FEED EFFICIENCY, CARCASS AND TEMPERAMENT TRAITS IN F_2 NELLORE-ANGUS STEERS

A Dissertation

by

TONYA SUE AMEN

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

December 2007

Major Subject: Animal Breeding

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ABSTRACT

Feed Efficiency, Carcass and Temperament Traits in F_2 Nellore-Angus Steers.

(December 2007)

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Feed efficiency in fed F_2 Nellore-Angus steers produced through embryo transfer was evaluated using two methods: residual feed intake (RFI) and NRC-based model predicted residual consumption (MPRC). Sire and family(sire) both contributed to differences in model predicted residual consumption ($P = 0.036$ and $P < 0.001$, respectively), but not in RFI ($P = 0.117$ and 0.455, respectively). This indicates that variation exists among the sires and families studied, and the opportunity exists to improve MPRC through selection; it also indicates these 2 evaluation methods could result in different conclusions about feed efficiency.

Five aspects of temperament were also evaluated (aggressiveness, nervousness, flightiness, gregariousness, and overall temperament) on a 9-point scale shortly after weaning. Sire had a significant effect on all 5 aspects of temperament evaluated, but family was only responsible for variation in aggressiveness, nervousness, and overall temperament. Contemporary group had no effect on aggressiveness, but did contribute significantly to variation in all other temperament traits. All temperament traits were highly correlated with one another ($r = 0.81$ to 0.98). Recipient dam temperament was lowly correlated with gregariousness and overall temperament ($r = 0.16$ and 0.15, respectively), and the correlations with recipient dam temperament approached significance for aggressiveness, nervousness and flightiness. This suggests that the temperament of the recipient female may have a small effect on the temperament of the calf. This population was structured to identify QTL for economically important traits and appears to be useful to identify genetic markers for feed efficiency and animal temperament.

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TABLE OF CONTENTS

LIST OF TABLES

INTRODUCTION

Cattle operations are plagued with a relatively low average return on investment compared to many other business ventures. Decreasing input costs to increase profitability will be very beneficial. Feed costs represent the majority of expense for cattle operations, so reducing the amount of feed required by an individual to achieve the same production response could increase overall efficiency at both the cow-calf level as well as the feedyard level. This is especially relevant as it has been shown that a relatively small portion of the nutrients provided to cattle are actually used for the production of beef; 70-75% of total energy requirements are used for maintenance alone (Ferrell and Jenkins, 1985) .

Pond et al. (1995) estimated that 60% of beef production costs are associated with providing feed for cattle. It becomes clear then, that anything that can be done to reduce the amount of feed required in order to achieve necessary performance would be economically important.

According to Taylor and Field (1999), when everything else is held constant, a 5% improvement in feed efficiency would be equivalent to:

- Reducing ration cost by $8 per ton
- Decreasing the purchase cost of feeder calves by $1.75 per cwt
- Increasing ADG by 0.6 pounds per day
- Decreasing interest rate on capital from 15% to 9.5%

This dissertation follows the style of Journal of Animal Science.

The potential advantages associated with improvements in efficiency are clear; however, Johnson et al. (2003) reported that observations of maintenance requirements and energetic efficiency haven't changed significantly in the last 100 years even though other significant advancements in production have been made. This is likely due to the fact that identifying individuals that excel in efficiency traits and using them for breeding purposes is problematic.

Accurate evaluation of the efficiency of feed utilization and its incorporation as a selection criterion in a breeding program is extremely important, but, has been an elusive goal due to the difficulty in measuring the trait and its correlation with other important production characters. Using the data gathered here, a bank of phenotypes with adequate variation can be established to detect QTL segregating for traits relating to feed efficiency. These QTL can then be used to increase the opportunity and accuracy of selecting breeding animals to improve feed efficiency in their offspring.

The objective of this research was to study the genetic aspects of feed intake and feed efficiency in *Bos indicus – Bos taurus* cross steers. Furthermore, we evaluated the relationship of feed efficiency with temperament, carcass and meat traits. Using data collected from steers involved in the McGregor Genomics project at Texas A&M University, the aim was to characterize differences in these traits so future researchers can use the phenotypes to locate QTL that may then be used in selection programs.

LITERATURE REVIEW

Traditionally, beef cattle producers have focused on making improvements in production based on traits related to output, such as body weight. This has occurred primarily because these are the traits that establish sale value, and are easiest to measure. Accurately and efficiently evaluating feed inputs is also very important. Using the Cornell Value Discovery System (Tedeschi et al., 2001), Fox et al. (2001) were able to simulate the effects of growth rate and feed efficiency on cost of gain and profitability for a steer with a final weight of 531.8 kg (Table 1). Improving gain by 10% resulted in a predicted 18% improvement in profitability; however, it was predicted that improving efficiency by 10% would result in a 43% increase in profitability. Furthermore, van der Westhuizen et al. (2004) found profitability to be correlated with feed conversion ratio (FCR) and residual feed intake (RFI) (-0.92 and -0.59, respectively) in young Bonsmara bulls in South Africa. Based on these results, it is clear that it is crucial to not only measure production outputs, but also to consider inputs such as feed intake to increase profitability and efficiency in beef production systems.

Table 1. The effect of improvement in feedlot gain and efficiency on profit[1]

	Average Steer	10% higher ADG	10% higher efficiency
Dry Matter intake, kg/day	8.5	9.9	8.5
Daily Gain, kg	1.46	1.60	1.64
Feed/Gain Ratio	2.64	2.57	2.35
Feed Cost, $	176	172	157
Non Feed Cost, $	98	91	89
Total Cost of Gain, $	274	263	246
Profit, $	65	77	93

[1] Adapted from Fox et al., 2001

Exton et al. (2000) attempted to estimate the value of genetic improvement in net feed efficiency (NFE) from an economic standpoint at the commercial cow-calf level, the feedlot level, and to the southern Australia beef cattle industry as a whole. For a 100 cow herd, the assumptions were made that initially, 3 genetically superior bulls (based on NFE) would be purchased and that they would be replaced every 3 years. In the first year, these bulls would be bred to unimproved cows and the resulting progeny in year 2 would be 2% superior for NFE. By year three, after making the decision to invest in bulls genetically similar for NFE, female progeny would be available to start replacing the original unimproved cowherd. Over a 25-year period, the size of the cowherd could be increased to 110 head with no further feed expense. Over this same period this equated to a 42% return on investment, or an annual benefit of $6.95 per cow for selecting bulls genetically superior for NFE. At the feedyard $8.08/hd could be saved on feed costs initially, and it was estimated that this would increase to over $35/hd over 25 years. The authors concluded that the net present value (NPV) of genetic improvement in NFE (assuming a 0.5% adoption rate) to the commercial sector, feedlot sector, and the southern Australian beef cattle industry as a whole to be $52 million, $10 million, and $62 million, respectively.

This review of literature will explore feed intake, methods of measuring efficiency, traits correlated with or causing differences in efficiency, selecting for improved efficiency of growth and factors relating to temperament.

Measuring Feed Efficiency

The two most obvious contributors to feed efficiency are feed intake and weight gain. Weight gain of individual animals is easy and inexpensive to obtain; individual feed intake is not. It is logical, then that selection schemes in the past have focused on the former. This logic was supported by the work of Koch et al. (1963) who reported that the genetic correlations between the efficiency of feed utilization (calculated as the +/- deviation from the regression of gain on consumption) and gain, feed consumption and gain, and feed efficiency (measured as feed conversion ratio) and feed consumption were 0.79, 0.64, and 0.04, respectively. They concluded that, "…selecting for gain should be effective and lead to both increased feed efficiency and increased feed consumption." Since that time, the advantages and disadvantages of different methods of evaluating feed efficiency, and their correlation with other traits, have been investigated in numerous studies.

Ratios. Feed efficiency has traditionally been defined as the ratio of weight gain to feed intake or its inverse, feed intake per unit gain in body weight (feed conversion ratio). Though this method is widely used and easily interpreted, it fails to partition the amount of feed actually needed for animal maintenance and growth. Using ratios, 3 factors are needed to evaluate feed efficiency: feed consumed, weight gain, and time. To evaluate feed efficiency, one of the factors is held constant and variation in the others evaluated. For example, all animals are put on feed at the same time and fed for an equal number of days, then variation in weight gain and feed intake is assessed. Conversely, animals could be fed the same amount or fed for a specific weight gain, but would then be on feed for varying amounts of time. According to Koch et al. (1963) each of these situations creates unique challenges from an analysis standpoint. In the former example (time held constant), differences will exist for body weight of the animal, and thus, maintenance requirements and composition of gain; plus, intake will vary. In the latter example (weight or intake held constant), time on feed will vary, and thus the animals will be evaluated under different environmental conditions.

Using ratios to evaluate efficiency is also difficult from a selection standpoint because selection for FCR can be accompanied by changes in growth rate and mature cow size (Mrode et al., 1990). Specifically, FCR is negatively correlated with growth; so, selecting for desirable FCR in calves will most likely lead to larger mature cow size, and thus, to an increase in expense of feed at the cow-calf level. Furthermore, FCR has been found to be genetically related to rib fat (r = 0.38) and P8 rump fat (r = 0.40, Robinson and Oddy, 2004). So, selecting for improved FCR, would likely lead to leaner animals as well, although this would not be obvious by only evaluating the phenotypic correlations.

Residual Feed Intake. Residual feed intake (RFI), also known as Net Feed Intake (NFI) or net feed efficiency (NFE), is defined as the difference between actual and predicted feed intake relative to weight and ADG, such that negative RFI indicates those animals that consume less than predicted to achieve a given rate of gain, which is more desirable. Residual feed intake has been evaluated on a biologically diverse array of cattle, including *Bos indicus* and *Bos taurus*, and varying reports have been given concerning its effectiveness as a tool for use in modern beef cattle production.

Herd and Bishop (2000) evaluated growth and efficiency traits on Hereford bulls placed on test from approximately 200 to 400 d of age. Body weight at the beginning and end of test, and feed intake were measured; metabolic body weight, daily gain, and carcass lean (predicted from ultrasound at the end of test) were calculated; then, maintenance energy requirements and RFI were estimated. Next, an attempt was made to estimate the correlation between mature cow weight (MCW) and RFI using the live weight of the dams of the tested bulls at 4.5 years of age. No animals had records for both RFI and MCW, so estimating the phenotypic correlation was impossible; however, using an animal model in ASREML the genetic correlation was estimated to be -0.09, which was not statistically different from zero. The authors indicated that selection could potentially be made for improved RFI without adversely affecting mature weight of the cow herd.

Arthur et al. (2001b) showed RFI to be phenotypically (r = 0.53) and genetically (r = 0.66) correlated with FCR in Angus bulls and heifers tested post-weaning in southern Australia, and genetically correlated with FCR (r > 0.85) when evaluated in Charolais bulls in France (Arthur et al., 2001a). This agrees with Herd and Bishop (2000) who found RFI to be positively correlated with both FCR and lean feed conversion ratio (LFCR) in Hereford bulls (200 to 400 d old) sired by horned, polled, and British Hereford bulls.

As discussed earlier, selection for traditional measures of feed efficiency such as FCR can be accompanied by changes in growth rate and mature cow size (Mrode et al., 1990). However, some have suggested that RFI is independent of size and growth rate (Herd and Bishop, 2000; Richardson et al., 2001).

Nkrumah et al. (2004) evaluated the relationship of efficiency, growth, and carcass traits in crossbred steers and bulls managed and tested under feedlot conditions in Canada. Crosses were made between Angus, Charolais, or University of Alberta hybrid (UAX) bulls and UAX cows. Hybrid animals were created by crossing composite lines consisting of Angus, Charolais, Galloway, Hereford, Simmental, and other beef breeds along with Holstein and Brown Swiss. Residual feed intake was found to be phenotypically correlated with dry matter intake, metabolizable energy intake, FCR and the partial efficiency of gain (r = 0.75, 0.83, 0.62, and -0.89, respectively); RFI was not related to average daily gain or metabolic weight (and due to the nature of it's calculation we would not expect it to be). This led the authors to propose that RFI, used for selection, is more likely to improve the efficiency of production as well as the partial efficiency of gain without altering the growth or body size of the animal.

Model Predictions. An inherent difficulty of evaluating efficiency is the requirement for individual intake to be measured on the animals in question. Several models are available that can predict feed intake. Using data from steers that came from a heterosis experiment involving Hereford, Angus, and Shorthorn, Williams et al. (2006) evaluated the feed intake predictions from 2 models: the Decision Evaluator for the Cattle Industry (DECI) and the Cornell Value Discovery System (CVDS). Predictions for daily feed required for maintenance, cold stress, gain, and combinations of these factors were made with each model and compared to observed values from the steers after the post-weaning feeding period. For both models, the prediction for daily feed intake required for maintenance had the highest phenotypic correlation with intake observed in the British crossbred steers (0.78 and 0.86 for CVDS and DECI, respectively).

Factors Affecting Feed Efficiency

One major issue in improving the efficiency of feed utilization in cattle is determining exactly what makes one animal more efficient than another. The effects of many factors on efficiency have been discussed in the literature. Meissner and Roux (1984) wrote that, "The efficiency with which feed energy is utilized in growing cattle and sheep is a function of intake, body composition, and maintenance energy requirements." While this statement likely encompasses the major factors affecting efficiency, maintenance energy requirements are affected by many other variables.

Johnson et al. (2003) suggested several measures of production potential (gain, body weight, and prolificacy) as well as metabolism for maintenance and growth as potential factors affecting efficiency. Similarly, Herd et al. (2004) suggested 5 processes that likely affect ultimate efficiency: feed intake, digestion of feed, metabolism, activity of the animal and thermoregulation. Brown et al. (2004) showed exit velocity as a measurement of temperament to be negatively correlated with ADG, body weight, and dry matter intake (DMI ; $P < 0.10$) in growing Bonsmara bulls and Santa Gertrudis steers. Further, Robinson and Oddy (2004) reported that more efficient animals made fewer trips to the bunk. So, feeding behavior or temperament may also play an important role in efficiency.

Nkrumah et al. (2006) evaluated 306 Continental x British cross steers for post-weaning feedlot performance and efficiency. At the conclusion of the feeding period, residual feed intake was calculated, and 27 steers were sorted into groups based on high (RFI > 0.5 SD above the mean), medium (RFI ± 0.5 SD from the mean) and low (RFI < 0.5 SD below the mean) levels of residual feed intake (with high designating the least efficient cattle and low representing the most efficient). These steers were used in a digestion and metabolism trial, which allowed for digestion and energy partitioning to be evaluated and compared with measures of feedlot performance and efficiency.

Dry matter intake did not differ ($P > 0.10$) among the 3 RFI groups during the digestion/metabolism study. However, differences in DMI between the 3 RFI groups *did* exist during the feeding phase (*P* = 0.01). Phenotypic correlations between selected traits measured at the feed yard and those taken during the digestibility/metabolism study are presented in Table 2. Residual feed intake was correlated with metabolizable energy (ME), heat production (HP), and retained energy (RE); however, FCR was significantly correlated only with HP. Furthermore, low RFI steers produced less methane than medium and high RFI steers (24% and 28% less, respectively) which implies that production of methane may greatly affect feed efficiency in cattle.

Table 2. Correlations between feedlot growth, intake, efficiency, behavior and post-feed yard digestibility and metabolism[1]

Trait[2]	MP	ME	HP	RE
RFI	0.44*	-0.44*	0.68***	-0.67***
FCR	0.19	-0.09	0.37*	-0.24
DMI	0.38*	-0.48**	0.31[a]	-0.53**
ADG	0.05	-0.27[a]	-0.09	-0.18
FA	-0.14	0.22	0.42	0.004
FD	0.51**	-0.55**	0.25	-0.60**

[1] Adapted from Nkrumah et al. (2006).
[2] MP = Methane Production, ME = Metabolizable Energy, HP = Heat Production, RE = Retained energy, RFI = Residual Feed Intake, FCR = Feed Conversion Ratio, DMI = Dry Matter Intake, ADG = Average Daily Gain, FA = Feed bunk attendance, FD = Feeding duration.
[a] $P < 0.10$.; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Breed Effects. Commerford et al. (1991) evaluated unadjusted and maintenance-adjusted FCR in the feedlot for a four-breed diallel of Simmental, Limousin, Polled Hereford, and Brahman. Unadjusted FCR was the highest for Brahman-sired calves and calves with Simmental, Limousin, or Brahman dams. Adjusting FCR to fat or age constant values showed no re-ranking. When FCR was adjusted for maintenance, Brahman-sired calves were still the least efficient (though not significantly different from Simmental-sired calves); however, calves from Hereford and Brahman dams were more efficient than calves from Simmental and Limousin dams. Furthermore, when evaluating mating types (sire x dam), no reciprocal differences existed for *Bos taurus* crosses; however, among *Bos indicus* crosses, reciprocal differences were evident. For Simmental – Brahman calves, those with Simmental sires had a FCR of 7.08 compared to 8.10 for calves with Simmental dams. Similarly, Limousin x Brahman calves had a FCR of 7.22 compared to 7.74 for Brahman x Limousin calves. Conversely, among Hereford – Brahman crosses, calves with Hereford dams were more efficient (6.60) than those with Hereford sires (7.07). The same reciprocal cross trends existed for fat-constant and age-constant FCR.

Frisch and Vercoe (1969) evaluated 1.5 to 2-year old Brahman, Africander, and Shorthorn x Hereford bulls and steers for intake and gain on an *ad libitum* forage diet. Feed was offered to them in stalls at 8:00 am and 4:00 pm daily; the remainder of the time they were kept in a shaded yard with access to water and a mineral lick. When adjusted for weight, Brahman ate less than Africander and the British crosses that ate the most. When adjusted for intake, Brahman gained the most followed by Africander and Shorthorn x Hereford. They concluded that the Brahman cattle were the most efficient possibly due to having the lowest maintenance requirements.

Meissner and Roux (1984) compiled data from Kenya, Denmark, and South Africa that included crossbred temperate (> 50% *Bos taurus*) and tropical (> 50% *Bos* *indicus*) cattle. They concluded that, when primarily *Bos indicus* breeds were excluded, the differences in FCR between breeds were primarily due to differences in size.

Intake. As feed intake increases, retained energy also increases, but not linearly; in fact, as feed intake increases, retained energy increases at a decreasing rate (Ferrell, 1988). This could be because as intake increases, rate of turnover of fluid and particulate digesta in the rumen increases (Merchen, 1988) and the proportion of energy lost as feces increases (Ferrell, 1988); thus, energy required for digestion increases (Herd et al., 2004).

Rate of Maturity/Body Composition. Klosterman and Parker (1976) studied feed efficiency in Charolais (C), Hereford (H), and crossbred C x H and Angus (A) x H cows bred to C and H bulls. Efficiency was evaluated as total digestible nutrients (TDN) required by the cow and calf, kg of TDN needed per unit of edible beef produced, and total net energy in the empty body per unit of metabolizable energy available from the total feed fed to the cow and calf prior to slaughter.

For this study, 1/age of slaughter x 100 (which is the reduced form of weight per day of age/slaughter weight) was used as a covariate and was responsible for significant variation in all 3 measures of efficiency. For example, the covariate was moderately correlated with total TDN required by the cow and calf ($r = -0.52$) when calves were fed to a fat-constant end point. This indicated that animals with a faster rate of maturity used feed more efficiently. Ferrell and Jenkins (1985) cited conflicting evidence as to the effect that body composition has on maintenance energy requirements across a wide range of species, sexes, and ages.

Temperament/Behavior. Temperament (Brown et al., 2004) and eating behavior (Frisch and Vercoe, 1969; Robinson and Oddy, 2004; Cammack et al., 2005; Nkrumah et al., 2006) have been shown to be related to feed intake and efficiency traits and will be discussed in depth in the section entitled “Temperament”.

Production Potential. Ferrell and Jenkins (1985) reported that Angus-Hereford crossbred cows and Charolais cross cows had similar maintenance requirements per unit of body size and that the maintenance requirements for Jersey cross and Simmental cross cows were higher per unit of body weight. They suggested that maintenance energy requirements per unit of body weight are related more to genetic potential for milk production than to body size.

Liver/Viscera. The review by Owens et al. (1993) cited several studies that concluded the phenomenon of compensatory growth after periods of nutrient restriction can be entirely explained by changes in the mass of the gastro intestinal tract and liver. Similarly, Ferrell and Jenkins (1985) concluded that energy spent by the liver and gastrointestinal tract is responsible for a large portion of maintenance energy requirements.

Conclusions. According to Ferrell and Jenkins (1985), most of the variation observed in total energy requirements is due to variation in energy required for maintenance. Research has supported differences in maintenance requirements for those characters discussed above, though it is doubtful any of them are working singularly to influence efficiency. Rather, a complex interaction among many forces is likely leading to the observed variation in feed efficiency.

Selection for Improved Efficiency and Its Correlation with Other Traits

If genetic variation can be recognized and quantified in a population, it is possible to make improvements in phenotype through selection. This has been accomplished in beef cattle production primarily in growth and other size traits that are easily observed. However, up to this point, there has been little success (possibly due to little effort) in making advancements in feed efficiency (Johnson et al., 2003). Australian research has indicated significant genetic variation in feed efficiency in the Australian cattle population and that efficiency traits, RFI specifically, seem to be moderately heritable (Archer et al., 1999; Arthur et al., 2004; Robinson and Oddy, 2004). With this in mind, potential for improvement in feed efficiency through selection seems probable.

Kennedy et al. (1993) evaluated heritability and response to selection for RFI in dairy cattle over a range of heritabilities, and genetic and environmental correlations for feed intake (f) and production (p). They concluded that RFI is simply a linear combination of its component traits, and therefore behaves as an index. As a result, single trait selection for phenotypic RFI is the same as multiple trait selection for its component traits. This also implies that the heritability of RFI, its correlation with production traits, and its response to selection is based heavily on the heritability and correlation of its component traits. Heritability estimates for RFI were determined by simulation. The lowest estimate was 0.028 and occurred when the genetic correlation between feed intake and production was highest (0.90), the corresponding environmental correlation was moderate (0.50), and the heritabilities of feed intake and production were 0.10 and 0.30, respectively. The highest heritability estimate for RFI (0.841) was obtained when respective parameters for h^2f , h^2p, r_{efp} (e = environmental), r_{gfp} (g = genetic) were 0.5, 0.1, 0.9, and 0.1. Ideally then, to achieve optimum response to selection for RFI, the genetic correlation between feed intake and production would be negative, such that a decrease in feed intake has a resulting increase in production. Further, it is apparent that an increase in h^2 for feed intake also increases h^2 for RFI.

Estimates of heritability and genetic correlations of RFI with other measures of interest in cattle are presented in Table 3. Arthur et al. (2001b) found RFI to be moderately heritable (0.39 ± 0.03). Herd and Bishop (2000) estimated heritability of RFI to be 0.16 ± 0.08. It seems possible that improvement should be able to be made in feed efficiency through selection; however, its effect on correlated traits may be as important a consideration as the direct selection response.

Table 3. Heritability of RFI and its genetic correlation with other traits of interest

	Arthur	Herd	Robinson	Nkrumah
Heritability	0.39	0.16	0.18	-
Weight Gain	-	-	0.09	-
Metabolic Weight	-0.06	0.22	-0.20	-0.02
FCR	0.66	0.70	0.41	0.62
ADG	-0.04	0.09	-	-0.03
FI	0.69	-	0.43	0.75
Rib Fat	-	-	0.48	-
Rump Fat	-	-	0.72	-

Arthur et al. (2001b); Herd and Bishop (2000); Robinson and Oddy (2004); Nkrumah et al. (2004)

Bishop et al. (1991) reported a corresponding improvement in the feed conversion (FC) of progeny from sires that were selected for high and low rates of conversion (less feed per unit of gain vs. more feed per unit of gain, respectively). Improvements for unadjusted FC as well as FC adjusted for maintenance requirements were observed in progeny from sires selected for high FC.

Richardson et al. (2001) showed that when parents were selected for low RFI, the steer progeny also had lower RFI and consumed less feed, but still weighed the same at the end of the feeding phase as steers from parents with high RFI. Similarly, after 5 years of selection for efficient vs. non-efficient animals (low RFI vs. high RFI, respectively), progeny of low RFI lines were found to consume less feed, and had similar growth performance prior to one year of age as compared to high RFI lines (Arthur et al. 2001c). This is in contrast to Hoque et al. (2005) who evaluated the genetic relationship between efficiency traits in Wagyu bulls, and growth and carcass traits in their offspring. They reported negative genetic correlations between RFI in bulls and body weight in their progeny (r = -0.27 to -0.61), which would indicate that as RFI improved, body weight increased.

Much of the research for improvement in efficiency has focused on the selection of sires with desirable efficiency traits and the ultimate performance of their offspring from a feed efficiency standpoint. To truly improve the efficiency of the production system as a whole, we must also be able to improve feed efficiency in the cowherd. Archer et al. (2002) showed a high genetic correlation between efficiency traits (FCR and RFI) measured in heifers post-weaning and those traits measured in the same animals as mature cows after the birth of their second calf. They concluded that the opportunity exists to improve the efficiency of the cowherd through selection of young heifers who are desirable from an efficiency standpoint.

However, the use of RFI for selection purposes is problematic for several reasons. First, re-ranking of animals for RFI may occur in different environments or contemporary groups, and correlations may exist with some carcass traits. A significant diet x breed interaction was reported for RFI in Hereford and Angus bulls (Fan et al., 1995). During a post-weaning gain test, bulls ranked differently for RFI depending on if they were fed high or medium-energy diets (both *ad libitum*). On the high-energy diet, the RFI for Hereford and Angus bulls was 0.45 and 1.18 Mcal of ME/d, respectively. On the medium energy diet, Hereford and Angus bulls had an average RFI of -1.86 and -2.46 Mcal of ME/d, respectively.

More recently, feed intake was measured and net feed efficiency (NFE) calculated on 410 Charolais-cross steers in Canada at 2 different phases (Crews et al., 2003). During the growing phase, steers were fed a diet that consisted primarily of barley silage for 84 d, while during the feeding phase a barley-grain based diet was fed for 112 d. The genetic correlation between NFE during the growing phase and NFE during the finishing phase was 0.55, which indicates that animals may rank differently for NFE depending on if they are fed roughage or forage based diets.

It seems logical to believe that if animals that are efficient on one diet are not the same animals that are efficient on another diet, then selecting for cattle that are efficient in the feedyard may not automatically lead to more efficient replacement females who thrive in a predominately forage-based environment. In fact, Arthur et al. (2004) listed finding an accurate method for evaluating individual intake in the pasture as a major challenge for the future of efficiency focused research.

Kause et al. (2006) reported different genetic correlations between daily feed intake, daily gain, and body weight in rainbow trout depending on if they consumed a normal protein (NP) vs. a high protein (HP) diet. On the NP diet, genetic and phenotypic correlations between gain and feed intake were moderately to highly correlated at the beginning (0.95 and 0.74, respectively) and end (0.96 and 0.51, respectively) of the test. On the high protein diet, the correlations were high at the beginning of the test (0.87 and

0.73 for genetic and phenotypic, respectively), but much lower at the end (0.29 and 0.27 for genetic and phenotypic, respectively). When daily gain was the only selection criteria, the estimated genetic improvement in gain was 17.6 to 18.6%, and the estimated genetic improvement in efficiency was 8.4 to 9.3% on NP and HP diets, respectively. When selection was made for gain and against feed intake, no genetic improvement in efficiency was predicted on the NP diet. However, on the HP diet selecting for gain and against feed intake was predicted to improve the genetic response in feed efficiency from 9.3% to 11.4%.

Residual feed intake has also been reported to be correlated with other production traits, including carcass traits. In the Hereford cattle described earlier, Herd and Bishop (2000) showed RFI to be negatively phenotypically correlated with predicted carcass lean content (LEAN) and lean growth rate (r = -0.22 ± 0.04 and -0.33 ± 0.04, respectively) when LEAN was standardized to a mean of 0.60 each year with a coefficient of variation of 0.04. This suggests that selection for lower (more efficient) RFI may increase carcass leanness, and this trend seems to exist across several studies.

Robinson and Oddy (2004) evaluated RFI in temperate (Angus, Hereford, Murray Grey, and Shorthorn) and tropically adapted (Brahman, Belmont Red, and Santa Gertrudis) feedlot cattle finished for Japanese, Korean, and the Australian domestic markets. They found RFI to be highly genetically correlated with fat thickness measured by ultrasound between the 12th and 13th rib (r = 0.48 ± 0.12) and at the P8 rump site (r = 0.72 ± 0.17). Much lower phenotypic correlations existed (r = 0.11 and 0.13 for P8 fat and rib fat, respectively). Residual feed intake was also found to be lowly genetically (r =

0.22 ± 0.17) and phenotypically (r = 0.12) correlated with intramuscular fat as measured by ultrasound.

After a single generation of selection for high and low post-weaning RFI in Angus sires, fat differences were reported in their progeny (McDonagh et al., 2001). When born to low or high RFI Angus, Hereford, and Shorthorn dams, the steers with low RFI (more efficient) parents were reported to have less rib fat (9.2 vs. 10.1 mm; $P < 0.05$) and rump fat (11.5 vs. 12.1 mm; $P = 0.10$) than steers with high RFI (less efficient) parents (McDonagh et al., 2001). In the same research, no differences were found in carcass weight (HCW), dressing percentage, or longissimus muscle area (REA) between low and high RFI steers. From a meat quality standpoint no difference existed in marbling score (MARB), lean color, fat color, shear force, or calpain activity immediately following slaughter. However, low RFI steers had 13% higher calpastatin activity than high RFI steers (5.2 vs. 4.6 units, respectively; $P < 0.05$).

In Charolais-cross steers, NFE measured during an 84-d growing phase was weakly genetically correlated with HCW, REA, and MARB (r = 0.10, 0.15, and 0.08, respectively) and moderately genetically correlated with fat thickness (r = -0.24). However, at the feeding phase (high concentrate diet) NFE was lowly genetically correlated with fat thickness (r = -0.09) and moderately genetically correlated with HCW, REA and MARB (r = 0.26, 0.52, and -0.44, respectively; Crews et al., 2003).

In Duroc pigs, Hoque et al. (2007) found RFI to be positively correlated (both genetically and phenotypically) with intramuscular fat, and negatively correlated with loin eye area. They also reported both RFI and FCR to be positively correlated with backfat thickness.

It is possible that selection for RFI may impact physiological processes other than growth efficiency. For example, Van Eerden et al. (2004) showed that low RFI chickens had a lower antibody response to Salmonella protein than high RFI birds. This suggests that selecting for improved RFI may adversely affect the animal's ability to mount an immune response. As far as can be determined, this has not been reported or evaluated in other species.

If variation in efficiency traits and selection strategies exist, how can this information be implemented into widespread use in an industry? In Australia, estimated breeding values for RFI have been developed for Angus and Hereford cattle (Arthur et al., 2004).

Snowder and Van Vleck (2003) evaluated selection strategies for improving economic efficiency in Targhee lambs. They concluded that using a selection index consisting of ADG, total feed intake, and body weight provided greater opportunity for economic improvement than other selection methods which included direct selection for ADG and against total feed intake as well as the use of a two-trait index comprised of ADG and total feed intake. Costs for the economic evaluation were obtained from personal communication with 2 commercial lamb feed yards.

Owing to the importance of crossbreeding in the modern beef cattle industry, some studies have evaluated heterosis for feed efficiency. When evaluated in a diallel of Simmental, Limousin, Polled Hereford, and Brahman, estimates for the hybrid vigor between pairs of breeds for FC ranged from -0.87 (between Hereford and Brahman) to 0.19 (between Limousin and Hereford) where negative values represent more desirable efficiency (Commerford et al., 1991). Effects of the purebred, as well as maternal effects and general combining ability (referring to the contribution of the breed to a crossbreeding program) were also evaluated for each breed. Most of the variation observed in FC was the result of differences among the pure breeds; however, Hereford had a significant negative effect on FCR (-0.25; $P < 0.05$) from the standpoint of combining ability, such that the use of Hereford sires or dams produced more efficient steers than would have been predicted from straightbreds.

Physiological Indicators. Fenton et al. (2001) estimated the cost of including RFI as part of selection criteria in Australian beef cattle to be around $500A per animal. Because it is costly to measure feed efficiency traits in cattle, some have suggested indirect selection through detection of physiological indicators. Moore et al. (2003) found the concentration of plasma insulin-like growth factor-1 (IGF-1) to have a positive genetic correlation with RFI in Angus cattle in Australia. Kahi et al. (2003) modeled the Australian Hereford population in an attempt to predict dollar return and profit per cow when using 5 different selection scenarios to meet the demands of 4 different marketing options. They determined that testing all bulls for IGF-1 concentration about 9 months of age, measuring the top 5% for RFI, and using the results in a selection scheme with other commonly measured traits (birth weight, weaning weight, and carcass traits) yielded the most profit per cow for all 4 selection schemes. Similarly, when incorporated into a selection scenario, the highest profit in Australian export markets was obtained when all bulls and cows were tested for IGF-1 concentration, followed by evaluation of RFI on the top 5% of bulls as determined by IGF-1 (Wood et al., 2004).

Similarly, IGF-1 and feed efficiency were found to have negative correlations (-0.45 and -0.65, respectively) with $index in Large White and Duroc pigs (da Gloria Taela et al., 2006), which led the authors to conclude that low IGF-1 indirectly improves feed efficiency and thus, could improve profits. Transgenic sheep (heterozygous for an additional copy of a gene encoding growth hormone) had a higher IGF-1 concentration (342.1 ng/mL) and higher RFI (149 g/day) than non-transgenic controls (89.5 ng/mL and 18 g/day for IGF-1 and RFI, respectively) from the same flock (Briegel and Adams, 2006).

Additionally, IGF-1 concentration has been shown to be genetically and phenotypically correlated with ultrasound rib and rump fat, IMF (Johnston et al., 2001; Moore et al., 2003), P8 fat, and ADG (Johnston et al., 2001). Johnston et al. (2001) reported a low genetic and moderate phenotypic correlation (r = 0.20 and 0.62, respectively) between ultrasound P8 fat and IGF-1 in temperate breeds (Angus, Hereford, Shorthorn, and Murray Grey) in Australia. Similar genetic and phenotypic correlations were observed between scanned rib fat and IGF-1 (r = 0.20 and 0.72, respectively). Furthermore, IGF-1 was moderately genetically correlated with intramuscular fat observed in the carcass (r = 0.47). Insulin-like growth factor-1 was also found to be lowly correlated with feedlot ADG (r = -0.25), but was not significantly phenotypically correlated with the same trait. Moore et al. (2003) observed similar results for the correlation of IGF-1 with scanned rib and rump fat, and intramuscular fat (all r = 0.31 to 0.33) in Angus cattle.

Heritability estimates for IGF-1 concentration have ranged from 0.32 (Johnston et al., 2001) to 0.36 (Moore et al., 2003) to a high of 0.53 (da Gloria Taela et al., 2006).

Quantitative Trait Loci. In mice, 3 QTL for net feed intake (NFI) have been detected, along with one for daily feed intake (DFI) which overlapped with one of the

NFI QTL. A 13% difference in DFI and 12% difference in NFI existed in alternate homozygotes for the latter QTL (Fenton et al., 2001). In cattle, Pitchford et al. (2002) identified 5 QTL potentially having an effect on feed intake in Limousin – Jersey backcross steers and heifers. One of these QTL resulted in progeny that ate 14% less; however, as was the case with the other QTL identified, it was only found in one family and thus was not a "fixed" gene in either of the parent populations.

Temperament

Fordyce et al. (1985) defined temperament as "the response of cattle to man", such that animals with a poor temperament attempt to escape or react extremely when approached or confined. This section of the literature review discusses methods for evaluating temperament, factors affecting temperament, and the genetic aspects of temperament including heritability and selection.

Measuring Temperament

Subjective Scores. Subjective scores are typically evaluated in one of two manners: while animals are restrained in a chute or scale (Hearnshaw et al., 1979; Fordyce et al., 1982; Fordyce et al., 1985; Grandin, 1993) or while cattle are unrestrained in a pen (Fordyce et al., 1982; Fordyce et al., 1985; Gauly et al., 2001).

Hearnshaw et al. (1979) scored animals for temperament in the squeeze chute on a scale of 0 to 5: 0 = "stands very quietly, offers no resistance, only casual tail switching"; 1 = "generally quiet, offers token resistance, steady movement in bail head"; 2 = "involves slightly excited movement, straining and paddling, may kick"; 3 = "excited, vigorous abrupt movement, straining, paddling; may jump or kneel"; 4 = "very disturbed, frightened, wild movements, etc.; may jump and goes down in the chute"; 5 =

"unmanageable and dangerous". Similarly, Grandin (1993) suggested assigning temperament scores in the squeeze chute on a scale of 1 to 4 in which 1 = "calm, little movement", 2 = "squirming, occasional shaking of restraint device", 3 = "continuous vigorous movement and shaking of restraint device", 4 = "frenzied rearing, twisting, or violently struggling". This method was subsequently used in several other studies (Voisinet et al., 1997a and b).

Gauly et al. (2001) used an unrestrained test to evaluate temperament in cattle. Animals were initially observed in groups of 10, then 1 animal was separated from the rest and pushed into a smaller area to be observed, and the time it took to accomplish this was recorded. The animal was then observed alone for 30 s after which time a person entered the pen and stood still, the time spent running in the presence and absence of a person was recorded (TSR1 and TSR2, respectively). An overall temperament score (1 to 5 scale, where 1 = calm and 5 = very excited) was assigned for this time period, which was referred to as "before handling". Next, the handler attempted to move the animal into a corner and hold it for 30 s, if this was successful, the handler attempted to touch the animal. Time to get the animal to the corner, how long it stayed there, and how long it allowed itself to be touched were also recorded and an overall temperament score (1 to 5) was given for this "after handling" period.

Fordyce et al. (1982) evaluated cattle for temperament in both restrained and unrestrained situations. Animals were evaluated for movement response (MOV) and audible respiration (BLO) on a 7 point scale (1 = stands quietly; 7 = struggles violently) when in a single-file alley, when in a squeeze chute, and in a head-catch. Animals were also evaluated for temperament in the pen based on their rate of movement (SPEED) and flight distance (FD). Animals were sorted from the group and pushed into the pen alone and assigned a score for SPEED (1 = standing and walking, 5 = gallops), then an observer entered the pen and attempted to walk toward the animal and the closest distance the animal would tolerate between them was recorded as FD. Only moderate correlations were obtained between restrained and unrestrained temperament scores, suggesting different aspects of temperament were being evaluated. Correlations between unrestrained temperament scores (SPEED and FD) were high (r = 0.71). Fordyce et al. (1996) reported high phenotypic and genetic correlations between SPEED and FD at different ages, which suggests that unrestrained measures of temperament may be more repeatable than restrained methods.

Flight Speed. Curley et al. (2006) evaluated 3 methods of temperament scoring (exit velocity, and 1 to 5 in a pen and in a chute) on 3 separate occasions (each 60 d apart) in yearling Brahman bulls. Chute score was evaluated on a 1 to 5 scale (1 = calm; 5 = extremely excited) while the animal was unrestrained on a scale. As the animal exited the chute, exit velocity (EV) (defined as rate at which the bulls exited the working chute) was recorded. Bulls then moved to a squeeze chute where blood was drawn to be tested for serum cortisol concentration. Immediately after blood had been drawn, pen score was evaluated on groups of 5 animals in a 5 x 10 m pen. Pen score and EV were both found to be correlated with cortisol concentration, chute score was not, which led the researchers to conclude that EV was a more valuable tool for assigning temperament than the subjective measures of chute score and pen score.

On the contrary, early research by Tulloh (1961) suggested that the speed with which animals moved may not be related to temperament. Hereford, Angus, and

Shorthorn steers and heifers were evaluated for behavior entering the scale, the squeeze chute, and the head-catch (these 3 scores being primarily related to the speed with which the animal entered) and then given a final temperament score while in the squeeze chute. The former 3 scores were found to be unrelated to each other as well as to temperament score.

Factors Affecting Temperament

Breed. *Bos indicus* cattle and their crosses tend to have more excitable temperaments than *Bos taurus* breeds (Hearnshaw and Morris, 1984; Fordyce et al., 1988; Voisinet, 1997a). When evaluated in the pen and squeeze chute, Shorthorn bulls received lower (more docile) scores than Brahman-cross bulls for audible respiration and overall temperament in the squeeze chute, as well as degree of movement when held alone in a pen (Fordyce et al., 1988). Similar results were found by Voisenet et al., (1997a) in *Bos taurus* (Simmental x Red Angus, Tarentaise x Angus, and Angus) and *Bos indicus* (Braford, Red Brangus, and Simbrah) steers. Temperament scores (1 = calm, no movement; 5 = rearing, twisting or violently struggling) were assigned to animals while they were standing unrestrained on a scale. *Bos indicus*-cross steers had significantly higher scores ($P < 0.001$) than *Bos taurus* steers (3.46 ± 0.09 vs. 1.80 ± 0.10, respectively).

Using the method of Hearnshaw et al. (1979), Hearnshaw and Morris (1984) evaluated temperament scores on calves at weaning in 3 different sets of calves. In the first data set, calves were sired by Hereford, Simmental, Friesian, or Brahman bulls and out of Hereford cows. Brahman-cross calves had a significantly higher temperament score than calves sired by any other breed (1.96 vs. a mean of 1.05 for the other breeds).

Females from the first data set were bred back to Hereford, Simmental, Friesian, or Brahman bulls and temperament scores were obtained for the calves at weaning and for the cows. Again, calves with Brahman sires or grandsires had significantly higher temperament scores than calves by other breeds. No significant differences were found for temperament among *Bos taurus* breeds. In the third data set, Brahman-, Braford-, and Africander-sired calves were compared for temperament. In the first 2 years of the study, significant sire breed differences existed for temperament for all 3 breeds (Brahman = 1.84, Braford = 1.38, Africander = 1.25); while sires ranked the same in the third year, differences were not statistically significant.

Gauly et al. (2001) evaluated temperament using the previously described method in Simmental and German Angus cattle. During the restraint test, Simmental cattle were found to run longer than the German Angus before and after the handler entered the restraint pen ($P < 0.001$). Also, it took the handler more time to move the Simmental cattle than the German Angus (35 vs. 27 s for the first test and 47 vs. 32 s for the second test, respectively). Once the handler was able to move the animals to the corner, the Angus stayed there longer than Simmental (24 vs. 21 s and 23 vs 15 s for the first and second test, respectively). Simmental cattle also appeared to be more aggressive as 4.9% showed aggression in the first test and 7.9% showed aggression in the second test compared to 3.0% for the German Angus for both test times.

Sex. Gelbvieh, Charolais, and Simmental cross bulls and steers with an average on-test weight of 260 kg were scored for temperament using the scale described by Grandin (1993) on 5 different occasions for bulls and 4 different occasions for steers. She concluded that steers tend to be less temperamental than bulls. Forty percent of steers received a temperament rating of 1 (calm, little movement in the squeeze chute), while only 25% of bulls received a ranking of 1. Furthermore, 9% of bulls were behaviorally agitated (received a rating of 4 or 5) at all 4 temperament scoring sessions, while only 3% of steers were behaviorally agitated at all 3 times they were run through the chute.

Gauly et al. (2001) found heifer calves to be more difficult to handle than their male counterparts when temperament was evaluated twice, 2 and 3 weeks after weaning. Female calves took longer to separate from the group, spent more time running when held alone in a pen and when in the presence of a handler, and heifers escaped more frequently when a handler attempted to hold them in a corner. In contrast, Hearnshaw et al. (1979) found no difference in temperament between steers and heifers scored at weaning.

Weight and Body Composition. In the Shorthorn and Brahman-cross bulls and cows described earlier, Fordyce et al. (1988) found the fattest animals to have lower (more docile) temperament scores when evaluated based on degree of movement around a pen. Tulloh (1961) reported a significant relationship between live weight and temperament, as did Fordyce et al. (1985). In the latter study, 232 *Bos indicus* cross steers were evaluated for temperament in the manner described above (Fordyce et al., 1985). Negative correlations were found between weight and movement response (r = - 0.35; $P < 0.001$), audible respiration (r = - 0.22; $P < 0.01$), and total temperament (r = - 0.34; $P < 0.001$) such that docile animals were found to be heavier than nervous animals.

Previous Handling. Grandin (1993) assigned balking ratings to Continental cross bulls (5 observations) and steers (4 observations) both upon entering a single-file scale and when entering a squeeze chute to have blood drawn. Animals balked less frequently at the scale as time progressed, until at the final observation, none of the animals balked at the scale, which suggests that animals became accustomed to the process of moving through the scale over time. At the squeeze chute, however, 13% of bulls balked during session 1, while 42% balked at session 5. In steers, balking remained steady from observation 1 (21%) to observation 4 (22%). Blood was drawn while the animals were in the chute, and the increase in balking suggests that the animals remembered an unpleasant experience from a previous handling session.

Curley et al. (2006) evaluated temperament on Brahman bulls using EV on three separate occasions, each 60 d apart. As time progressed, EV reduced; suggesting that the animals became accustomed to being handled over time. In this case, animals were only weighed, unrestrained prior to being evaluated for EV.

Selection for Improved Temperament and Its Correlation with Other Traits

Reported heritability estimates for temperament vary widely and seem to depend on the method used for determining temperament and the breeds involved (Table 4). Hearnshaw and Morris (1984) found temperament to be moderately heritable (h^2 = 0.46) for *Bos indicus*-sired calves and lowly heritable (h^2 = .03) for *Bos taurus*-sired calves, though it should be noted that the project was designed primarily as a sire-breed comparison, not a test of genetic variability and the progeny per sire was low (3.77, on average). Low to moderate heritability estimates were obtained for German Angus and Simmental cattle for overall temperament before and during handling (Gauly et al., 2001).

Morris et al. (1994) found different heritability estimates for temperament scores in several different herds and among different breeds and crosses in calves, yearlings, and cows (h^2 = 0.23, 0.32, and 0.22, respectively). Likewise, Fordyce et al. (1996) found different heritability estimates at different ages for both temperament score and flight distance, which was defined as the minimum tolerated distance an animal would allow a handler to approach. Brahman and Sahiwal cross bulls were evaluated for temperament and flight distance at weaning, at 12 mo of age, and at 24 mo of age. Temperament score was lowly heritable at all ages, but flight distance was moderate at the first two ages and high at 2 years of age (Table 4).

Table 4. Heritability estimates for measures of temperament

Study[1] Type of test	Heritability	S.E.
Hearnshaw and Morris		
Bos indicus	0.46	0.37
Bos taurus	0.03	0.28
Overall	0.44	0.25
Gauly		
Before handling - Angus[2]	0.13/0.11	0.11/0.07
During handling - Angus[2]	0.61/0.18	0.17/0.07
Before handling - Simmental[2]	0.17/0.35	0.12/0.21
During handling - Simmental[2]	0.55/0.52	0.15/0.20
Morris		
Calves	0.23	0.12
Yearlings	0.32	0.24
Cows	0.22	0.15
Fordyce		
Temperament – weaning	0.14	0.11
Temperament – 12 mo	0.12	0.11
Temperament – 24 mo	0.08	0.10

Table 4 continued

Study[1] Type of test	Heritability	S.E.
Flight distance – weaning	0.40	0.15
Flight distance – 12 mo	0.32	0.14
Flight distance – 24 mo	0.70	0.23

[1] from Hearnshaw and Morris (1984); Gauly et al. (2001); Morris et al. (1994); Fordyce et al. (1996)

[2] Heritability and standard error for Test 1/Test 2

Temperament has been shown to affect many traits of importance in beef cattle including daily gain (Burrow and Dillon, 1997; Voisinet et al., 1997a; Brown et al., 2004), carcass and meat traits (Voisinet et al., 1997b), and feed intake (Brown et al., 2004). Voisinet et al. (1997a) evaluated temperament in *Bos indicus* and *Bos taurus* steers (n = 292) and heifers (n = 144) in 2 different ways; unrestrained on a scale (Experiment 1) and restrained in a squeeze chute (Experiment 2). For both experiments, cattle with a more excitable temperament had lower ADG ($P < 0.001$). In *Bos taurus* breeds for Experiment 1, cattle with the most docile temperament had 0.19 kg/d higher gain than those with the least docile temperament, and scores for *Bos indicus*-influenced cattle followed a similar trend.

Burrow and Dillon (1997) measured flight speed each week on 2 groups of 5/8 Brahman 3/8 Shorthorn steers and heifers in the feed yard. The first group received a minimum amount of handling by men both on foot and on horseback for 10 days only at weaning time, but received little handling before or after weaning. The second group was handled similarly through weaning, but after they were grazed on pasture for 4 months which required being gathered and moved between paddocks on a regular basis; plus, the calves were gathered and weighed once a month. Prior to analysis, mean scores for flight speed were separated into 5 categories based on 0.10 s time intervals. In the first group, flight speed was related to ADG and final weight such that steers with the fastest flight speed gained less (0.79 vs. 1.13 kg/d) and weighed less at the end of the test (297 vs. 346 kg) than animals with the slowest flight speeds. The second group had overall slower flight speeds than the first group, and no significant differences were detected in gain or body weight based on flight speed. Similarly, in Bonsmara bulls and Santa Gertrudis steers, Brown et al. (2004) showed exit velocity (EV) to be negatively correlated with ADG, body weight, and DMI ($P < 0.10$).

Voisinet et al. (1997b) evaluated the effect of temperament (using a 4-point scale in the squeeze chute) on meat quality traits in *Bos indicus* influenced cattle. They reported cattle with high temperament scores to have a higher incidence of dark cutters ($P = 0.01$) and higher Warner-Bratzler shear force ($P < 0.001$) than more docile cattle. Of the most excitable animals (temperament score of 5), 25% were borderline dark cutters, while only 6.7% of the calm animals were borderline dark cutters. Mean Warner-Bratzler shear force values for calm and excitable animals were 2.86 and 3.63 kg, respectively. Stated differently, 40% of the excitable animals measured higher than 3.9 kg, while only 11% of the calm animals had a shear force greater than 3.9 kg, with 3.9 kg being the threshold value for acceptability for tenderness in food service.

Burrow and Dillon (1997) found no relationship between flight speed and fat thickness or carcass bruising, which was similar to Brown et al. (2004) who found no relation between EV and carcass backfat or intramuscular fat. However, in the group of calves that had extensive handling prior to entering the feedyard, those with slower flight speeds had higher dressing percentages ($P < 0.001$; Burrow and Dillon, 1997). Conversely, Brown et al. (2004) found EV to be positively correlated with longissimus muscle area ($P < 0.01$). These seeming contradictions may be indicative of Tulloh's (1961) assertion that speed of movement is not necessarily related to temperament.

Feeding Behavior and Feed Efficiency. Feeding behavior may play a role in efficiency as several studies have shown that the eating rate (Frisch and Vercoe, 1969; Robinson and Oddy, 2004), feeding duration and bunk attendance (Robison and Oddy, 2004; Nkrumah et al., 2006) affect different measures of intake and efficiency in *Bos indicus* and *Bos taurus*, and crosses of those biological types.

Robinson and Oddy (2004) evaluated RFI and FCR on temperate and tropical breeds of cattle fed for the Korean, Japanese, and Australian domestic markets and calculated their genetic and phenotypic correlations with feeding time (in minutes per day), number of eating sessions per day, and eating rate (in grams per minute). Feeding time had a moderate to high genetic correlation with RFI and FCR (0.35 and 0.78, respectively), but had only a low phenotypic correlation (0.16 and -0.05, respectively). Similar results were obtained for number of eating sessions per day. Eating rate (g/min), on the other hand was negatively genetically correlated with FCR (-0.83) and RFI (-0.07), suggesting that animals that eat faster were more efficient. Eating rate was also genetically ($r = 0.29$) and phenotypically ($r = 0.20$) correlated with metabolic body weight such that heavier animals ate more feed per minute.

More recently, Nkrumah et al. (2006) reported differences between low, medium and high RFI groups feeding duration ($P < 0.01$), and bunk attendance ($P = 0.01$). This followed the report of Robinson and Oddy (2004) who observed that more efficient cattle made fewer trips to the bunk.

In composite ram lambs (1/2 Columbia, ¼ Hampshire, ¼ Suffolk; 11 to 17 wk old), the genetic and phenotypic correlations between RFI and time spent feeding daily were 0.22 and 0.10, respectively. The genetic and phenotypic correlations between RFI and daily feeding events were 0.20 and 0.10, respectively. Residual feed intake and daily feed intake had genetic and phenotypic correlations of 0.61 (Cammack et al., 2005).

Summary

Accurate evaluation of the efficiency of feed utilization and its incorporation as a selection criteria in a breeding program is extremely important, but to this point, has been an elusive goal. Some research has suggested that RFI may hold promise for making improvements in efficiency; however, as has been discussed here, RFI does have several limitations. On the one hand, RFI based on phenotypic regression is not genetically independent of its component traits and, as a result, selection could have an effect on body weight (Kennedy et al., 1993), fatness (Robinson and Oddy, 2004) and other production traits. Furthermore, ranking of animals based on RFI can change depending on diet (Fan et al., 1995). However, due to the nature of its derivation, RFI lends itself to use as a selection index, which would allow for selection pressure to be placed upon it, and thus it could be included in a breeding program using multiple trait selection.

Developing a metric for assessing differences in efficiency that incorporates both input and output variables and is not heavily dependent on contemporary group would certainly be beneficial. Also, temperament may be need to be incorporated when evaluating feed efficiency. Furthermore, due to the time and expense limitations of evaluating feed intake on large numbers of animals, the discovery of QTL or genes related to efficiency would be extremely valuable. The focus of the ensuing research is: (1) the development of a new metric for describing feed efficiency and its relationship with other production traits, and (2) to provide phenotypic analysis that will be used in future QTL analysis and gene discovery.

MATERIALS AND METHODS

Materials

This study utilized F_2 Nellore-Angus steers from 6 contemporary groups produced by embryo transfer from 13 F_1 Nellore-Angus donor females and 4 Nellore-Angus F_1 sires. All F_1 parents were Nellore-sired. Steers were born in the Spring and Fall calving seasons of 2003 through 2005, and those born in the same year and season were managed in the same contemporary group (Table 5). Disposition (temperament) scores were assigned approximately 30 d after weaning, individual feed intake and body weight were measured at the McGregor research center during the feeding phase, and carcass and meat traits were evaluated after harvest at the TAMU Rosenthal Meat Science and Technology Center. All procedures involving animals were approved by the Texas A&M Institutional Animal Care and Use Committee; AUP # 2002-116 and 2005-147.

Table 5. Contemporary group designation

Birth Year/Season	Contemporary Group	n
Spring 2003	1	22
Fall 2003	2	26
Spring 2004	3	34
Fall 2004	4	32
Spring 2005	5	36
Fall 2005	6	30

Temperament (Disposition) Scoring. Shortly after weaning, calves were evaluated for 5 aspects of temperament (aggressiveness, nervousness, flightiness, gregariousness, and overall temperament) by a panel of 4 university evaluators using a subjective scale of 1 to 9. Aggressiveness represents the animal's combativeness towards evaluators (1 is non-aggressive, and 9 is extremely aggressive). Nervousness refers to the animal's agitation and fear with behavior including walking and running, vocalization, and physically shaking (1 is totally calm and 9 is extremely nervous). Flightiness signifies the animal's desire to keep away or get away from evaluators where 1 is totally quiet and 9 is extremely flighty. Gregariousness refers to an animal's desire to get back to the group of individuals from which it came and/or to where it is going such as sticking head through fence toward group, looking at the group, and how it acted in a pair as compared to being separated, where 1 is totally willing to be separated from the group and 9 is unwilling to be separated. Overall disposition is not an average of the others traits, but instead, is scored as a separate trait as an overall assessment, where 1 is completely docile and 9 is wild.

To execute temperament scoring, initially 2 calves were cut from a group (of about 15 head) in the holding pen into the adjacent evaluation area and allowed to settle (usually 1 to 2 minutes). Then one calf was pushed back to the holding pen and the remaining calf was evaluated individually for temperament. When all of the evaluators had completed temperament scoring, the calf exited the scoring area through a gate opposite that which it entered.

Recipient females are also scored for disposition shortly after calving on a scale of 1 to 5, where 1 represents a docile disposition and 5 represents a wild and/or aggressive disposition.

Individual Feed Intake. After weaning, the calves were placed on grass for an approximate 130-day growing period, after which individual feed intake was evaluated using a Calan gate system beginning at an average age of 11 to 13 months (ration in Table 6). During this time, the steers were housed in a partially covered facility in pens of 4 and weighed every 28 days. Feed was offered *ad libitum* with refused feed being collected at 7-d intervals, weighed, and fresh feed offered if refused feed began to build up. The diet was periodically checked for dry matter content, which was found to average 90%. A small number of animals were not adequately trained to eat from the Calan gate bunks and were fed individually in adjacent pens. All animals were evaluated for disposition at the end of the feeding period by a single evaluator.

Table 6. Ration formulation

Ingredient	%[a]
Ground milo	20.00
Ground corn	31.25
Cottonseed meal	9.00
Cottonseed hulls	25.00
Molasses	10.00
Premix[1]	3.00
Ammonium chloride	0.25
R-1500[2]	1.50

[a] Expressed as a percent on an as-fed basis

[1] Composition of premix: ground limestone, 60%; trace mineralized salt, 16.7% (NaCl, 98%; Zn, 0.35%; Mn, 0.28%; Fe, 0.175%, Cu, 0.035%, I, 0.007%, Co, 0.007%); mono-dicalcium phosphate, 13%; potassium chloride, 6.7%; Vitamin premix, 3.3% (vitamin A, 2,200,000 IU/kg; vitamin D, 1,100,000 IU/kg, vitamin E, 2,200 IU/kg); Zinc oxide, 0.33%.

[2] R-1500 contains 1.65 g monensin sodium (Rumensin™) per kg.

Carcass and Meat Traits. Following a feeding period of approximately 140 d (approximately 18 mo of age), the steers were harvested at the Rosenthal Meat Science and Technology Center at Texas A&M. Carcasses were weighed (HCW), and 24 hours postmortem, longissimus muscle area (REA), fat thickness (FT), kidney pelvic and heart fat, and marbling scores were recorded by TAMU meat scientists, with USDA yield grade (YG) calculated from the component traits. All animals were evaluated for disposition in the holding pens immediately prior to being stunned.

Statistical Analysis. Using the NRC (2000) beef cattle model, daily feed intake was predicted based on observed weight gain for each animal and standardized input for animal type, age, sex, condition, and breed. This model predicted intake (MDMI) was then subtracted from observed DMI and the difference defined as model predicted residual consumption (MPRC) such that those animals that consumed less than predicted (and thus, were more efficient) had negative MPRC. This method was utilized in addition to traditional residual feed intake in order to make simultaneous use of data from multiple contemporary groups (Table 7). Mixed procedures of SAS were then used to analyze MPRC with fixed factors of sire and family nested within sire. Initial analysis also included contemporary group (CG); however, substantial imbalance existed with sire and family across contemporary groups, so it was subsequently omitted from final analyses.

In a separate analysis, regression procedures of SAS were used to regress observed DMI on ADG and average weight while on feed to obtain predicted values for DMI as well as residuals (RFI) within each contemporary group. Then, the Mixed procedure was used to analyze RFI with fixed factors of sire and family nested within sire. Spearman's rank correlation was then used to evaluate the degree of re-ranking that occurred for sires, families, and CG between RFI and MPRC.

Temperament was evaluated through analysis of variance with fixed effects of sire, family nested within sire, and contemporary group (CG). Finally, correlations were calculated for temperament traits with measures of efficiency, carcass traits, temperament group (group of approximately 15 calves from which sorting was done), and temperament sequence (the order in which calves were temperament scored).

Table 7. Distribution of contemporary group and family combinations

	Contemporary Group						
Family	1	2	3	4	5	6	Total
70	1	5	4	2	1	4	17
71	2	2	5	5	2	1	17
72	5	0	5	0	2	7	19
73	2	3	0	0	0	0	5
74	4	0	0	0	0	0	4
75	5	0	0	2	4	0	11
76	2	3	0	0	0	0	5
77	1	5	1	1	11	0	19
80	0	7	3	16	0	1	27
81	0	1	13	3	5	5	27
82	0	0	0	0	0	6	6
83	0	0	3	2	4	2	11
84	0	0	0	1	7	4	12
Total	22	26	34	32	36	30	180

RESULTS AND DISCUSSION

Residual Feed Intake

Residual feed intake was calculated within each contemporary group (CG) for all steers (n = 180) by regressing observed dry matter intake (DMI) on ADG and average body weight while on feed (MWT) and subtracting the predicted values from observed DMI. Next, an analysis of variance was conducted with RFI as the dependent variable and fixed factors of sire and family nested within sire as independent variables. Using this method, neither sire nor family nested within sire contributed to variation in RFI (Table 8).

Table 8. Residual feed intake fixed effects

	F-value	*P*-value
Sire	1.99	0.117
Family (Sire)	0.98	0.455

In order to assess the relationship of RFI with DMI and ADG, correlations were calculated across all animals, by sire, by family, and by CG. Simple means for DMI and ADG were 9.30 kg day^{-1} and 1.03 kg day^{-1}, respectively. Overall, RFI was moderately correlated with DMI (r = 0.50; $P < 0.001$) and, as expected, was not correlated with ADG (r = 0.00; $P = 1.00$).

Within sire groups, the mean RFI ranged from -0.16 to 0.19, and the correlation between RFI and DMI ranged from 0.40 to 0.76 kg ($P = < 0.001$ to 0.015), while no correlation ($P > 0.05$) existed between RFI and ADG (Table 9). Within each sire group, DMI and ADG were moderately to highly correlated (0.55 to 0.77, all $P < 0.05$; Table 9).

Table 9. Correlations of residual feed intake with observed dry matter intake and average daily gain by sire

			Daily dry matter intake			Average daily gain			ADG/DMI[1]	
Sire	n	Mean RFI	Mean (kg/d)	r	*P*-value	Mean (kg/d)	r	*P*-value	r	*P*-value
297J	34	-0.04	9.64	0.41	0.015	1.05	-0.18	0.301	0.73	< 0.001
432H	24	-0.01	8.79	0.76	< 0.001	0.95	0.05	0.829	0.55	0.006
437J	59	0.19	9.75	0.53	< 0.001	1.09	0.06	0.673	0.75	< 0.001
551G	63	-0.16	8.89	0.40	0.01	1.00	-0.03	0.816	0.77	< 0.001

[1] ADG/DMI = correlation between average daily gain (kg/d) and dry matter intake (kg/d)

Table 10. Correlations of residual feed intake with observed dry matter intake and average daily gain by contemporary group

			Daily dry matter intake			Average daily gain			ADG/DMI[*1]	
Contemporary group	n	Mean RFI	Mean (kg/d)	r	*P*-value	Mean (kg/d)	r	*P*-value	r	*P*-value
1	22	0	9.08	0.68	< 0.001	0.94	0	1.0	0.60	0.003
2	26	0	9.66	0.35	0.082	0.93	0	1.0	0.87	< 0.001
3	34	0	8.77	0.53	< 0.001	1.00	0	1.0	0.80	< 0.001
4	32	0	8.80	0.57	< 0.001	0.91	0	1.0	0.72	< 0.001
5	36	0	10.30	0.53	< 0.001	1.37	0	1.0	0.80	< 0.001
6	30	0	9.09	0.58	< 0.001	0.95	0	1.0	0.72	< 0.001

[*1] ADG/DMI = correlation between average daily gain (kg/d) and dry matter intake (kg/d)

Table 11. Correlation of residual feed intake with observed dry matter intake and average daily gain by family

			Daily dry matter intake			Average daily gain			ADG/DMI[*1]	
Family	n	Mean RFI	Mean (kg/d)	r	*P*-value	Mean (kg/d)	r	*P*-value	r	*P*-value
70	17	0.26	9.95	0.50	0.043	1.02	-0.29	0.260	0.54	0.025
71	17	-0.33	9.33	0.25	0.333	1.08	-0.09	0.740	0.91	< 0.001
72	19	-0.14	8.57	0.74	< 0.001	0.96	0.03	0.894	0.57	0.011
73	5	0.48	9.62	0.84	0.073	0.89	0.58	0.304	0.92	0.028
74	4	0.53	9.11	0.998	0.002	0.80	0.40	0.596	0.37	0.628
75	11	0.21	9.87	0.78	0.004	1.18	0.49	0.129	0.81	0.003
76	5	-0.24	8.40	0.24	0.699	0.88	-0.10	0.874	0.92	0.029
77	19	-0.13	10.26	0.52	0.022	1.25	-0.18	0.451	0.46	0.048
80	27	-0.18	8.22	0.53	0.005	0.83	0.08	0.674	0.78	< 0.001
81	27	0.08	9.59	0.50	0.009	1.11	-0.01	0.942	0.77	< 0.001
82	6	0.05	9.63	0.09	0.862	0.99	-0.31	0.544	0.84	0.038
83	11	0.43	10.30	0.41	0.210	1.11	-0.03	0.927	0.79	0.004
84	12	-0.11	8.44	0.31	0.324	1.03	-0.15	0.635	0.87	< 0.001

[*1] ADG/DMI = correlation between average daily gain (kg/d) and dry matter intake (kg/d)

As expected, the mean RFI for each contemporary group was zero. Within contemporary groups, the correlation between RFI and DMI ranged from 0.35 to 0.68. Higher correlations, ranging from 0.60 to 0.87, were observed between ADG and DMI (Table 10).

Family means for RFI ranged from -0.33 kg/d (most efficient) to 0.53 kg/d (least efficient). As expected, RFI and ADG were not significantly correlated for any of the families. However, significant ($P < 0.05$) correlations between RFI and DMI by family did exist and ranged from 0.09 to 1.00 (Table 11).

The results reported here for the correlation of RFI with DMI and ADG are similar to those of Nkrumah et al. (2004) who reported a phenotypic correlation of 0.75 between RFI and DMI in *Bos taurus* crossbred bulls and steers. More recently, Nkrumah et al. (2007) reported moderate phenotypic correlations between RFI and DMI (r = 0.64; $P < 0.001$) and between DMI and ADG (r = 0.60; $P < 0.001$) in progeny of Angus, Charolais, or Alberta Hybrid bulls and Alberta Hybrid cows.

Table 12. Correlation of carcass traits with residual feed intake

Carcass trait	n	Mean	Standard deviation	Correlation w/ RFI	*P*-value
Marbling R[1]	172[2]	418.0	86.24	0.10	0.182
Marbling L[1]	180	421.8	89.52	0.12	0.095
Carcass weight (kg)	180	297.1	40.63	0.07	0.369
Fat thickness (cm)	180	1.4	0.46	0.06	0.388
Longissimus muscle area (cm^2)	180	72.6	7.12	-0.04	0.639
USDA Yield Grade	180	3.2	0.67	0.14	0.065

[1] The right side of the carcass was electrically stimulated, the left side was not
[2] The electrical stimulator was non-functioning 1 day

Pearson's correlation coefficients between RFI and carcass traits were calculated across all animals. No significant correlations were found, though there was a trend for RFI to have a slight (r = 0.14) positive correlation with USDA Yield Grade ($P = 0.065$), such that more efficient animals tended to have lower numerical yield grades and less efficient animals tended to have higher numerical yield grades (Table 12).

In cattle, past research has generally reported moderate correlations between RFI and measures of fatness, where more efficient animals tended to be leaner. In Hereford cattle, Herd and Bishop (2000) showed RFI to be negatively phenotypically correlated with predicted carcass lean content based on ultrasound (r = -0.22 ± 0.04) such that lower RFI (more efficient animals) should produce a carcass with a great proportion of lean content. Likewise, Robinson and Oddy (2004) found RFI to be genetically correlated with fat thickness measured at between the 12th and 13th rib and at the P8 rump site (r = 0.48 and 0.72, respectively, when adjusted for age and r = 0.58 and 0.79, respectively, when adjusted for carcass weight). Nkrumah et al. (2007) found slightly lower phenotypic correlations between RFI and ultrasound fat thickness (r = 0.25; $P < 0.01$) and carcass grade fat (r = 0.23; $P < 0.01$). Furthermore, they found a negative phenotypic correlation between RFI and lean meat yield (r = -0.21; $P < 0.01$) and a positive correlation between RFI and yield grade (r = 0.22; $P < 0.01$). In contrast, Baker et al. (2006) found no significant correlation between RFI and fat measured by ultrasound or fat thickness, KPH and yield grade in the carcass.

Previously, researchers have made an attempt to account for differences across contemporary groups by using the model:

$$DFI = \mu + CG + ADG + MMWT + CG*ADG + CG*MMWT + RFI$$

where DFI is daily feed intake, CG is contemporary group, ADG is average daily gain, MMWT is metabolic mid-weight, and RFI is the residual from the model (W.S. Pitchford, University of Adelaide, Pers. Comm). For the current dataset, residuals were obtained using the above recommendation and analyzed using the same model that was used to analyze RFI (residuals as the dependent variable and fixed factors of sire and family nested within sire as independent variables). Results using this adjustment across contemporary groups were identical to those obtained here for calculation of RFI within each contemporary group.

Model Predicted Residual Consumption (MPRC)

Based on RFI, comparing animals from different contemporary groups may be problematic because the regression equation derived to obtain residuals is unique to the particular group of animals being evaluated. Developing an efficiency index from a stable model may allow for the comparison of data within and among contemporary groups.

As such, Model Predicted Residual Consumption (MPRC) was evaluated on 180 steers. Using the NRC (2000) beef cattle model, daily feed intake was predicted based on observed weight gain for each animal and standardized input for animal type, age, sex, condition, and breed. This model predicted intake (MDMI) was then subtracted from observed DMI, and the difference defined as model predicted residual consumption (MPRC) such that those animals that consumed less than predicted (and thus, were more efficient) had negative MPRC. Variation in MPRC was attributable to the fixed effects of sire and family nested within sire (Table 13).

Table 13. Model predicted residual consumption fixed effects

	F-value	*P*-value
Sire	2.92	0.0356
Family (Sire)	4.61	<0.001

The mean MPRC for all animals was -0.01 kg day^{-1} (n = 180), indicating that on average, steers from this study consumed 0.01 kg less per day than the NRC model predicted. Least squares means for MPRC by sire group ranged from a low of -0.31 ± 0.21 kg day $^{-1}$ to a high of 0.71 ± 0.34 kg day^{-1} (Table 14), showing that differences did exist in the progeny of various sires and thus, the possibility may exist to map QTL and discover genes relating to efficiency in this population. Differences in average MPRC between the sires are presented in Table 15.

Table 14. Means and least squares means for MPRC by sire

Sire	n	Mean (kg d^{-1})	Standard deviation	Least squares means (kg d^{-1})	SEM	*P*-value^{1}
297J	34	0.31	1.45	0.31	0.23	0.180
432H	24	0.27	1.25	0.71	0.34	0.039
437J	59	0.03	1.42	0.33	0.22	0.126
551G	63	-0.34	1.60	-0.31	0.21	0.140

[1] Indicates probability that least squares means are different from zero

Table 15. Differences among sires for MPRC[1]

Sire	297J	432H	437J	551G
297J		0.40	0.02	0.62
432H	0.336		0.38	1.01
437J	0.952	0.349		0.64
551G	0.048	0.012	0.034	

[1] Absolute value of the difference in average MPRC between sires is above the diagonal, *P–value* for the difference from the t-test is below the diagonal.

Simple means and least squares means for MPRC by family (sire) were identical and ranged from -1.32 ± 0.39 kg day $^{-1}$ to 1.45 ± 0.60 kg day^{-1} across all families (Table 16). Closer scrutiny of the values for MPRC shows that the same sires were responsible for families with negative and positive MPRC. This is not surprising since families with the same sire had different dams. Since the dam contributes ½ of the genes to any particular calf and each dam is a Nellore-Angus F_1, it's reasonable to believe the females in this population could be segregating for different genes relating to efficiency traits.

Table 16. Means and least squares means for model predicted residual consumption (MPRC) by family nested within sire

Sire Family	n	Mean (kg d^{-1})	Standard deviation	Least squares means (kg d^{-1})	SEM	*P*-value[1]
297J						
70	17	0.90	1.43	0.90	0.33	0.007
71	17	-0.27	1.25	-0.27	0.33	0.404
432H						
72	19	-0.04	1.17	-0.04	0.31	0.909
73	5	1.45	0.82	1.45	0.60	0.017

Table 16 continued

Sire Family	n	Mean (kg d^{-1})	Standard deviation	Least squares means (kg d^{-1})	SEM	*P*-value[1]
437J						
74	4	1.37	0.96	1.37	0.68	0.044
75	11	-0.52	1.38	-0.52	0.41	0.200
81	27	-0.12	1.39	-0.12	0.26	0.653
82	6	0.94	0.52	0.94	0.55	0.090
83	11	-0.01	1.65	-0.01	0.41	0.973
551G						
76	5	0.73	0.51	0.73	0.60	0.226
77	19	-1.00	2.00	-1.00	0.31	0.001
80	27	0.37	0.92	0.37	0.26	0.160
84	12	-1.32	1.47	-1.32	0.39	<0.001

[1] Indicates probability that least squares means are different from zero

By sire, the range in mean for RFI was -0.16 to 0.19 kg/d and by family the range in means for RFI was -0.33 to 0.53 kg/d. For MPRC, much larger ranges in means were observed. For sire, the range in means for MPRC was -0.34 to 0.31 kg/d, and by family the range was -1.32 to 1.45 kg/d. The larger range observed for MPRC may be because the calculation of MPRC does not hold weight gain or feed intake constant. It is possible that *Bos indicus* and *Bos taurus* cattle differ in efficiency for different reasons and MPRC allows these differences to be seen. Furthermore, the larger range in means for MPRC compared to RFI may prove to be beneficial in the future when QTL analysis is done, because models that provide more spread in the residuals tend to be more valuable in QTL mapping.

Correlations were calculated for MPRC, daily DMI, and ADG across all animals as well as by sire, by family, and by CG. Overall, MPRC was lowly correlated with DMI (r = 0.11; *P* = 0.142) and moderately correlated with ADG (r = -0.51; *P* < 0.001). By sire, mean MPRC ranged from -0.34 to 0.31 kg/d and tended to be moderately positively correlated with DMI and moderately negatively correlated with ADG (Table 17). These results indicate that more efficient animals (negative MPRC) tend to consume less and gain more. Similarly, by family and CG, correlations tended to be moderate and were positive for DMI and negative for ADG, with the exception of family 71, which had large negative correlations between RFI, ADG, and DMI (Tables 18 and 19).

Table 17. Correlation of model predicted residual consumption (MPRC) with observed dry matter intake and average daily gain by sire

			Daily DMI		Average Daily Gain	
Sire	n	Mean MPRC	r	*P*-value	r	*P*-value
297J	34	0.31	0.08	0.64	-0.59	< 0.001
432H	24	0.27	0.67	< 0.001	-0.13	0.553
437J	59	0.03	0.16	0.222	-0.43	< 0.001
551G	63	-0.34	-0.09	0.477	-0.66	< 0.001

Results reported here for RFI and previously in other studies have shown no significant correlation of RFI with ADG. This has been interpreted to mean that selecting for reduced RFI can be used to improve efficiency without affecting growth. This interpretation would mean that, theoretically, selection for reduced RFI would produce steers that are more efficient in the feedyard, and that their female counterparts could be kept as replacements without an increase in the mature size (and thus the maintenance requirements) of the cowherd. This conclusion should be considered carefully as the very nature of the calculation of RFI (regressing DMI on ADG and BW) forces the correlation between ADG and RFI to be zero because it forces all of the variation in performance into DMI.

Another cause for concern is the use of RFI in genetic evaluations. We have shown here that using the previously published adjustment for RFI calculation across contemporary groups yielded the same result as calculating RFI individually within each contemporary group. Thus, the RFI on an individual animal is not static; the merit of the contemporary group would influence the RFI of an individual.

Table 18. Correlation of model predicted residual consumption (MPRC) with observed dry matter intake and average daily gain by family

				Daily DMI		Average Daily Gain	
Family	Sire	n	Mean MPRC	r	*P*-value	r	*P*-value
70	297J	17	0.90	0.54	0.025	-0.36	0.156
71	297J	17	-0.27	-0.56	0.020	-0.83	< 0.001
72	432H	19	-0.04	0.60	0.007	-0.14	0.574
73	432H	5	1.45	0.77	0.131	0.45	0.446
74	437J	4	1.37	0.90	0.103	-0.07	0.93
75	437J	11	-0.52	0.09	0.80	-0.45	0.161
76	551G	5	0.73	-0.05	0.931	-0.42	0.482
77	551G	19	-1.00	-0.09	0.701	-0.91	< 0.001
80	551G	27	0.36	0.63	< 0.001	0.05	0.804
81	437J	27	-0.12	0.32	0.105	-0.22	0.264
82	437J	6	0.94	0.47	0.342	-0.05	0.919
83	437J	11	-0.01	-0.03	0.931	-0.57	0.065
84	551G	12	-1.32	-0.31	0.330	-0.69	0.013

Table 19. Correlation of model predicted residual consumption (MPRC) with observed dry matter intake and average daily gain by contemporary group

			Daily DMI		Average Daily Gain	
Contemporary group	n	Mean MPRC	r	P-Value	r	P-Value
1	22	0.52	0.41	0.057	-0.44	0.039
2	26	1.28	0.63	< 0.001	0.21	0.302
3	34	0.06	0.54	0.001	-0.03	0.845
4	32	0.40	0.68	< 0.001	-0.00	0.980
5	36	-2.28	0.21	0.216	-0.33	0.046
6	30	0.69	0.79	< 0.001	0.19	0.326

Using a path analysis, Koch et al. (1963) showed that in bulls and heifers from British breeds, 38% of the variation in weight gain could be attributed to genetic differences in feed efficiency, 25% was attributable to genetic differences in feed consumption and the remainder (37%) was due to environment. With this in mind it also seems highly unlikely that weight gain has no effect on feed efficiency.

In fact, the 2 basic contributors to feed efficiency are feed intake and weight gain; so, it is reasonable to believe that some animals may be more efficient because they require less feed, while others may be more efficient because they gain more, and, it may or may not be the same genes controlling gain and feed intake. So, it would also be logical to assume that, for some families or sires, efficiency would be more highly correlated with ADG, while in other families efficiency may be more highly correlated with DMI. From this standpoint, MPRC may provide a more truthful picture of the factors contributing to a family's efficiency (or lack of) as compared to RFI.

Spearman's rank correlation was calculated between RFI and MPRC overall, by sire, by family, and by CG. Across all animals, RFI and MPRC were moderately correlated (r = 0.57; P < 0.001) indicating that there was some degree of re-ranking of sires depending on if efficiency was measured by MPRC or RFI. By sire, this correlation ranged from moderate to high (Table 20), supporting the theory that some sires may pass on genes related to differences in intake and other sires may pass on genes related to differences in growth, both of which may affect the apparent efficiency of their progeny, but for different reasons.

Table 20. Spearman's rank correlation between model predicted residual intake and residual feed intake by sire

Sire	n	Spearman's correlation	*P*-value
297J	34	0.77	< 0.001
432H	24	0.84	< 0.001
437J	59	0.47	< 0.001
551G	63	0.47	< 0.001

This is further supported by the analysis of the correlations between MPRC and RFI by family, where for some families the two are not correlated (*P* > 0.05), while for other families they are highly correlated (Table 21). When evaluated by contemporary group, the correlation between RFI and MPRC was generally high (Table 22), which is not unexpected because intake was predicted by contemporary group in order to obtain RFI.

Table 21. Spearman's rank correlation for model predicted residual intake and residual feed intake by family

Family	Sire	n	Spearman's correlation	*P*-Value
70	297J	17	0.78	< 0.001
71	297J	17	0.63	0.007
72	432H	19	0.84	< 0.001
73	432H	5	0.90	0.037
74	437J	4	0.40	0.600
75	437J	11	0.15	0.670
76	551G	5	0.70	0.188
77	551G	19	0.50	0.031
80	551G	27	0.86	< 0.001
81	437J	27	0.55	0.003
82	437J	6	0.54	0.266
83	437J	11	0.31	0.355
84	551G	12	0.70	0.011

Table 22. Spearman's rank correlation for model predicted residual intake and residual feed intake by contemporary group

Contemporary group	n	Spearman's correlation	*P*-value
1	22	0.70	< 0.001
2	26	0.90	< 0.001
3	34	0.98	< 0.001
4	32	0.89	< 0.001
5	36	0.88	< 0.001
6	30	0.81	< 0.001

Pearson's correlation coefficients were calculated between MPRC and carcass traits (Table 23). Model predicted residual consumption was found to be moderately positively correlated with marbling score on both the electrically stimulated and non-stimulated sides of the carcass such that steers with lower MPRC (more efficient) had less marbling, and vice versa. A weak trend (*P* = 0.07) existed between MPRC and carcass weight. No other carcass traits were correlated with MPRC.

Table 23. Correlation of carcass traits with model predicted residual consumption

Carcass trait	mean	SDM	CV	r	*P*-value
Marbling right[1]	418.0	86.2	0.21	0.29	< 0.001
Marbling left[1]	421.8	89.5	0.21	0.33	< 0.001
Carcass weight (kg)	297.1	40.6	0.14	0.14	0.067
Fat thickness (cm)	1.4	0.46	0.32	-0.01	0.846
REA (cm^2)[2]	72.6	7.11	0.10	0.02	0.743
USDA Yield Grade	3.2	0.67	0.21	0.07	0.341

[1] The right side of the carcass was electrically stimulated, the left side was not.
[2] REA = Longissimus muscle area.

Previously, Herd and Bishop (2000) reported RFI to be negatively phenotypically correlated with predicted carcass lean content (LEAN) and lean growth rate in Hereford cattle when lean was standardized to a mean of 0.60 for each year. Later, Robinson and Oddy (2004) found RFI to be genetically correlated with fat thickness measured by ultrasound between the 12th and 13th rib (r = 0.48) and at the P8 rump site (r = 0.72) both when adjusted for age and for carcass weight in temperate and tropical cattle breeds; RFI was lowly phenotypically correlated with these same traits (r = 0.11 and 0.13 for rump and rib fat, respectively). McDonagh et al. (2001) found differences in rib fat and rump fat in British-cross calves of sires and dams selected for high and a low RFI.

In cattle, Robinson and Oddy (2004) found RFI to be weakly genetically and phenotypically correlated with intramuscular fat as measured by ultrasound, and Hoque et al. (2007) found positive genetic and phenotypic correlations between the same traits. However, McDonagh et al. (2001) found no difference in marbling in the progeny of low and high RFI sires and dams.

Temperament

Temperament was evaluated shortly after weaning by 4 trained evaluators. Aggressiveness, nervousness, flightiness, gregariousness, and overall temperament were evaluated on a 1 to 9 scale, with 1 denoting the most calm, quiet, etc. behaviors and 9 denoting extremely aggressive, agitated, etc. behaviors.

Analysis of variance was used to evaluate each aspect of temperament with fixed factors of sire, family nested within sire, and contemporary group. All of these effects contributed to differences in each of the temperament measurements ($P < 0.10$; Table 24). It is important to reiterate that embryo transfer was used to produce all of the calves in this analysis. So, the effect the dam had on temperament (as observed in family(sire)) is only due to learned behavior. This is in agreement with Fordyce and Goddard (1984) who showed a low correlation (0.09) between overall temperament in cows and their daughters (produced through natural service) when temperament was evaluated on a subjective scale during pregnancy palpation. They also reported a heritability of zero for overall temperament, which led them to conclude that the influence cows have on their progeny is non-genetic, which is supported by the results reported here.

Table 24. Analysis of variance results for temperament traits

	Sire		Family(sire)		Contemporary group	
Trait	F- value	*P*-value	F-value	*P*-value	F-value	*P*-value
Aggressiveness	7.37	< 0.001	2.89	0.003	1.41	0.224
Nervousness	5.16	0.002	2.15	0.028	2.77	0.020
Flightiness	4.89	0.003	1.81	0.070	3.21	0.009
Gregariousness	4.76	0.003	1.80	0.072	3.80	0.003
Overall Temp	5.36	0.002	2.12	0.031	2.82	0.018

Aggressiveness. Least squares means for aggressiveness by sire ranged from 1.91 to 3.49 (Table 25). Differences between the sires for aggressiveness are presented in Table 26. When analyzed by family nested within sire, least square means ranged from a low of 1.60 to a high of 5.72 (Table 27). By contemporary group, least squares means were more consistent, with a low of 2.22 and a high of 3.16 (Table 28).

Table 25. Means and least squares means for aggressiveness by sire

Sire	n	Mean	Standard deviation	Least squares mean	SEM
297J	34	1.90	1.37	1.91	0.26
432H	24	2.47	1.57	2.46	0.38
437J	59	3.27	1.83	3.49	0.25
551G	63	2.31	1.29	2.16	0.23

Table 26. Differences among sires for aggresiveness[1]

Sire	297J	432H	437J	551G
297J		0.55	1.58	0.25
432H	0.235		1.03	0.30
437J	< 0.001	0.023		1.33
551G	0.476	0.500	< 0.001	

[1] Absolute value of the difference in average aggressiveness score between sires is above the diagonal, *P*-value for the difference is below the diagonal.

Table 27. Means and least squares means for aggressiveness by family nested within sire

Sire Family	n	Mean	Standard deviation	Least squares mean	SEM
297J					
70	17	2.29	1.60	2.24	0.36
71	17	1.50	0.98	1.60	0.36
432H					
72	19	2.41	1.47	2.60	0.35
73	5	2.70	2.11	2.34	0.70
437J					
74	4	5.63	1.56	5.72	0.81
75	11	2.59	1.65	2.61	0.47
81	27	3.76	1.76	3.90	0.31
82	6	2.58	1.24	2.86	0.66
83	11	2.27	1.56	2.36	0.45
551G					
76	5	2.00	1.02	1.64	0.68
77	19	2.39	1.42	2.14	0.36
80	27	2.12	1.21	2.14	0.33
84	12	2.71	1.36	2.71	0.45

Table 28. Means and least squares means for aggressiveness by contemporary group

Contemporary Group	n	Mean	Standard deviation	Least squares mean	SEM
1	22	2.83	1.94	2.41	0.36
2	26	2.81	1.56	3.16	0.32
3	34	2.59	1.67	2.27	0.30
4	32	2.02	1.53	2.24	0.33
5	36	2.76	1.52	2.70	0.30
6	30	2.48	1.51	2.22	0.33

Nervousness. Overall, animals scored higher for nervousness than for aggressiveness. Least squares means ranged from 3.06 to 4.70 by sire (Table 29; differences between sires for nervousness are presented in Table 30), 2.52 to 6.01 by family nested within sire (Table 31), and 3.24 to 4.73 by contemporary group (Table 32).

Table 29. Means and least squares means for nervousness by sire

Sire	n	Mean	Standard deviation	Least squares mean	SEM
297J	34	2.96	1.80	3.06	0.30
432H	24	4.24	1.58	4.29	0.44
437J	59	4.64	1.95	4.70	0.29
551G	63	3.86	1.69	3.75	0.27

Table 30. Differences among sires for nervousness[1]

Sire	297J	432H	437J	551G
297J		0.55	1.58	0.25
432H	0.235		1.03	0.30
437J	< 0.001	0.023		1.33
551G	0.476	0.500	< 0.001	

[1] Absolute value of the difference in average score between sires is above the diagonal, *P*-value for the difference is below the diagonal.

Table 31. Means and least squares means for nervousness by family nested within sire

Sire Family	n	Mean	Standard deviation	Least squares mean	SEM
297J					
70	17	3.51	1.80	3.60	0.42
71	17	2.40	1.66	2.52	0.42
432H					
72	19	4.12	1.62	4.21	0.41
73	5	4.70	1.47	4.36	0.80
437J					
74	4	6.31	0.90	6.01	0.94
75	11	4.36	2.06	4.07	0.54
74	4	6.31	0.90	6.01	0.94
75	11	4.36	2.06	4.07	0.54
81	27	5.11	1.79	5.21	0.36
82	6	4.04	1.49	4.61	0.77
83	11	3.50	2.17	3.49	0.53
551G					
76	5	3.65	1.13	3.32	0.80
77	19	3.75	1.87	3.23	0.42
80	27	3.61	1.63	4.00	0.38
84	12	4.67	1.65	4.46	0.53

Table 32. Means and least squares means for nervousness by contemporary group

Contemporary Group	n	Mean	Standard deviation	Least squares mean	SEM
1	22	4.51	1.80	4.24	0.41
2	26	4.02	1.79	4.30	0.37
3	34	4.00	1.76	3.78	0.35
4	32	3.10	1.67	3.24	0.38
5	36	4.68	2.09	4.73	0.35
6	30	3.73	1.72	3.37	0.38

Flightiness. Least squares means for flightiness were similar to those observed for nervousness. By sire, least squares means ranged from 2.75 to 4.43 (Table 33), differences between sires are presented in Table 34. By family nested within sire, the range in least squares means was 2.31 to 5.80 (Table 35). Least squares means for contemporary group ranged from 2.85 to 4.53 (Table 36).

Table 33. Means and least squares means for flightiness by sire

Sire	n	Mean	Standard deviation	Least squares mean	SEM
297J	34	2.63	1.85	2.75	0.31
432H	24	3.93	1.76	3.98	0.47
437J	59	3.78	2.00	4.43	0.31
551G	63	3.63	1.86	3.50	0.29

Table 34. Differences among sires for flightiness[1]

Sire	297J	432H	437J	551G
297J		1.24	1.69	0.75
432H	0.031		0.45	0.49
437J	< 0.001	0.417		0.94
551G	0.082	0.379	0.032	

[1] Absolute value of the difference in average flightiness score between sires is above the diagonal, *P*-value for the difference is below the diagonal.

Table 35. Means and least squares means for flightiness by family nested within sire

Sire Family	n	Mean	Standard deviation	Least squares mean	SEM
297J					
70	17	3.10	2.06	3.19	0.45
71	17	2.16	1.55	2.31	0.44
432H					
72	19	3.78	1.73	3.90	0.44
73	5	4.50	1.97	4.07	0.84
437J					
74	4	6.13	0.43	5.80	1.0
75	11	4.14	2.20	3.83	0.57
81	27	4.81	1.89	4.94	0.38
82	6	3.58	1.52	4.22	0.82
83	11	3.36	2.15	3.38	0.56
551G					
76	5	3.40	1.35	2.97	0.84
77	19	3.54	2.05	2.95	0.45
80	27	3.34	1.77	3.75	0.40
84	12	4.54	1.84	4.32	0.56

Table 36. Means and least squares means for flightiness by contemporary group

Contemporary Group	n	Mean	Standard deviation	Least squares mean	SEM
1	22	4.26	1.85	4.00	0.44
2	26	3.87	2.11	4.16	0.39
3	34	3.67	1.80	3.44	0.37
4	32	2.76	1.74	2.85	0.40
5	36	4.52	2.17	4.53	0.38
6	30	3.37	1.72	3.03	0.40

Gregariousness. Least squares means for gregariousness ranged from 2.79 to 4.32 by sire (Table 37; differences in Table 38), 2.28 to 5.84 by family nested within sire (Table 39), and 2.69 to 4.43 by contemporary group (Table 40).

Table 37. Means and least squares means for gregariousness by sire

Sire	n	Mean	Standard deviation	Least squares mean	SEM
297J	34	2.65	1.82	2.79	0.29
432H	24	4.01	1.58	4.00	0.44
437J	59	4.16	1.86	4.32	0.28
551G	63	3.54	1.79	3.45	0.27

Table 38. Differences among sires for gregariousness[1]

Sire	297J	432H	437J	551G
297J		1.21	1.53	0.67
432H	0.024		0.32	0.54
437J	< 0.001	0.536		0.86
551G	0.096	0.290	0.033	

[1] Absolute value of the difference in average gregariousness score between sires is above the diagonal, *P*-value for the difference is below the diagonal.

Table 39. Means and least squares means for gregariousness by family nested within sire

Sire Family	n	Mean	Standard deviation	Least squares mean	SEM
297J					
70	17	3.12	2.00	3.30	0.41
71	17	2.19	1.54	2.28	0.41
432H					
72	19	3.91	1.64	4.04	0.41
73	5	4.40	1.40	3.96	0.78
437J					
74	4	6.56	0.55	5.84	0.93
75	11	4.36	1.92	3.86	0.53
81	27	4.36	1.68	4.55	0.35
82	6	3.25	1.36	4.20	0.76
83	11	3.09	1.92	3.14	0.52
551G					
76	5	3.55	1.32	3.11	0.78
77	19	3.49	1.86	2.97	0.42
80	27	3.27	1.79	3.62	0.38
84	12	4.21	1.86	4.12	0.52

Table 40. Means and least squares means for gregariousness by contemporary group

Contemporary Group	n	Mean	Standard deviation	Least squares mean	SEM
1	22	2.72	1.68	4.37	0.41
2	26	3.60	1.92	3.89	0.36
3	34	3.54	1.56	3.44	0.35
4	32	2.85	1.89	3.03	0.37
5	36	4.35	2.04	4.43	0.35
6	30	2.98	1.33	2.69	0.37

Overall Temperament. Across sire groups, least squares means for overall temperament ranged from 2.66 for sire 297J to 4.37 for sire 437J (Table 41; differences between sires in Table 42). Across families, the range was 2.18 for family 71 to 6.17 for family 74 (Table 43). Least squares means by contemporary group ranged from a low of 2.83 for CG 4 to a high of 4.39 for CG 5 (Table 44). All temperament measurements were highly correlated with one another and with overall temperament (Table 45).

Table 41. Means and least squares means for overall temperament by sire

Sire	n	Mean	Standard deviation	Least squares mean	SEM
297J	34	2.54	1.73	2.66	0.30
432H	24	3.80	1.69	3.84	0.45
437J	59	4.28	2.01	4.37	0.29
551G	63	3.44	1.78	3.34	0.28

Table 42. Differences among sires for overall temperament[1]

Sire	297J	432H	437J	551G
297J		1.18	1.71	0.68
432H	0.033		0.52	0.50
437J	< 0.001	0.328		1.02
551G	0.102	0.349	0.015	

[1] Absolute value of the difference in average flightiness score between sires is above the diagonal, *P*-value for the difference is below the diagonal.

Table 43. Means and least squares means for overall temperament by family nested within sire

Sire Family	n	Mean	Standard deviation	Least squares mean	SEM
297J					
70	17	3.04	1.81	3.15	0.43
71	17	2.04	1.53	2.18	0.43
432H					
72	19	3.68	1.72	3.77	0.42
73	5	4.25	1.67	3.92	0.81
437J					
74	4	6.50	0.98	6.17	0.96
75	11	3.93	2.17	3.61	0.55
81	27	4.70	1.84	4.83	0.36
82	6	3.42	1.51	3.97	0.79
83	11	3.27	2.09	3.26	0.54
551G					
76	5	3.30	1.33	2.97	0.81
77	19	3.39	2.06	2.85	0.43
80	27	3.10	1.58	3.49	0.39
84	12	4.31	1.79	4.07	0.54

Table 44. Means and least squares means for overall temperament by contemporary group

Contemporary Group	n	Mean	Standard deviation	Least squares mean	SEM
1	22	4.23	1.89	3.89	0.42
2	26	3.58	1.83	3.89	0.38
3	34	3.54	1.71	3.33	0.36
4	32	2.66	1.73	2.83	0.39
5	36	4.35	2.19	4.39	0.36
6	30	3.29	1.73	3.00	0.39

Table 45. Correlations between temperament measures[1]

	Nerv	Flight	Greg	Ovall
Aggressiveness	0.86	0.85	0.81	0.90
Nervousness		0.98	0.95	0.98
Flightiness			0.95	0.98
Gregariousness				0.96

[1] All $P < 0.001$

To ascertain if the temperament score of the recipient dam affected the temperament of the calf, the correlation coefficients between each of the temperament traits and overall temperament of the dam were calculated (Table 46). Recipient dam temperament was lowly positively correlated with gregariousness and overall temperament and these same correlations approached significance for aggressiveness, nervousness and flightiness (Table 46), such that higher temperament scores in the dam corresponded with higher temperament scores in the offspring. This suggests that the environment provided by the recipient does affect the temperament of the calf at weaning. Keeping in mind that family(sire) was responsible for variation in all of the temperament traits likely means that both genetics and learned behavior play a role in the temperament of the calf.

Also calculated was the correlation of the temperament traits with temperament group, which is the group the animal was temperament scored in, and temperament sequence, which is the animals sequence in their temperament group. Temperament sequence was positively correlated with all of the temperament traits such that animals that came later in the sequence had higher temperament scores. It is difficult to determine if calves appeared later in the sequence because they had a poor temperament and were difficult to handle, or if they became agitated during the scoring process and the fact that they were late in the sequence caused them to have a higher temperament score.

Table 46. Correlation of calf temperament traits at weaning with recipient temperament, weaning temperament group and sequence within group

	Correlation		
Temperament trait	Recipient temperament	Temperament group	Temperament sequence
Aggressiveness	$0.12^{\dagger}$	-0.11	0.20^{*}
Nervousness	$0.14^{\dagger}$	-0.06	0.20^{*}
Flightiness	$0.14^{\dagger}$	-0.04	0.21^{*}
Gregariousness	0.16^{*}	-0.02	0.27^{***}
Overall Temp	0.15^{*}	-0.02	0.22^{*}

† $P \leq 0.10$; $^{*}P \leq 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$

Correlations of RFI and MPRC with temperament traits were calculated (Table 47). Residual feed intake was weakly phenotypically correlated with nervousness and flightiness, such that animals with higher temperament scores (less docile) had more positive (less efficient) RFI; no significant correlation existed between RFI and any other temperament traits. Model predicted residual consumption was not correlated with any temperament traits.

Table 47. Correlation of temperament traits with residual feed intake and model predicted residual consumption

Temperament trait	Mean[1]	Standard deviation	Correlation w/ RFI	*P*-value	Correlation w/ MPRC	*P*-value
Aggressiveness	2.6	1.61	0.08	0.302	0.00	0.965
Nervousness	4.0	1.87	0.15	0.046	-0.08	0.308
Flightiness	3.7	1.98	0.16	0.029	-0.07	0.328
Gregariousness	3.6	1.86	0.14	0.064	-0.09	0.241
Overall Temp.	3.6	1.93	0.13	0.088	-0.09	0.225

[1] Scale 1-9

Fox (2004) found no relationship between RFI or FCR and subjective temperament scores (obtained in the chute and in a pen) in growing Bonsmara bulls. Burrow and Dillon (1997) found flight speed to be related to ADG and final weight such that steers with the fastest flight speed gained less (0.79 vs. 1.13 kg/d) and weighed less at the end of the test (297 vs. 346 kg) than animals with the slowest flight speeds in animals that had received minimal previous handling. However, in animals that received more extensive handling post-weaning no significant differences were detected in gain or body weight based on flight speed. It should also be noted that the second group had overall slower flight speeds than the first group. Similarly, in Bonsmara bulls and Santa Gertrudis steers, Brown et al. (2004) showed exit velocity (EV) to be negatively correlated with ADG, body weight, and DMI ($P < 0.10$).

Correlations between temperament traits and carcass traits are shown in Table 48. Aggressiveness, nervousness, flightiness and overall temperament were weakly negatively correlated ($P < 0.05$) with fat thickness. Nervousness, flightiness, gregariousness and overall temperament were weakly correlated with YG ($P < 0.01$). No other significant correlations existed between carcass and temperament traits.

Table 48. Correlations between temperament and carcass traits

Trait[1]	Marbling right[2]	Marbling left[2]	Carcass weight (kg)	Fat thickness (cm)	REA[3] (cm^2)	Yield Grade
Aggr	$-0.13^{\dagger}$	-0.11	-0.02	-0.16^{*}	0.04	-0.11
Nerv	-0.12	-0.09	-0.11	-0.18^{*}	-0.01	-0.16^{*}
Flight	-0.12	-0.01	-0.10	-0.18^{*}	0.01	-0.16^{*}
Greg	-0.08	-0.07	-0.10	$-0.14^{\dagger}$	0.03	-0.15^{*}
Ovall	$-0.13^{\dagger}$	-0.09	-0.10	-0.17^{*}	0.01	-0.15^{*}

† $P < 0.10$; $^{*}P \leq 0.05$

[1] Aggr = aggressiveness; Nerv = nervousness; Flight = Flightiness; Greg = gregariousness; Ovall = Overall temperament

[2] The right side of the carcass was electrically stimulated, the left side was not.

[3] REA = Longissimus muscle area.

Previously, Burrow and Dillon (1997) found no relationship between flight speed and fat thickness or carcass bruising, and Brown et al. (2004) found no relationship between EV with carcass backfat or intramuscular fat. It is possible that these objective temperament measures are not accounting for the same aspects of behavior as the subjective measure used in the research reported here. It is also possible that different breeds, families, or groups of animals are affected differently by differences in temperament.

Correlations among carcass traits are presented in Table 49. Marbling on both sides of the carcass (electrically stimulated and not) was moderately correlated with both fat thickness and YG (*P* < 0.001). Carcass weight was moderately correlated with FT, REA, and YG (*P* < 0.001), but not with marbling. A moderate correlation existed between FT and REA (*P* < 0.01) and, as expected, a high correlation existed between FT and YG (*P* < 0.001).

Table 49. Correlations between carcass traits

Carcass trait	Marbling left[a]	Carcass weight (kg)	Fat thickness (cm)	REA (cm^2)	USDA Yield Grade
Marbling right[a]	0.92^{***}	0.07	0.27^{***}	0.00	0.26^{***}
Marbling left[a]		0.10	0.28^{***}	0.03	0.26^{***}
Carcass weight (kg)			0.43^{***}	0.50^{***}	0.57^{***}
Fat thickness (cm)				0.22^{**}	0.83^{***}
REA (cm^2)[b]					-0.11

† $P \leq 0.10$; $^{*}P \leq 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$

[a] The right side of the carcass was electrically stimulated, the left side was not.

[b] REA = Longissimus muscle area.

SUMMARY

Is it possible to make improvements in feed efficiency in beef cattle? Arthur et al. (2004) believed that in Australia potential existed to improve efficiency measured as residual feed intake (RFI) through selection because variation existed in their population, and studies have shown feed efficiency to be moderately heritable. In the research discussed here, sire and family both contributed to differences in NRC-based model predicted residual consumption (MPRC; $P = 0.036$ and $P < 0.001$, respectively), but not to differences in RFI ($P = 0.117$ and 0.455, respectively). This indicates that variation exists among the sires and families studied, and the opportunity exists to improve MPRC through selection, and that different conclusions may be reached by these two evaluation methods.

By sire, the range in means for RFI was -0.16 to 0.19 kg/d, and by family the range in means for RFI was -0.33 to 0.53 kg/d. For MPRC, much larger ranges in means were observed, which may be due in part to not having contemporary group in the model. Across sires, the range in means for MPRC was -0.34 to 0.31 kg/d, and by family the range was -1.32 to 1.45 kg/d. The larger range observed for MPRC may be observed because the calculation of MPRC does not hold weight gain or feed intake constant. It is possible that *Bos indicus* and *Bos taurus* cattle differ in efficiency for different reasons, and MPRC may allow these differences to be seen. Furthermore, the more substantial range in mean for MPRC compared to RFI may prove to be beneficial in the future when QTL analysis is done, because models that provide more spread in the residuals tend to be more valuable in QTL mapping.

Results reported here for RFI and previously in other studies have shown no correlation of RFI with ADG. This has been interpreted to mean that selecting for reduced RFI can be used to improve efficiency without affecting growth. This interpretation would mean that, theoretically, selection for reduced RFI would produce steers that are more efficient in the feedyard, and that their female counterparts could be kept as replacements without an increase in the mature size (and thus the maintenance requirements) of the cowherd. This elucidation of the results should be met with some caution, however, as the very nature of the calculation of RFI (regressing DMI on ADG and BW) forces the correlation between ADG and RFI to be zero. Another cause for concern is the use of RFI in genetic evaluations. We have shown here that using the previously published adjustment for RFI calculation across contemporary groups yielded the same result as calculating RFI individually within each contemporary group. Thus, it would appear that the merit of the contemporary group would influence the RFI of an individual.

The correlation of MPRC with DMI was highly significant for one sire ($r = 0.67$; $P < 0.001$), and MPRC and ADG were moderately negatively correlated for the other three sires ($r = -0.43$ to -0.66; $P < 0.001$). This suggests that feed intake may be the primary force affecting efficiency in some cattle, while gain may affect efficiency more in other cattle. Similar inconsistent results were observed for the correlation of MPRC with ADG and DMI by family.

Spearman’s rank correlation was calculated between RFI and MPRC overall, by sire, by family, and by CG. Across all animals, RFI and MPRC were moderately correlated ($r = 0.57$; $P < 0.001$) indicating that there was some degree of re-ranking of sires depending on if efficiency was measured by MPRC or RFI. By sire, this correlation ranged from moderate to high, supporting the theory that some sires may pass on genes related to differences in intake and other sires may pass on genes related to differences in growth, both of which may affect the apparent efficiency of their progeny, but for different reasons.

This is further supported by the analysis of the correlations between MPRC and RFI by family, where for some families the two are not correlated, while for other families they are highly correlated When evaluated by contemporary group, the correlation between RFI and MPRC was generally to high, which is not unexpected because intake was predicted by contemporary group in order to obtain RFI.

Five aspects of temperament were also evaluated shortly after weaning (aggressiveness, nervousness, flightiness, gregariousness, and overall temperament). Sire had a significant effect on variation for all 5 aspects of temperament evaluated. Family was responsible for variation in aggressiveness, nervousness, and overall temperament. Contemporary group had no effect on aggressiveness, but did contribute significantly to variation in all other temperament traits. Also, all temperament traits were highly correlated with one another.

Recipient dam temperament measured at calf birth was lowly correlated with calf gregariousness and overall temperament after weaning and these same correlations approached significance for aggressiveness, nervousness and flightiness. This suggests that the temperament of the recipient female may have a small effect on the temperament of the calf.

This population demonstrates genetic variation in feed efficiency and temperament and should prove useful for QTL mapping of these traits. This population also demonstrates that feed efficiency is a complex trait to study and that evaluation methods may impact conclusions about genetic and environmental influences affecting feed intake and efficiency.

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