<td>0.46**</td>
<td>-0.31**</td>
<td>0</td>
<td>0.28**</td>
<td>0.19*</td>
</tr>
<tr>
<td>ADG</td>
<td>0.69**</td>
<td>0.26**</td>
<td>0.41**</td>
<td>0.23**</td>
<td>0.30**</td>
<td>0.52**</td>
<td>-0.18**</td>
<td>0</td>
<td>0.16**</td>
<td>0.11</td>
<td>0.11</td>
</tr>
<tr>
<td>DMI</td>
<td>0.15*</td>
<td>0.34**</td>
<td>0.05</td>
<td>0.29**</td>
<td>0.41**</td>
<td>-0.26**</td>
<td>0</td>
<td>0.20**</td>
<td>0.09</td>
<td>0.09</td>
<td>-0.17*</td>
</tr>
</tbody>
</table>

\(^1\) RFI\(_{reg}\) = Residual feed intake in which predicted feed intake was calculated by using a multivariate linear model adjusting for ADG and mid-weight
\(^2\) RFI\(_{NRC}\) = Residual feed intake in which predicted feed intake was calculated using prediction equations from the NRC (2000).

MidBW\(^1\) = 42 d weight on test

SC\(^4\) = adjusted 365 d scrotal circumference

HH\(^5\) = hip height

REA\(^6\) = Rib eye area

IMF\(^7\) = intramuscular fat %

TS\(^8\) = temperament score

EV\(^9\) = exit velocity

** P < 0.01

* P< 0.1
Table 5. Spearman Rank Correlation Coefficients

<table>
<thead>
<tr>
<th></th>
<th>RFI_{reg}</th>
<th>F:G</th>
<th>MidBW</th>
<th>ADG</th>
<th>DMI</th>
<th>Adjusted 365d of age</th>
<th>TS</th>
<th>EV</th>
<th>Testosterone</th>
<th>T3</th>
<th>T4</th>
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<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>RFI_{reg}</td>
<td>0.70**</td>
<td>0.67***</td>
<td>0.01</td>
<td>0.05</td>
<td>0.58**</td>
<td>-0.05</td>
<td>-0.08</td>
<td>0.02</td>
<td>0.07</td>
<td>0.03</td>
<td>-0.01</td>
</tr>
<tr>
<td>RFI_{NRC}^2</td>
<td>0.64**</td>
<td>-0.58**</td>
<td>-0.11</td>
<td>-0.27**</td>
<td>-0.46**</td>
<td>-0.14*</td>
<td>-0.23**</td>
<td>-0.37**</td>
<td>0.16*</td>
<td>-0.05</td>
<td>-0.17*</td>
</tr>
<tr>
<td>FCR</td>
<td>0.13*</td>
<td>-0.41**</td>
<td>0.28**</td>
<td>-0.1</td>
<td>-0.08</td>
<td>-0.20**</td>
<td>-0.05</td>
<td>-0.09</td>
<td>-0.07</td>
<td>0.01</td>
<td>-0.03</td>
</tr>
<tr>
<td>MidBW^3</td>
<td>0.58**</td>
<td>0.69**</td>
<td>0.29**</td>
<td>0.54**</td>
<td>0.03</td>
<td>0.34**</td>
<td>0.50**</td>
<td>-0.30**</td>
<td>-0.02</td>
<td>0.32**</td>
<td>0.09</td>
</tr>
<tr>
<td>ADG</td>
<td>0.71**</td>
<td>0.27**</td>
<td>0.44**</td>
<td>0.25**</td>
<td>0.36**</td>
<td>0.52**</td>
<td>-0.20**</td>
<td>-0.03</td>
<td>0.15*</td>
<td>0.08</td>
<td>0.09</td>
</tr>
<tr>
<td>DMI</td>
<td>0.21**</td>
<td>0.38**</td>
<td>0.12</td>
<td>0.33**</td>
<td>0.46**</td>
<td>-0.24**</td>
<td>-0.02</td>
<td>0.21**</td>
<td>0.05</td>
<td>0.08</td>
<td>-0.20**</td>
</tr>
</tbody>
</table>

RFI_{reg} = Residual feed intake in which predicted feed intake was calculated by using a multivariate linear model adjusting for ADG and mid-weight

RFI_{NRC}^2 = Residual feed intake in which predicted feed intake was calculated using prediction equations from the NRC (2000).

MidBW^3 = 42 d weight on test

SC^5 = adjusted 365 d scrotal circumference

HH^5 = hip height

REA^6 = Rib eye area

IMF^7 = Intramuscular fat %

TS^8 = temperament score

EV^9 = exit velocity

** P < 0.01

* P < 0.1
Table 6. Estimations of heritability using two methods calculation

<table>
<thead>
<tr>
<th>item</th>
<th>Half-Sib analysis</th>
<th>MTDFREML</th>
</tr>
</thead>
<tbody>
<tr>
<td>RFI (NRC)(^1)</td>
<td>0.34</td>
<td>0.44</td>
</tr>
<tr>
<td>RFI (reg)(^2)</td>
<td>0.21</td>
<td>0.39</td>
</tr>
<tr>
<td>FCR</td>
<td>0.40</td>
<td>0.36</td>
</tr>
<tr>
<td>205 d weight</td>
<td>0.28</td>
<td>0.38</td>
</tr>
<tr>
<td>ADG</td>
<td>0.32</td>
<td>0.43</td>
</tr>
<tr>
<td>DMI</td>
<td>0.36</td>
<td>0.46</td>
</tr>
<tr>
<td>Scrotal Circumference(^4)</td>
<td>0.32</td>
<td>0.33</td>
</tr>
<tr>
<td>Hip height(^4)</td>
<td>0.36</td>
<td>0.29</td>
</tr>
<tr>
<td>Rump Fat(^4)</td>
<td>0.21</td>
<td>0.33</td>
</tr>
<tr>
<td>Rib Fat(^4)</td>
<td>0.37</td>
<td>0.16</td>
</tr>
<tr>
<td>Rib eye area(^4)</td>
<td>0.02</td>
<td>0.53</td>
</tr>
<tr>
<td>IMF(^3,4) (%)</td>
<td>0.49</td>
<td>0.55</td>
</tr>
<tr>
<td>Exit velocity</td>
<td>0.20</td>
<td>0.39</td>
</tr>
<tr>
<td>Temperament Score</td>
<td>0.00</td>
<td>0.20</td>
</tr>
<tr>
<td>T(_3) Beginning of Test</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>T(_3) Middle of Test</td>
<td>0.14</td>
<td>0.35</td>
</tr>
<tr>
<td>T(_3) End of Test</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>T(_4) Beginning of Test</td>
<td>0.31</td>
<td>0.33</td>
</tr>
<tr>
<td>T(_4) Middle of Test</td>
<td>0.48</td>
<td>0.51</td>
</tr>
<tr>
<td>T(_4) End of Test</td>
<td>0.57</td>
<td>0.54</td>
</tr>
</tbody>
</table>

\(^1\) RFI (regression) = Residual feed intake in which predicted feed intake was calculated by using a multivariate linear model adjusting for ADG and mid-weight

\(^2\) RFI (NRC) = Residual feed intake in which predicted feed intake was calculated using prediction equations from the NRC (2000).

\(^3\) IMF = intramuscular fat %

\(^4\) Adjusted 365 d measurement
**Table 7. Genetic and Phenotypic Correlations**

<table>
<thead>
<tr>
<th></th>
<th>RFI(reg)</th>
<th>RFI(NRC)</th>
<th>FCR</th>
<th>Temperament Score</th>
<th>Exit Velocity</th>
</tr>
</thead>
<tbody>
<tr>
<td>RFI(_{\text{reg}})(^1)</td>
<td>0.39</td>
<td>0.76</td>
<td>0.74</td>
<td>0.00</td>
<td>0.02</td>
</tr>
<tr>
<td>RFI(_{\text{NRC}})(^2)</td>
<td>0.49</td>
<td>0.44</td>
<td>0.72</td>
<td>0.00</td>
<td>-0.14</td>
</tr>
<tr>
<td>FCR</td>
<td>0.16</td>
<td>0.41</td>
<td>0.36</td>
<td>-0.03</td>
<td>0.04</td>
</tr>
<tr>
<td>Temperament Score</td>
<td>0.02</td>
<td>0.07</td>
<td>0.07</td>
<td>0.20</td>
<td>0.00</td>
</tr>
<tr>
<td>Exit Velocity</td>
<td>-0.05</td>
<td>-0.77</td>
<td>-0.09</td>
<td>-0.02</td>
<td>0.39</td>
</tr>
</tbody>
</table>

Genetic (below diagonal), Phenotypic (above diagonal) Correlations and Heritability (diagonal)

\(^1\) RFI\(_{\text{reg}}\) = Residual feed intake in which predicted feed intake was calculated by using a multivariate linear model adjusting for ADG and mid-weight

\(^2\) RFI\(_{\text{NRC}}\) = Residual feed intake in which predicted feed intake was calculated using prediction equations from the NRC (2000).
Figure 1a  Predicted feed intake calculated using prediction equations provided by NRC based on maintenance and growth requirements
Figure 1b. Predicted feed intake calculated using regression method.