SOURCES OF BIOLOGICAL VARIATION IN RESIDUAL FEED INTAKE IN GROWING AND FINISHING STEERS

A Dissertation

by

ERIN GWEN BROWN

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 2005

Major Subject: Nutrition

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Approved by:

Chair of Committee,	Gordon E. Carstens
Committee Members,	Thomas H. Welsh, Jr.
	Ronald D. Randel
	T.D.A. Forbes
Chair of Nutrition Faculty,	Nancy Turner

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ABSTRACT

Sources of Biological Variation in Residual Feed Intake in Growing and Finishing Steers. (December 2005)

Erin Gwen Brown, B.S., Texas A&M University;

M.S., Michigan State University

Chair of Advisory Committee: Dr. Gordon E. Carstens

Objectives of this research were to characterize residual feed intake (RFI) in growing and finishing steers and examine phenotypic correlations between performance, feed efficiency, carcass, digestibility, and physiological indicator traits. The research included two growing studies and one finishing study. Braunvieh-sired crossbred steers (n = 169) and Santa Gertrudis steers (n = 120) were individually fed a roughage-based diet for 77 d during the growing phase. Santa Gertrudis steers (n = 120) were individually fed a grain-based diet for 80 d during the finishing phase. Individual body weight (BW) and feed intake data were recorded. Residual feed intake was calculated as the difference between actual dry matter intake (DMI) and DMI predicted from linear regression of DMI on mid-test metabolic BW. During the growing phase, initial ultrasound measures of 12th rib fat thickness (FT) and final ultrasound measures of Longissimus muscle area (LMA), FT, and intramuscular fat (IMF) were obtained. During the finishing phase, initial and final LMA, FT, and IMF ultrasound measurements were obtained. Finishing steers were slaughtered at 1.0 cm of FT and

carcass cooler traits measured. Blood samples were collected at the start and end of each feeding period and analyzed for physiological indicators. Temperament traits were also measured at the start and end of each feeding period.

Growing and finishing steers with low RFI consumed 19-22% less feed than growing and finishing steers with high RFI, but did not differ in average daily gain (ADG). Consequently, steers with low RFI were also more efficient as measured by feed conversion ratio and partial efficiency of growth. Steers with low RFI had less FT compared to steers with high RFI. Initial serum IGF-I was correlated with RFI in growing steers indicating that IGF-I could be a potential indicator trait for RFI in growing cattle. Additionally, RFI was correlated with digestibility to indicate more efficient cattle had higher dry matter digestibility. Results indicate that RFI has potential to allow producers to select more efficient animals without increasing growth rate. Moreover, serum IGF-I may facilitate early detection and more accurate selection of animals that are superior for growing RFI.

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CHAPTER I

INTRODUCTION AND LITERATURE REVIEW

Introduction

Feed inputs represent the largest variable cost in producing beef. However, genetic selection has remained focused on output traits, such as growth and carcass quality. The overall goal of the beef industry is to improve profitability, which can be achieved through reductions in feed inputs and increases in product outputs. To accomplish these goals, the beef industry needs to select cattle that are more efficient at utilizing feed resources. Numerous feed efficiency traits have been evaluated, but some of these traits are related to growth rate, such that gain and mature size would be increased if used in selection programs. Therefore, it is important to evaluate each feed efficiency trait in order to determine the most appropriate trait to use in selection programs. Along with selecting more efficient animals, there is a need to understand sources of biological variation associated with feed efficiency. Moreover, it is important to determine if feed efficiency traits are related to changes in reproductive performance or carcass quality traits. This review describes several feed efficiency traits and sources of the biological variation associated with differences in feed efficiency.

This dissertation follows the style of Journal of Animal Science.

Measures of feed efficiency

Feed conversion ratio. Traditionally feed efficiency has been measured as feed:gain or feed conversion ratio (FCR; Table 1.1). Feed conversion ratio is a gross measure of feed efficiency that does not attempt to partition feed intake into growth and maintenance components (Arthur et al., 1996; Hennessy and Arthur, 2004). Feed requirements for maintenance are estimated to account for 60-65% of the total feed cost associated with the cow herd (Montano-Bermudez and Nielsen, 1990), thus Arthur et al. (1996) proposed that feed efficiency traits should attempt to account for variation in maintenance energy requirements. Additionally, FCR has been shown to be negatively correlated genetically with growth and mature size (Koots et al., 1994), thus selection pressure applied against FCR will likely increase ADG and mature size. Consequently, selection based on FCR will not necessarily improve feed efficiency of integrated beef operations.

Residual gain efficiency. Residual gain efficiency was first proposed by Koch et al. (1963) as an alternative feed efficiency trait. Residual gain efficiency (RGE) was calculated as the difference between actual ADG and expected ADG, with expected ADG derived using linear regression model of actual ADG on DMI and mid-test $BW^{.75}$. A positive RGE indicates animals were more efficient as they gain more than expected for a given DMI and liveweight. In growing bulls, Fox (2004) reported that RGE was strongly correlated with ADG (r = 0.75), but was not correlated with DMI.

Partial efficiency of growth. Partial efficiency of growth (PEG) is defined as the ratio of ADG to DMI expected for growth. Expected DMI available for growth is

Table 1.1. Feed efficiency traits

Feed Efficiency Trait	Calculation	Favorable Phenotype
Feed conversion ratio (FCR)	Ratio of DMI to ADG	Low
Residual gain efficiency (RGE)	Difference between actual ADG and expected ADG based on DMI and BW	High
Partial efficiency of growth (PEG)	Ratio of ADG to DMI used for growth	High
Residual feed intake (RFI)	Difference between actual DMI and expected DMI based on ADG and BW	Low

computed as actual DMI minus expected DMI for maintenance. Dry matter intake for maintenance can be calculated as 0.077×mid-test $BW^{.75} \div NE_m$ concentration of the diet (NRC, 1996). However, using PEG has challenges associated with establishing maintenance requirements for the growing animal (Archer et al., 1999).

Partial efficiency of growth appears to have merit as an alternative feed efficiency trait to FCR. In growing bulls and steers, Lancaster et al. (2005b) and Nkrumah et al. (2004) found that ADG was less strongly correlated to PEG (r = 0.24 to 0.29) than FCR (r = -0.67 to -0.63). The correlations between DMI and PEG (r = -0.51 to -0.52) were stronger than between DMI and FCR (r = 0.13 to 0.49). These results suggest that PEG is less reflective of changes in growth rate compared to FCR, and selection for improved PEG would result in greater reductions in DMI compared to selection for FCR.

Residual feed intake. Residual feed intake (RFI) is an alternative measure of feed efficiency that has gained considerable attention in recent years. Koch et al. (1963) first proposed the use of RFI as an attempt to partition feed intake into growth and maintenance components. Residual feed intake is computed as the difference between actual feed intake and expected feed intake. Cattle that deviate from the expected intake determined by the residual portion can be identified as more or less efficient. Cattle with a numerically lower residual (negative RFI value) would consume less feed than expected for their body size and level of production, and be more efficient. Cattle with a numerically higher residual (positive RFI value) would consume more feed than expected for their body size and level of production, and be less efficient. Two methods have been used to compute expected feed intake in determining RFI. The first method uses feeding standards (e.g., NRC, 2000) to predict expected feed intake based on the animal's BW, ADG, and concentration of energy of the diet. The second method uses multiple linear regression of DMI on ADG and mid-test $BW^{.75}$ within a contemporary group of cattle (Arthur et al., 1996). Liu et al. (2000) used the beef NRC (2000) to estimate expected feed intake in calculating RFI in growing bulls, and found that RFI was strongly correlated with ADG (r = -0.55) and moderately correlated with BW (r = -0.26) (Table 1.2). In contrast, RFI computed using linear regression to estimate expected feed intake was not correlated with BW or ADG in the growing bulls. Likewise, when feeding standards were used to compute RFI in growing bulls, Arthur et al. (2001b) found that RFI was phenotypically correlated with ADG (r_p = -0.38) and BW (r_p = -0.35), whereas RFI computed from linear regression was independent of BW and ADG. Hennessy and Arthur (2004) used feeding standards to compute RFI and observed positive correlations between RFI and ADG (r = 0.67) and BW (r = 0.39). The positive correlations observed is in contrast to the findings of Arthur et al. (2001b) and Liu et al. (2000). These results suggest that the use of feeding standards to estimate expected feed intake in computing RFI will result in inconsistent correlations between RFI and its component traits (e.g. ADG, BW).

Although, RFI is phenotypically independent of the component traits when multiple linear regression is used to compute expected DMI, RFI may not always be genetically independent of ADG. Arthur et al. (2001b) observed a weak genetic correlation (r_g = -0.10) between RFI computed using linear regression and ADG.

Table 1.2. Phenotypic correlations[a] between residual feed intake and performance and efficiency traits

Trait[b]	Hennessy and Arthur, 2004	Arthur et al., 2001	Liu et al., 2000
		RFI_{equ}	
BW	**0.39**	**-0.35**	**-0.26**
ADG	**0.67**	**-0.38**	**-0.55**
DMI	**0.88**	**0.49**	0.00
		RFI_{reg}	
BW	0.03	0.03	0.00
ADG	0.01	0.01	0.00
DMI	**0.46**	**0.60**	**0.48**

[a]Correlations in bold are different from zero at $P < 0.05$.
[b]BW = body weight; ADG = average daily gain; DMI = dry matter intake; RFI_{equ} = residual feed intake calculated from feeding standards; RFI_{reg} = residual feed intake calculated from linear regression.

Herd and Bishop (2000) reported RFI was independent of ADG (r_g = 0.09), although genetic correlations between RFI and MBW were moderately correlated (r_g = 0.22), but not different from zero.

Feed efficiency traits in various production phases

Cattle are fed and developed on various types of diets, including high-roughage and high-grain diets. For instance, a bull might be developed on a roughage diet and produce offspring that are fed in a feedyard on a high-grain diet. It would be beneficial to know if a bull developed on one-type of diet is efficient when fed another type of diet and how well his offspring would perform on varying diets. However, few studies have examined the influence of diet and(or) stage of production on feed efficiency traits. Crews et al. (2003) examined the relationship between RFI in steers measured at two stages of production. They observed a positive genetic correlation (r = 0.55) between RFI measured in growing steers fed a high-roughage diet and the same steers fed a high-grain diet, indicating that these two measures of RFI tended to be biologically similar. Arthur et al. (2001c) found that the genetic correlation between feed efficiency traits measured in bulls fed the same diet at 15 and 18 months of age was much higher for RFI (r_g = 0.75) than for FCR (r_g = 0.42). Similarly, Archer et al. (2002) measured RFI and FCR in the same females when measured as heifers and later as mature cows. The genetic correlation between the growing and mature females RFI (r_g = 0.98) was higher than that observed for FCR (r_g = 0.20), suggesting that RFI may be the more appropriate trait to assess feed efficiency across various production phases. However, correlations between different stages of production for PEG and RGE have not been reported to date.

Sources of biological variation in residual feed intake

Genetic variation in RFI provides opportunities to select for more efficient cattle (low RFI) that consume significantly less feed with little effects on growth rate or mature body size. The sources of the biological variation in RFI remain largely unknown. Herd et al. (2004) estimated that individual animal differences in digestibility, heat increment, body composition, and physical activity accounted for 14, 9, 5, and 5% of the variation in RFI in growing cattle (Figure 1.1). However, 67% of the variation in RFI was not associated with known sources of variation in RFI.

Body composition. Differences in body composition may account for ~5% of the variation in RFI (Richardson and Herd, 2004). In bulls and heifers divergently selected for RFI, backfat was correlated both genetically ($r_g = 0.17$) and phenotypically ($r_p = 0.14$) with RFI (Arthur et al., 2001a), suggesting that low RFI cattle are leaner. Positive phenotypic correlations between ultrasound estimates of carcass backfat thickness and RFI were also observed in growing steers (Carstens et al., 2002). Growing cattle with low RFI have been reported to have less carcass backfat and rump fat, and more whole-body protein compared to high RFI cattle (Basarab et al., 2003; McDonagh et al., 2001; Richardson et al., 2001b). Differences were not observed in Longissimus muscle area, intramuscular fat, marbling, shear force or dressing percentage between

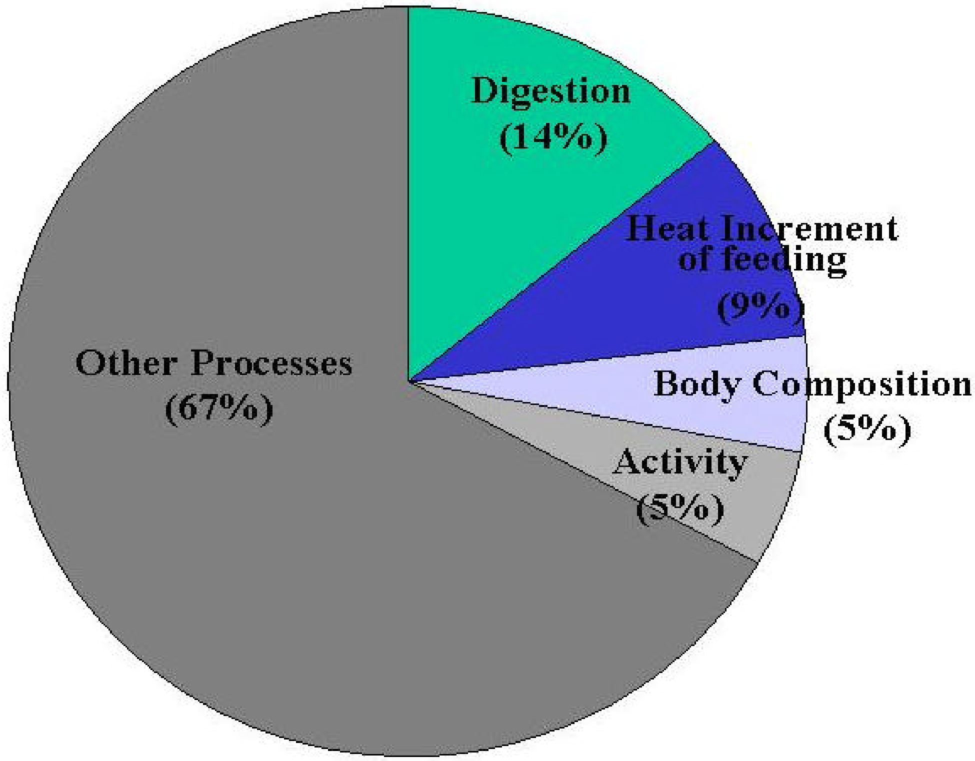

Figure 1.1 Estimates of the percentage contribution of different mechanisms to variation in residual feed intake (adopted from Herd et al. 2004).

divergently selected high and low RFI steers (McDonagh et al., 2001). However, there was a 13% increase in calpastatin in the divergently selected low RFI steers compared to high RFI steers. Calpastatin is an inhibitor of calpain activity and has been previously linked with toughness following 14 d of post mortem aging (Whipple et al., 1990). These results suggest that continuous selection of low RFI cattle may result in indirect selection for cattle that produce less tender beef. Richardson et al. (2001b) did not observe differences in carcass weight or dressing percentage between high and low divergently selected RFI steers. These results indicate that low RFI cattle tended to be leaner, but LMA and marbling are not adversely affected, compared to high RFI cattle.

Metabolizability. An increase in metabolizable energy can result from increases in digestibility, or reductions in urinary and gaseous (e.g., methane) energy losses. Methane emissions account for about 6-10% of gross energy losses in beef cattle (Johnson and Johnson, 1995). Redirecting feed fermentation products to decrease methane emission would improve efficiency of feed utilization, allowing for lower feed intake and less fecal waste produced. Herd et al. (2002) estimated that cattle divergently selected for low RFI after two generations would produce 15% less methane than cattle divergently selected for high RFI. Reductions in methane could be a consequence of lower DMI and(or) lower rates of methane production per unit of DMI. Recently, Nkrumah et al. (2005b) reported that low RFI steers produced 28% less methane compared to high RFI steers.

Herd et al. (2004) estimated that variation in digestion accounted for about 14% of the biological variation associated with RFI. Nkrumah et al. (2005b) reported that RFI tended (*P* < 0.10) to be correlated with apparent digestibility of DM (r = -0.33) and CP (r = -0.34), indicating that steers with low RFI had higher DM and CP digestibility compared to steers with high RFI. In contrast, FCR was not correlated with apparent digestibility of DM or CP. In growing cattle divergently selected for low and high RFI after one generation, digestibility estimates were examined on roughage- and grain-based diets (Richardson et al., 2001a). When fed the roughage-based diets, low RFI bulls and heifers tended (*P* < 0.10) to have higher digestibility compared to the high RFI bulls and heifers (68.1 vs 67.1%). Likewise, low RFI steers had higher digestibility than high RFI steers when a grain-based diet was fed (79.5% vs 77.3%).

Channon et al. (2004) hypothesized that differences in RFI could be attributed to differences in site of starch digestion. Barajas and Zinn (1998) reported that greater ruminal starch digestion was associated with higher fecal pH and lower fecal starch content in growing steers fed a corn diet. These results indicate that cattle with higher fecal pH would have more starch digestion occurring in the rumen and possibly the small intestine. Orskov (1986) reported that increasing amounts of starch to the large intestine would result in lower fecal pH and lower fecal DM.

Channon et al. (2004) observed negative correlations between fecal dry matter and RFI in Angus, Shorthorn, and Hereford crossbred steers fed a 75% rolled barley diet, indicating that more efficient cattle would have higher fecal dry matter contents. The higher fecal dry matter content is an indicator of reduced hindgut fermentation and more efficient starch digestion in the rumen and small intestine. They also observed negative correlations between fecal dry matter and DMI, indicating more efficient starch digestion by cattle with lower DMI. Additionally, fecal pH can be a reflection of the site of starch digestion. The lower fecal pH reflected the higher concentration of acid resulting from more hindgut fermentation. Fecal nitrogen content was not correlated with RFI, but fecal dry matter was negatively correlated with fecal nitrogen content. Increased fecal nitrogen results from increased starch flow to the lower intestinal tract and microbial protein excreted in fecal material. The higher starch digestion in low RFI cattle could indicate differing rumen bacterial populations or host characteristics compared to high RFI cattle.

Heat production. Recently, Nkrumah et al. (2005b) found that RFI was correlated with heat production measured by respiration calorimetry (r = 0.68) and retained energy (r = -0.67) in growing steers. Basarab et al. (2003) also found that high RFI steers produced 9% more heat, had 12% higher retained energy and a 10% higher metabolizable energy intake compared to low RFI steers. Basarab et al. (2003) reported that a steer with a RFI of -1.5 RFI used 67% of metabolizable energy for heat production and 33% of metabolizable energy for retained energy whereas a steer with a RFI of 1.5 used 75% of metabolizable energy for heat production and 25% of metabolizable energy for retained energy (Basarab et al. 2003). This suggests that less efficient cattle partition more energy towards heat production and less towards retained energy compared to efficient cattle. Richardson et al. (2001b) found that residual heat production (energy used for maintenance, activity, and lost as heat increment of feeding) was not different between the high and low RFI steers, but that high RFI steers had 35% higher residual heat production per kg of protein deposited compared to low RFI steers. This implies that low RFI steers are more efficient at depositing energy in protein gain and/or maintaining protein tissue once it has been deposited.

Activity level. Differences in activity level are estimated to contribute ~5% of the biological variation in residual feed intake (Herd et al. 2004). Cattle with low RFI may spend more time being sedentary, thus utilizing less energy for activity. Richardson et al. (2001a) used pedometers to measure the activity level of divergently selected low and high RFI bulls. They reported a significant positive phenotypic correlation (r = 0.32) between RFI and pedometer count, indicating that more efficient cattle spent less time walking or running compared to the less efficient cattle. In the same study, the amount of time spent lying, standing, and walking was recorded. Although, no significant differences were observed between high and low RFI cattle, the more efficient cattle spent numerically more time lying down compared to less efficient cattle. This could also mean more time spent ruminating while the animal was lying down.

Activity level is typically thought of as the time spent walking or moving, but it can also include time spent going to the feed bunk, and time the animal spends eating or grazing. Cammack et al. (2005) reported positive genetic correlations between RFI and amount of time spent feeding and number of feeding visits in growing ram lambs. This would indicate that low RFI lambs spent less time eating and less time going to the feed bunk. It could be assumed that if the lambs were spending less time going to the feed bunk, the lambs would spend less time walking and more time lying down, and ruminating. Likewise, Dehaer et al. (1993) observed that more efficient pigs (low RFI) spent less time eating per day and less time at the feed bunk compared to pigs with high

RFI. Lancaster et al. (2005b) examined feeding duration and frequency, and eating rate in growing bulls. Bulls with low RFI spent twenty min/d less time at the feed bunk and had 5% fewer meals per day compared to bulls with high RFI. In contrast, there were not differences in eating rate between low and high RFI bulls. They did not measure time spent walking or lying down. These studies suggest that cattle with low RFI may use less energy for activity and that differences in energy expanded for activity is an important source of biological variation in RFI.

Physiological indicators

Multiple physiological indicator traits have been examined in an attempt to identify traits that are indicative of RFI that could aid in reducing costs and improve the accuracy of identifying animals with superior genetics for RFI. Some of these physiological indicators have included hormones, metabolites, and temperament traits.

Insulin-like growth factor-I. Examination of endogenous growth promoting hormones could explain differences in feed intake and utilization in low and high RFI cattle. Insulin-like growth factor-I (IGF-I) is a known mitogen for cell proliferation and is secreted primarily from the liver in response to growth hormone. Several studies have found that circulating concentrations of IGF-I are moderately to highly heritable in beef cattle (Davis and Simmen, 2000; Johnston et al., 2001). Three Australian studies determined circulating concentrations of IGF-I to be genetically correlated in a positive manner with FCR and RFI (Johnston et al., 2002; Moore et al., 2005; Moore et al., 2003) in growing cattle fed a high-roughage diet. These results suggests that selection for low serum IGF-I concentrations may produce cattle with low RFI. In support of these studies, positive phenotypic correlations between serum IGF-I concentrations and RFI (r = 0.22; 0.38, respectively) were observed in growing bulls and steers (Brown et al., 2004). The Australian genetic improvement program is currently using serum IGF-I measurements with RFI data to generate estimated breeding values for RFI in Angus bulls. In a simulation study, Wood et al. (2002) found that measuring IGF-I concentrations in all bulls before subjecting them to RFI testing resulted in the highest percentage profit compared to testing all animals or testing only a portion of the cattle. These results suggested that using a two-stage selection scheme based on IGF-I may improve the accuracy of RFI and decrease the number of animals required to be tested.

Leptin. Measuring variation in concentrations of hormones that regulate feed intake may explain variation in RFI in cattle. Leptin, a hormone produced by adipocytes, has been associated with reductions in feed intake and increases in energy expenditure (Houseknecht et al., 1998). Richardson et al. (2004) found positive phenotypic correlations between serum leptin concentrations and RFI in steers divergently selected for high and low RFI fed a grain-based diet. In contrast, serum leptin concentrations were not correlated with RFI, DMI, FCR or ADG in growing bulls and steers (Brown et al., 2004). Nkrumah et al. (2005a) reported that single nucleotide polymorphisms in the promoter region of the bovine leptin gene were associated with serum leptin, ADG, and DMI, but not RFI or FCR. These results suggest that serum leptin is not a potential indicator trait for RFI in growing cattle, although additional research is warranted to determine if serum leptin is an indicator trait for RFI in finishing cattle.

Insulin. Insulin is an anabolic hormone, which promotes glucose uptake and is secreted by the pancreas. Differences in glucose uptake, and degradation of protein or lipid could result in differences in feed efficiency. Divergently selected high RFI birds had lower serum insulin concentrations in both the fasted and fed state compared to low RFI birds (Gabarrou et al., 2000). The lower insulin concentrations in the high RFI birds could result in lower uptake of glucose and greater lipid and protein degradation. Differences in protein turnover could explain some of the variation in RFI in growing animals. Richardson et al. (2004) observed a lower concentration of blood urea nitrogen in low RFI steers compared to high RFI steers that were divergently selected for RFI, suggesting a greater rate of protein degradation in the less efficient steers, as urea is a product of protein degradation. Divergently selected high RFI steers tended to have higher insulin concentrations than low RFI steers at the end of a feedlot test when the cattle were fed a high-grain diet (Richardson et al., 2004). Richardson et al. (2004) suggested that the differences in insulin concentrations could be attributed to increased fat deposition, as insulin can reduce lipolysis and stimulate lipogenesis in adipose tissue. However, if low RFI steers are more efficient due to reduced protein turnover, then the higher insulin concentrations in the divergently selected high RFI steers does not fit the hypothesis of lower protein degradation in low RFI cattle. An increase in leanness in ruminants has resulted in an increased insulin sensitivity of muscles and higher glycolytic energy metabolism (McCann and Reimers, 1986; McCann et al., 1986). High RFI steers may have a reduced insulin sensitivity of muscle, therefore reducing the effect of insulin on muscle protein degradation. A reduction in insulin sensitivity induces an increase in basal plasma insulin concentrations, which accompanies an increase in carcass fatness (Trenkle and Topel, 1978). These results indicate that insulin may be an indicator trait for RFI when cattle are depositing a higher proportion of fat.

Cortisol. It has been suggested that factors regulating growth are inversely related to the animal's ability to tolerate stress. Cortisol is released from the adrenal gland in response to stress via corticotropin-releasing hormone and vasopression release from the hypothalamus and adrenocorticotropic hormone from the pituitary gland. In growing calves, serum cortisol concentrations were negatively correlated with growth rates (Nikolic et al., 1996), suggesting that higher concentrations of cortisol suppress feed intake and growth. Since low RFI (more efficient) cattle consume substantially less feed that high RFI cattle, cortisol may be a potential indicator trait for RFI. Richardson et al. (2004) found that steers selected for high RFI tended to have higher serum cortisol concentrations than steers selected for low RFI. Theis et al. (2002) found that serum cortisol was negatively correlated with DMI and ADG in growing steers. However, serum cortisol was not significantly correlated with RFI in this study.

Temperament. Exit velocity (EV) has been proposed as an objective measure of temperament (Burrow et al., 1988). Curley et al. (2004) reported positive correlations between EV and serum cortisol concentrations in cows. Initial and final EV were negatively correlated with BW, ADG, and DMI in Bonsmara bulls, but EV was not correlated with FCR, RGE, or RFI (Fox, 2004). In the same study, initial chute score was not correlated to performance or efficiency traits. Likewise, growing cattle with faster exit velocities consumed significantly less feed and gained slower than calves with slower exit velocity (Lancaster et al., 2005a). First generation divergently selected high and low RFI cattle did not differ in EV when measured over a two week period on four different days (Richardson et al., 2001a). Additionally, Voisnet et al. (1997) observed that cattle with more excitable temperaments grew slower and produced less tender beef.

Glucose. The use of serum glucose concentrations as an indicator trait for RFI has not been examined extensively. Divergently selected high RFI birds had lower serum glucose concentrations compared to low RFI birds in the fasted state (Gabarrou et al., 2000). Glucose measured at weaning was not correlated with ADG, DMI, FCR, or RFI during the test period in divergently selected steers fed a feedlot ration (Richardson et al., 2004). However, glucose measured at the start of the test period was correlated with ADG ($r = 0.57$), FCR ($r = -0.46$), and RFI ($r = 0.40$).

Conclusion

Feed costs represent 60% of total costs for beef operations. However, past attempts to improve genetic merit of beef cattle have focused primarily on output traits. Any attempts to improve feed efficiency have been associated with FCR. Although this is an improvement in the right direction, FCR may not be the most appropriate feed efficiency trait due to its strong negative relationship with growth rate and mature size. Other feed efficiency traits need to be evaluated to determine the most appropriate trait based on responses associated with carcass traits and growth patterns. Additionally, understanding sources of biological variation are important so improvements in feed efficiency can be made. A better understanding of the sources of biological variation in RFI may facilitate identification of physiological indicator traits that would allow for more accurate selection of efficient cattle. Based on the review of literature, differences in body composition, heat production, digestibility, and activity level explain approximately 33% of the variation associated with RFI.

Overall objectives

The overall objective of this research was to further characterize RFI in individually fed Santa Gertrudis steers on a growing and a finishing diet.

Specific objectives of this study included:

1. To characterize feed efficiency traits in growing and finishing steers, and
2. To examine phenotypic correlations between feed efficiency traits measured during two production phases.
3. To examine phenotypic correlations between feed efficiency and carcass ultrasound traits in growing and finishing steers, and
4. To examine phenotypic correlations between feed efficiency and carcass composition and quality traits in finishing steers, and
5. To examine phenotypic correlations between feed efficiency traits and digestibility in growing and finishing steers, and
6. To examine phenotypic correlations between potential physiological indicators, and growth and feed efficiency traits in steers.

CHAPTER II

FEED EFFICIENCY IN GROWING STEERS. I. RELATIONSHIPS BETWEEN FEED EFFICIENCY AND CARCASS ULTRASOUND TRAITS

Introduction

Feed inputs represent the largest variable cost in producing beef. However, genetic selection has remained focused on output traits, such as growth and carcass quality that are moderately heritable and relatively easy to measure. Feed efficiency traits are also moderately heritable, but are more difficult and expensive to measure than growth traits. Past attempts to improve genetic merit of feed efficiency have concentrated on feed:gain or feed conversion ratio (FCR). Feed conversion ratio is moderately heritable, but is also negatively correlated with growth and mature size (Koots et al., 1994). Additionally, FCR does not attempt to partition feed intake into growth or maintenance components. Therefore, selection for improved FCR will likely not improve efficiency of integrated beef operations due to increases in mature size and higher maintenance requirements. In an attempt to select cattle for improved feed efficiency, numerous feed efficiency traits have been evaluated, including: FCR, residual feed intake (RFI), partial efficiency of growth (PEG), Kleiber ratio (KR), and relative growth rate (RGR). Numerous studies have examined relationships between RFI and FCR (Arthur et al., 1997; Arthur et al., 1996; Herd et al., 2003), but few have compared RFI with other measures of feed efficiency (Arthur et al., 2001b; Nkrumah et al., 2004).

Nkrumah et al. (2004) concluded that RFI and PEG are the most appropriate feed efficiency traits to use in growing cattle due to strong relationships between DMI and minimal responses in growth rates compared to FCR, KR, or RGR. Residual feed intake was independent of growth rate and has been shown to be moderately heritable (Archer et al., 1999; Arthur et al., 2001a). Partial efficiency of growth was weakly correlated (r = 0.24) with ADG compared to the strong correlations between ADG and FCR (r = -0.63), KR (r = 0.85), and RGR (r = 0.72) (Arthur et al. 2001a). Numerous studies have also evaluated the relationships between carcass composition and RFI and FCR (Arthur et al., 1997; Richardson et al., 2001b), but few have examined relationships between carcass traits and other measures of feed efficiency (Lancaster et al., 2005a; Nkrumah et al., 2004). Nkrumah et al. (2004) examined relationships between feed efficiency and carcass traits and reported that RFI, FCR, and PEG were not correlated with longissimus muscle area, 12th rib fat thickness, or carcass yield grade. Based on performance and carcass results, it appears that RFI and PEG would have the greatest potential to improve feed efficiency, with minimal influence on carcass traits. However, with the limited number of studies available additional research is warranted to examine relationships between various measures of feed efficiency and carcass traits. Therefore, the objectives were to characterize feed efficiency traits in growing steers and examine phenotypic correlations between feed efficiency and carcass ultrasound traits in growing steers.

Material and methods

Experimental animals. Study one used one hundred eighty crossbred steers obtained from the Spade Ranch (Lubbock, TX) that originated from one of three different herds. The steers were Braunvieh-sired progeny from a four-breed rotational breeding program (Angus, Simmental, Hereford, and Braunvieh). Four to six weeks prior to being transported to the McGregor research center (McGregor, TX), steers were weaned at about six mo of age, vaccinated for infectious bovine rhinotracheitis, parainfluenza-3, bovine virus diarrhea, bovine respiratory syncitial virus, *Haemophilus somnus*, *Pasteurella*, and *Clostridia* and treated for parasites. Upon arrival steers received booster vaccinations and were placed in a drylot and fed grass hay and range cubes (20% CP) for one week. Steers were stratified by initial BW (233.7 ± 25.6 kg BW) and herd of origin, and randomly assigned to one of two feeding locations (College Station (test group 1); n = 60 and McGregor (test group 2); n = 120). Within feeding location, steers were randomly allotted by BW into pens (6 steers/pen at College Station; 4 steers/pen at McGregor) equipped with Calan-gate feeders (American Calan, Northwood, NH). Steers were housed in 74.3 m^2 and 42.2 m^2 pens at College Station and McGregor, respectively.

Study two used one hundred twenty sire-identified Santa Gertrudis steers from the King Ranch (Kingsville, TX). At three to five mo of age, steers were vaccinated against infectious bovine rhinotracheitis, parainfluenza-3, bovine virus diarrhea, bovine respiratory syncitial virus, *Haemophilus somnus*, *Pasteurella*, and *Clostridia*. At six to eight mo of age, steers were weaned (weaning weight: 239.0 ± 35.8 kg), and administered booster vaccinations. Steers were backgrounded for two mo on rye grass before being shipped to the King Ranch feedyard and fed for 20 d (diet as-fed: 40% milo, 11% whole cottonseed, 5% cottonseed meal, 6% pressed brewers grain, 19.5% cotton burrs, 9.5% molasses, 4% alfalfa pellets, and 5% premix; 15% CP, 2.6 Mcal/kg ME). At 9 to 11 mo of age, steers (289.8 ± 33.6 kg BW) were transported to the research center at College Station, TX. Upon arrival, steers were randomly allotted by BW and sire progeny group to one of twenty pens equipped with Calan-gate feeders.

Feeding management. In both studies, steers were adapted to the experimental diets and trained to eat from Calan gates for 28-d. In study one, a roughage-based pelleted diet (Table 2.1) was fed to group one and two steers to minimize variation due to feeding location. In study two, steers were fed a diet consisting of chopped alfalfa, alfalfa pellets, cottonseed hulls, dry rolled corn, molasses, and premix (Table 2.1). The experimental diets were formulated to meet or exceed the requirements for growing steers. At the end of the adaptation period, steers were individually fed for 77 d. Steers in study one were approximately seven mo of age and weighed 247.9 ± 26.1 kg, while steers in study two were ten to twelve mo of age and weighed 296.6 ± 33.6 kg at the start of the 77-d feeding period. The diets were fed once (study one) and twice daily (study two) in amounts sufficient to allow ad libitum intake. Feed intakes were recorded daily and feed refusals weighed weekly for individual steers. Steers had ad libitum access to fresh drinking water. Anabolic implants were not administered to steers during the studies.

Table 2.1. Ingredient and nutrient composition of experimental diets

Diet	Study 1	Study 2
Ingredients (As-fed basis):		
Alfalfa meal	35.0	
Chopped Alfalfa		35.0
Pelleted Alfalfa		19.0
Dry Rolled Corn		15.5
Cottonseed hulls	30.0	21.5
Soybean hulls	13.5	
Wheat midds	10.0	
Rice bran	5.0	
Molasses	5.0	7.0
Premix[ab]	1.5	2.0
Nutrients (Dry matter basis):		
Dry matter, %	88.1	87.1
Crude protein, %	15.6	11.2
Metabolizable energy, Mcal/kg	2.14	2.13
Net energy for maintenance, Mcal/kg	1.28	1.27
Net energy for growth, Mcal/kg	0.71	0.70
Acid detergent fiber, %	34.7	32.0
Neutral detergent fiber, %	50.1	63.6
Calcium, %	1.05	0.98
Phosphorus, %	0.40	0.27

[a]Premix for study 1 contained trace minerals, vitamin E, pellet binder, ammonium chloride, and salt.
[b]Premix for study 2 contained 1.66 g/kg monensin, 0.55 g/kg tylosin, 6.5% CP, 675 mg/kg Cu, 1050 mg/kg Mn, 2850 mg/kg Zn, 15 mg/kg Se, 35 mg/kg I, 7.5 mg/kg Co, 132,300 IU/kg vitamin A, and 3308 IU/kg vitamin E.

In study one, diet samples were collected at 7-d intervals, whereas, in study two feed ingredient samples were collected at 14 d intervals. Composited diet (study one) and feed ingredient (study two) samples were sent to Dairy One Inc., Forage Testing Lab (Ithaca, NY) for chemical analysis (CNCPS option) (Table 2.1). Estimates of TDN were derived from chemical analysis results using equations from Weiss et al. (1992), and estimates of ME, NE_m, and NE_g determined according to NRC (1996).

Growth and ultrasound data. Steers were weighed at 7-d intervals in study one and at 14-d intervals during study two. Ultrasound measurements of 12^{th} rib fat thickness (FT) were obtained on d 0 and FT, longissimus muscle area (LMA) and percentage intramuscular fat (IMF) measured on d 77 and 70 in study one and two respectively. A Scanner 200 real-time ultrasound unit (Pie Medical Equipment Co., Maastrict, The Netherlands) equipped with an 18-cm, 3.5-MHz linear array transducer was used in study one, whereas, an Aloka SSD-500V real-time ultrasound unit (Walpole, MA) equipped with a 17-cm, 3.5-Mz linear array transducer was used in study two.

Animal care and use. All procedures were approved by the University Laboratory Animal Care Committee of Texas A & M University.

Derivation of statistical analyses. In study one, 11 steers were omitted from the study due to respiratory illness that impacted their weekly BW and feed intake patterns. In study two, one steer died and three steers were omitted from the study due to partial castration. As a result, data from 169 steers (College Station; n = 57 and McGregor n = 112) in study one, and 116 steers in study two were used in the final analysis. Growth rates of individual steers were computed from linear regression of BW on day of test using PROC REG of SAS (SAS, Inst., Cary, NC). The regression coefficients were used to derive initial and final BW, and mid-test $BW^{0.75}$ (MBW). Moisture analyses of diet (study one) and feed ingredients (study two) were used to compute average daily DMI from feed intake data.

Residual feed intake (RFI_p) was calculated as the difference between actual DMI and expected DMI from a phenotypic regression model using PROC GLM of SAS of actual DMI on ADG, MBW, test group, test group × MBW, and test group × ADG (Arthur et al., 2001b). To further characterize RFI_p, steers were ranked by RFI_p and separated into low, medium, and high RFI_p groups that were < 0.5 SD, ± 0.5, > 0.5 SD, respectively, from the mean RFI_p. To evaluate the influence of carcass ultrasound traits in the prediction of DMI, stepwise regression analysis was conducted using PROC REG of SAS to determine order in which carcass traits should be included to the base model. Using the order derived from stepwise regression analysis, carcass traits were progressively included in the linear regression model, and changes in the coefficient of determination used to evaluate the relative importance of their inclusion. Based on these results, an additional RFI trait was computed (RFI_c), that included final 12th rib fat thickness. Feed conversion ratio was calculated as the ratio of DMI to ADG. Partial efficiency of growth was computed as the ratio of ADG to the difference in actual DMI and expected DMI for maintenance (Arthur et al., 2001b). Expected DMI for maintenance was calculated as $0.077 \times MBW \div NE_m$ concentration of each diet.

Least squares procedures using PROC MIXED of SAS were used to examine the effects of RFI_p group on performance, feed efficiency, and carcass ultrasound traits with a model that included the random effects of test group, herd of origin within study, and the interaction of test group and RFI_p group. Differences in RFI_p group were determined by F-tests using Type III sums of squares. The PDIFF option of SAS was used to determine differences between RFI_p groups. Partial correlation coefficients among traits were determined using PROC CORR of SAS with the partial correlation option used to adjust for random effects of test group and herd of origin within test.

Results

Summary statistics for performance, feed efficiency, and ultrasound carcass traits are presented in Table 2.2. During the 77-d growing period, overall ADG and DMI were 1.1 and 9.4 kg/d, respectively. Feed conversion ratio averaged 8.74 (SD = 1.57) and ranged from 5.28 to 17.66. Partial efficiency of growth averaged 0.23 (SD = 0.05) ADG per DMI for growth and ranged from 0.11 to 0.43 ADG per DMI for growth. Residual feed intake averaged 0.00 kg/d (SD = 0.84) and ranged from -2.14 to 2.81 kg/d. This resulted in 4.95 kg of feed per d difference between the most and least efficient steers.

Differences in performance and feed efficiency traits are presented in Table 2.3 and partial correlations between performance and feed efficiency traits are presented in Table 2.4. Residual feed intake$_p$ was correlated (P < 0.001) with FCR and PEG, but was not correlated (P > 0.50) with ADG, MBW, initial or final BW. Dry matter intake was strongly correlated (P < 0.001) with ADG, initial and final BW, MBW, PEG, and RFI$_p$, but was not correlated (P > 0.55) with FCR. Feed conversion ratio was correlated (P < 0.05) with ADG, initial and final BW, and PEG, but was not correlated (P > 0.44) with MBW. Partial efficiency of growth was correlated (P < 0.001) with ADG, initial BW, and tended (P < 0.10) to be correlated with MBW, but was not correlated (P > 0.50) with final BW. Steers with low RFI$_p$ did not differ (P > 0.50) in initial or final BW, MBW, or ADG compared to steers with medium or high RFI$_p$. Steers with low RFI$_p$ consumed 10.9 and 18.9% less (P <0.001) feed than steers with medium and high RFI$_p$, respectively. The low RFI$_p$ steers were more efficient (P < 0.01) as measured by RFI, FCR, and PEG compared to both medium and high RFI$_p$ steers. Steers with low RFI and FCR values and high PEG values have the more desirable phenotypes.

Table 2.2. Summary statistics for traits measured during the three experimental tests in growing steers

	Study 1		Study 2
	Test 1	Test 2	Test 3
Number of steers	57	112	116
Initial BW, kg	249.2±26.16	255.5±28.65	291.1±33.79
Final BW, kg	332.8±31.29	330.3±35.35	395.4±39.03
Mid-test metabolic BW, kg^{75}	70.39±5.04	70.72±5.67	80.39±6.19
ADG, kg/d	1.09±0.21	0.97±0.20	1.26±0.21
DMI, kg/d	9.35±1.21	8.76±1.39	10.1±1.30
Residual feed intake, kg/d	0.00±0.69	0.00±0.89	0.00±0.89
Partial efficiency of growth[a]	0.21±0.03	0.21±0.05	0.25±0.05
Feed conversion ratio, kg of DMI/kg of gain	8.87±1.75	9.24±1.64	8.20±1.21
Initial 12th rib fat thickness , cm	0.31±0.07	0.31±0.06	0.25±0.07
Final longissimus muscle area, cm^2	53.49±4.97	52.72±5.07	60.55±6.57
Final 12th rib fat thickness, cm	0.44±0.06	0.38±0.07	0.32±0.16
Final intramuscular fat, %	2.91±0.44	2.83±0.36	1.88±0.72

[a]ADG/DMI for growth.

Table 2.3. Characterization of performance and feed efficiency traits in growing steers with low, medium, and high residual feed intake

Trait	Mean[b]	SD[c]	RFI group[a]			SE	*P*-value
			Low	Medium	High		
Number of steers	285		85	113	87		
Initial BW, kg	272.1	37.84	263.4	268.1	263.8	17.9	0.51
Final BW, kg	357.3	47.93	347.3	352.7	349.3	23.4	0.60
Mid-test metabolic BW, kg^{75}	74.59	7.50	72.93	73.82	73.11	3.65	0.55
ADG, kg/d	1.11	0.24	1.09	1.10	1.11	0.09	0.81
DMI, kg/d	9.41	1.44	8.31[x]	9.33[y]	10.25[z]	0.45	<0.001
Residual feed intake, kg/d	0.00	0.84	-0.94[x]	-0.05[y]	0.94[z]	0.05	<0.001
Partial efficiency of growth[d]	0.23	0.05	0.28[x]	0.22[y]	0.19[z]	0.01	<0.001
Feed conversion ratio, kg of DMI/kg of gain	8.74	1.57	7.87[x]	8.72[y]	9.56[z]	0.31	0.003
Adjusted residual feed intake, kg/d	0.00	0.82	-0.92	-0.02	0.88	0.06	<0.001

[a]Steers with low, medium, and high RFI were <0.05, ±0.05, and >0.05 SD from the mean RFI, respectively.
[b]Overall trait mean.
[c]Overall trait standard deviation.
[d]ADG/DMI for growth.
[xyz]Means with different superscripts in the same row differ ($P < 0.05$).

Table 2.4. Phenotypic correlations[a] between performance traits and measures of efficiency

Trait[b]	ADG	DMI	FCR	PEG	RFI_p	RFI_c
MBW	**0.38**	**0.63**	0.05	-0.11†	-0.03	-0.04
ADG		**0.63**	**-0.71**	**0.29**	-0.02	-0.02
DMI			0.04	**-0.50**	**0.62**	**0.61**
FCR				**-0.76**	**0.52**	**0.50**
PEG					**-0.87**	**-0.86**
RFI_p						**0.98**

[a]Correlations in bold are different from zero at $P < 0.05$.
†Correlations are different from zero at $P < 0.10$.
[b]MBW = mid-test $BW^{.75}$; ADG = average daily gain; DMI = dry matter intake; FCR = feed conversion ratio; PEG = partial efficiency of growth; RFIp = residual feed intake base model; RFI_c = adjusted RFI for back fat.

Correlations between RFI_p and initial FT were not different from zero (Table 2.5). Although initial FT was weakly correlated (*P* < 0.05) with initial and final BW, MBW, DMI, FCR, and PEG. Initial FT and ADG were not correlated (*P* > 0.36). Presented in Table 2.6 are means between low, medium, and high RFI steers for initial and final carcass ultrasound measurements. Steers with low and high RFI did not differ in initial FT (*P* > 0.70).

Correlations between RFI_p and final LMA and IMF were not different from zero. However, a weak correlation (*P* < 0.05) between RFI_p and final FT was observed. Steers with low RFI_p tended (*P* = 0.12) to have 10% less FT compared to steers with high $RFI_{p.}$ Feed conversion ratio and PEG were not correlated with final LMA or IMF. Feed conversion ratio was also not correlated with final FT. Partial efficiency of growth tended (*P* < 0.10) to be correlated with final FT. Average daily gain, initial and final BW, MBW, and DMI were correlated (*P* < 0.05) with final LMA and FT, but were not correlated (*P* > 0.15) with final IMF.

Table 2.5. Phenotypic correlations[a] between carcass ultrasound measurements and performance and efficiency traits in growing steers

Trait[b]	ADG	DMI	FCR	PEG	RFI_p	RFI_c
Initial 12th rib fat thickness	-0.06	**0.12**	**0.18**	**-0.16**	0.09	0.04
Final longissimus muscle area	**0.17**	**0.33**	0.06	-0.06	-0.01	-0.02
Final 12th rib fat thickness	**0.14**	**0.26**	0.02	-0.11†	**0.15**	-0.03
Final intramuscular fat	0.05	0.08	-0.01	-0.05	0.09	0.03

[a]Correlations in bold are different from zero at $P < 0.05$.
†Correlations are different from zero at $P < 0.10$.
[b]ADG = average daily gain; DMI = dry matter intake; FCR = feed conversion ratio or feed:gain; PEG = partial efficiency of growth; RFI_p = residual feed intake base model; RFI_c = adjusted RFI for 12th rib fat thickness.

Table 2.6. Characterization of carcass ultrasound traits in steers with low, medium, and high residual feed intake

	RFI_p group[a]				
Trait	Low	Medium	High	SE	*P*-value
Number of steers	85	113	87		
Initial 12th rib fat thickness, cm	0.29	0.30	0.29	0.022	0.70
Final longissimus muscle area, cm^2	55.24	56.15	55.73	2.52	0.61
Final 12th rib fat thickness, cm	0.37	0.37	0.41	0.04	0.12
Final intramuscular fat, %	2.52	2.49	2.62	0.34	0.40

[a]Low, medium, and high RFI steers were < 0.5 SD, ± 0.5 SD, and > 0.05 SD from the mean, respectively.
[xyz]Within a row, means without a common superscript letter differ ($P < 0.05$).

The significant correlation between final ultrasound FT and RFI_p, suggests that RFI_p should be adjusted for estimates of carcass fatness. Inclusion of final ultrasound FT in an adjusted model used to calculate RFI_p accounted for more of the variation in DMI (R^2 =0.67; RMSE = 0.83) compared to the base model (R^2 = 0.66; RMSE = 0.84) (Table 2.7). Inclusion of final LMA or IMF did not account for additional variation in DMI, so these carcass ultrasound traits were excluded from the linear regression model used to calculate RFI_c. The Spearman rank correlation between RFI_p and RFI_c was 0.97, indicating that RFI_c and RFI_p are highly related. Both RFI traits were similarly correlated with the performance and efficiency traits. As expected, RFI_c was not correlated with final FT, which was used to calculated DMI, and was not correlated with final LMA or IMF.

Discussion

As expected, steers with low RFI_p did not differ in initial and final BW, MBW, or ADG. Residual feed intake has been shown to be independent of growth and body size, unlike FCR (Arthur et al., 1997; Arthur et al., 2001b; Herd et al., 2003). Although, RFI_p was strongly correlated with PEG and FCR, similar to observations by Arthur et al. (2001b) and Nkrumah et al. (2004), the correlation between RFI_p and PEG was stronger than between RFI_p and FCR. Several previous studies have reported stronger correlations between RFI and PEG in growing steers, bulls, and heifers than correlations between RFI and FCR (Arthur et al., 2001b; Hennessy and Arthur, 2004; Nkrumah et al.,

Table 2.7. Amount of variation explained in feed intake models by inclusion of carcass traits

Model	R^2
Base model (BM)[a]	66.07
BM + FFT[b] + FFT × TEST GROUP	67.43
BM + FFT + FIMF[c] + FIMF × TEST GROUP	66.35
BM + FFT + FLMA[d] + FLMA × TEST GROUP	66.10
BM + GFT[e] + GFT × TEST GROUP	66.60

[a]DMI = $ß_0 + ß_1$MBW + $ß_2$ADG + $ß_3$TEST GROUP + $ß_4$MBW × TEST GROUP + $ß_5$ADG × TEST GROUP + error.

[b]Final 12[th] rib fat thickness.

[c]Final intramuscular fat.

[d]Final longissimus muscle area .

[e]Gain in 12[th] rib fat thickness.

2004). Feed conversion ratio was strongly correlated with ADG, and initial and final BW. Schenkel et al. (2004) and Bishop et al. (1991) also reported strong negative correlations between FCR and ADG. This indicates that selection pressure using FCR would likely result in increasing growth rates and mature size. Partial efficiency of growth was weakly correlated with initial BW and ADG and tended to be weakly correlated with MBW. These results suggest that selection programs using PEG would likely have minimal responses on growth rate. The lack of a significant correlation between PEG and final BW indicates that final mature size would likely not be affected.

Both PEG and RFI_p were strongly correlated with DMI such that selection for more favorable phenotypes would result in significant reductions in feed intake. While FCR was not correlated with DMI in the current study, Arthur et al. (2001b) and Nkrumah et al. (2004) reported correlations with FCR and DMI. However, the correlations reported between DMI and RFI and PEG were stronger than FCR in both of the published studies. Arthur et al. (2001b) suggested that in order to capture some of the variation in feed utilization for both growth and maintenance components then both weight and ADG need to be incorporated into feed efficiency traits. For the three feed efficiency traits examined, only RFI_p and PEG attempt to partition feed intake into growth and maintenance components. Selection programs that incorporate RFI_p and PEG would result in similar phenotypes.

Initial FT was not correlated with RFI_p. RFI tended to be positively correlated with initial FT in finishing steers (Herd et al., 2003) and bulls (Basarab et al., 2003). This might indicate that more efficient cattle would be leaner at the start of the feeding period. However, Fox (2004) reported a tendency for a negative correlation between initial FT and RFI in growing Bonsmara bulls. There was also a tendency for the low RFI bulls to have more FT at the start of the study. Conversely, divergently selected low RFI steers had 19% less FT than divergently selected high RFI steers at the start of the study (Richardson et al., 2001b). Differences in FT at the start of the studies could be attributed to differences in age, BW, genetics, or previous plane of nutrition between the various animals in each study. In the current study, PEG and FCR were correlated with initial FT in favorable directions to indicate that more efficient steers were leaner at the start of the study; however, the strength of the correlations was not great. Fox (2004) reported initial FT was not correlated with FCR in growing Bonsmara bulls. Initial FT was correlated with initial and final BW, MBW, and DMI suggesting that lighter cattle with lower DMI had less FT at the start of the study.

Final LMA was not correlated with either of the three feed efficiency traits measured in this study. In Bonsmara bulls, final LMA was not correlated with RFI or FCR (Fox, 2004). Lancaster et al. (2005a) reported no significant correlations between final LMA and RFI, FCR or PEG in growing Brangus heifers. Several previous studies have also reported no correlations between final LMA and RFI and FCR in steers, bulls, and heifers (Arthur et al., 2001a; Basarab et al., 2003; Nkrumah et al., 2004). Divergently selected low and high RFI steers did not differ in final LMA (Richardson et al., 2001b). Final LMA was correlated with ADG, MBW, initial and final BW, and DMI in this study. Arthur et al. (2001a) reported significant genetic and phenotypic correlations between LMA and DMI in Angus bulls and heifers. In hybrid bulls and steers, LMA was phenotypically correlated with ADG, MBW, and DMI (Nkrumah et al., 2004). These results suggest that cattle with faster growth rates, heavier BW, and higher intakes would have larger LMA at the end of the test.

The significant correlation between final FT and RFI_p is similar to reports in other studies (Arthur et al., 2001a; Nkrumah et al., 2004). However, Basarab et al. (2003) did not observe significant correlations between RFI and final ultrasound FT, but did observe a tendency for RFI to be correlated with carcass FT thickness, suggesting that low RFI cattle would be leaner. Nkrumah et al. (2004) observed 16% less ultrasound FT in low RFI steers and bulls compared to high RFI steers and bulls. The same low RFI steers had 24% less carcass FT compared to the high RFI steers at slaughter. Divergently selected low RFI steers showed a tendency to have 9% less chemical fat compared to high RFI steers (Richardson et al., 2001b). Although differences in body composition exist between low and high RFI groups, they explain approximately 5% of the variation in RFI (Richardson et al., 2001a). In the current study, PEG showed a tendency to be correlated with final FT in a direction to indicate more efficient cattle are leaner. Nkrumah et al. (2004) observed a significant negative correlation with PEG and ultrasound FT. In the current study, FCR was not correlated with final FT, which is inconsistent with Nkrumah et al. (2004), who reported a weak correlation between FCR and ultrasound FT. Likewise, Arthur et al. (2001a) did not observed genetic or phenotypic correlations between FCR and FT in Angus bulls and heifers. Average daily gain, MBW, and initial and final BW were also correlated with final FT. Arthur et al. (2001a) and Nkrumah et al. (2004) also reported similar correlations between DMI and

FT. Additionally, Nkrumah et al. (2004) reported significant correlations between FT and ADG and MBW in hybrid cattle. The faster growing cattle that would consume more feed would have more FT at the end of the test.

Intramuscular fat was not correlated with the feed efficiency traits measured in the current study. Nkrumah et al. (2004) reported no significant correlations between IMF and RFI and FCR, but did see a negative correlation between IMF and PEG. In Bonsmara bulls, final IMF was correlated with FCR and tended to be correlated with RFI (Fox, 2004). The correlations with IMF and FCR and RFI in the study by Fox (2004) were in undesirable directions. This is an indication that more efficient cattle might have less IMF, thus ultimately reducing marbling score. Although there was a weak significant correlation between PEG and IMF in finishing cattle in the study by Nkrumah et al., they did not observe significant correlations between PEG and carcass marbling. Basarab et al. (2003) did not observe correlations between RFI and IMF in finishing bulls, but observed a tendency for RFI to be correlated with carcass marbling score in an unfavorable direction. A reduction in FT would be welcome by the beef industry, but a reduction in IMF might not as it is related to quality grade and tenderness. In the current study, final IMF was not correlated with ADG, initial or final BW, MBW, or DMI. In contrast, ultrasound marbling score was correlated with ADG, MBW, and DMI in hybrid steers and bulls (Nkrumah et al., 2004). Caution must be used in selecting more efficient cattle as measured by FCR, PEG, or RFI so that marbling and tenderness are not adversely impacted. McDonagh et al. (2001) reported no change in carcass weight, dressing percentage, or tenderness in first generation divergently-selected high and low RFI steers. However, there was a reduction in subcutaneous fat and an increase in calpastatin concentrations in the longissmus dorsi muscle at slaughter. An increase in calpastatin activity could reduce tenderness of meat. If low RFI cattle have less IMF, then marbling could be reduced as well as reducing tenderness and juiciness of meat. A reduction in feed intake and an improvement in feed utilization would be welcomed by the beef industry, but reductions in tenderness and marbling would not.

The significant correlation between RFI_p and final FT suggested that RFI_p should be adjusted for carcass ultrasound traits. Stepwise regression indicated that the addition of final FT into the base model used to calculate RFI_p would explain additional variation in DMI. Therefore, calculation of a RFI_c value for each steer was made that included final FT. The inclusion of final LMA or IMF did not explain any more of the variation in DMI. Arthur et al. (2003) also observed an increase in the amount of variation explained by the model with the inclusion of FT, but the addition of other carcass traits did not explain any more of the variation. The inclusion of final FT in the model was deemed successful due to the lack of a significant correlation between RFI_c and the ultrasound measurements in the current study. Basarab et al. (2003) also calculated an adjusted RFI, which included gain in FT and gain in marbling score. They observed no correlations between ultrasound carcass traits as well as no correlations between most of the carcass traits collected after slaughter. Likewise, inclusion of FT into the regression model explained more of the variation in growing bulls and was independent of carcass ultrasound measurements (Schenkel et al., 2004). These results indicate that an adjusted RFI model could eliminate undesirable affects on carcass ultrasound and cooler traits.

Conclusion

Results in this study indicate that RFI_p is independent of growth rate and mature size, but highly correlated with DMI. Favorable RFI_p phenotypes have the potential to improve feed efficiency in cattle. Partial efficiency of growth was weakly correlated with growth rate, initial BW, and MBW indicating minimal responses in growth rate and mature size if PEG is used in selection programs. Both PEG and RFI_p were strongly correlated with DMI. Feed conversion ratio has a strong relationship with growth rate and mature size, and in this study not related to DMI. More efficient cattle as measured by PEG and RFI_p also were leaner. Adjusting the linear regression model for final FT may minimize the relationships between RFI and carcass ultrasound traits. The results from this study indicate that RFI and PEG have potential to improve feed efficiency in cattle with minimal responses to composition of growth rate and mature size.

CHAPTER III

FEED EFFICIENCY IN GROWING STEERS. II. PHYSIOLOGICAL INDICATORS OF PERFORMANCE AND FEED EFFICIENCY

Introduction

Residual feed intake (RFI) is an alternative feed efficiency trait that will facilitate selection of more efficient cattle with minimal effects on growth or compositional traits (Nkrumah et al., 2004; Basarab et al., 2003). Although using RFI in selection programs has great potential, wide spread adoption of this technology will be limited due to the difficulty and expense in measuring individual feed intake in cattle. Therefore, the discovery of indicator traits for RFI that are easier and less expensive to measure would be useful in early screening tests to reduce the number of animals that would need to be subjected to a complete RFI protocol.

Several studies have been conducted to determine the biological basis of variation in RFI in cattle (Richardson and Herd, 2004; Richardson et al., 2004; Richardson et al., 2001a; Richardson et al., 2001b). Various metabolic processes have been evaluated, but more than 60% of the variation in RFI remains unexplained.

Moore et al. (2005) reported that serum insulin-like growth factor-I (IGF-I) was genetically correlated (r_g = 0.41) with RFI in cattle. The Australian beef genetic improvement program is currently using serum IGF-I measurements along with RFI data to generate estimated breeding values for RFI in Angus bulls. Differences in body composition, which explains approximately 5% of the variation in RFI (Richardson et al., 2004), suggest that differences in serum leptin concentrations might exist between RFI groups. A positive correlation between serum leptin concentrations and RFI was observed in divergently selected RFI steers fed a high-grain diet (Richardson et al., 2004). In the same study, correlations between RFI and serum insulin concentrations were observed. Differences in energy substrate availability and utilization might account for observed differences in RFI. Divergently selected high RFI steers tended to have higher serum cortisol concentrations compared to divergently selected low RFI steers (Richardson and Herd, 2004). The difference in stress responsiveness could result in differences in energy requirements in low and high RFI cattle. Differences in heat production or heat loss could explain differences between high and low RFI cattle. Recently, Schaefer et al. (2005) observed that cows with low RFI had 9% lower average dorsal temperatures compared to cows with high RFI when measured using thermal imaging. These results suggest differences in efficiency lines could be attributed to thermoregulation. Heat may be lost from an animal due to less hair or feather coverage. Luiting et al. (1994) observed hens with lower RFI had smaller nude body areas compared to high RFI hens, from which they could lose energy. Additionally, the low RFI hens were better feathered compared to the high RFI hens. These factors could have an effect on thermal regulation and serve as a source of biological variation for RFI.

Although, there are numerous studies that have attempted to explain the variation in RFI due to metabolic and physiological responses in cattle fed high-grain diets, few have identified physiological indicator traits for RFI in growing cattle. The discovery of physiological indicator traits that are predictive of RFI would improve the accuracy and reduce the costs of identifying cattle with superior genetic merit for RFI. Therefore, the objectives were to examine relationships between potential physiological indicators and growth and efficiency traits in growing steers.

Material and methods

The experimental animals and design used in this study were described in the Chapter II. Briefly, study one used one hundred-eighty crossbred steers obtained from the Spade Ranch (Lubbock, TX) and study two used one hundred-twenty Santa Gertrudis steers from the King Ranch (Kingsville, TX). Steers were individually fed for 77-d on a high-roughage diet. Individual feed intake and BW were recorded for each steer and used to calculate the performance and feed efficiency traits described in Chapter II.

Blood collection and assays. Blood samples were collected from the jugular vein of each steer on d 0 and 70 for study one and d 0 and 77 for study two. Serum was harvested by centrifugation and aliquots frozen at -20ºC for later analysis. Insulin-like growth factor-I concentrations were determined by radioimmunoassay (RIA) procedures after removal of binding proteins (Strauch et al., 2003). Leptin concentrations in serum were determined at the University of Missouri using a double-antibody RIA (Delavaud et al., 2000). Insulin concentrations in serum were determined at the University of Missouri using a specific, double-antibody, equilibrium RIA as described by Elsasser et al. (1986) with modifications for steers in study two. Serum cortisol concentrations were determined by using a single antibody RIA procedure adapted from Willard et al. (1995).

In study one, d 70 serum cortisol concentrations were only determined for high and low RFI steers. Serum glucose concentrations were determined using an YSI Automatic Analyzer (Yellow Springs Instruments, Co., Yellow Springs, OH). Whole blood was collected to determine hematocrits.

Measurement of temperament. Temperament was assessed in each steer in study two using both a subjective and objective method. Chute score (1 = calm; 5 = continuous vigorous movement/excitement) was assigned to each steer by a single observer while confined, but not restrained in a squeeze chute (Voisinet et al., 1997) on d 0 and 70. Exit velocity was measured as the rate (m/s) at which a steer exited a squeeze chute and transversed a distance of 1.83 m on d 0 and 70 (Burrow et al., 1988).

Estimates of digestibility. In study two, fecal samples were collected for 10 consecutive d starting on d 52 of the study for 57 random steers in study two. Fecal samples were frozen and stored at 20ºC for subsequent analysis. Daily feed refusals during the 10-d fecal collection period were weighted and samples stored at -20°C for subsequent analysis. The feed refusals, fecal samples, and feed ingredient samples were freeze dried and ground in a Wiley mill equipped with a 1-mm screen. Feed refusals and feed samples were composited and analyzed for acid insoluble ash (AIA) by the methods described by Van Keulen and Young (1977).

Hair data. Hair samples were collected from a 4 cm^2 area on the left side of each steer near the last rib in study two. Hair fiber, curvature, and density were determined at the Texas A&M Experiment Station in San Angelo, TX using the methods described in ASTM Test Method D6500 (Annual Book of ASTM Standards, 2001).

Animal care and use. All procedures were approved by the University Laboratory Animal Care Committee of Texas A & M University.

Derivation of statistical analysis. Least squares procedures using PROC MIXED of SAS were used to examine the effects of RFI group on performance, feed efficiency, and physiological indicator traits with a model that included the random effects of test group, herd of origin within study, and the interaction of test group and RFI group. Differences in RFI group were determined by F-tests using Type III sums of squares. The PDIFF option of SAS was used to determine differences between RFI groups. Partial correlation coefficients among traits were determined using PROC CORR of SAS with the partial correlation option used to adjust for random effects of test group and herd of origin within test.

Results

Performance and feed efficiency data have been presented and discussed in chapter II. Briefly, steers in this study had an overall ADG of 1.11 kg/d (SD = 0.24), DMI of 9.41 kg/d (SD = 1.44), FCR of 8.74 kg of DMI/kg of gain (SD = 1.57), and PEG of 0.21 ADG/DMI for growth (SD = 0.06). Residual feed intake averaged 0.00 kg/d (SD = 0.84) and ranged from -2.14 to 2.81 kg/d. This resulted in 4.95 kg of feed per d difference between the most and least efficient steers.

Differences in performance and feed efficiency traits are presented in Table 2.3 and partial correlations between performance and feed efficiency traits are presented in Table 2.4. As expected, steers with low RFI did not differ in initial or final BW, or

MBW compared to steers with medium or high RFI, although the low RFI steers did consume 10.9 and 18.9% less feed than the medium and high RFI steers, respectively. Consequently, steers with low RFI had a 10 and 18% lower FCR compared to medium and high RFI steers, respectively, and ADG was similar for steers with low, medium, and high RFI. Steers with low RFI were also more efficient as measured by PEG compared to medium or high RFI steers.

Partial correlations between performance, feed efficiency traits, and physiological indicator traits are presented in Table 3.1 and 3.2 for the start and end of the test, respectively. Differences in the physiological indicator traits between the RFI groups are presented in Table 3.3 and 3.4 for the start and end of the test, respectively. Serum IGF-I at the start of test was correlated ($P < 0.01$) with RFI, PEG, FCR, and DMI, but not correlated ($P > 0.20$) with ADG. Steers with low RFI tended ($P < 0.10$) to have 15% lower serum IGF-I concentrations at the start of test compared to steers with high RFI at the start of test. Correlations between serum IGF-I at the end of test and RFI, PEG, and FCR were not different from zero. However, serum IGF-I at the end of test was positively correlated ($P < 0.05$) with DMI and ADG. Differences in serum IGF-I at the end of test were not observed between RFI groups.

Correlations between serum insulin at the start of test and performance and feed efficiency traits were not different from zero. However, at the end of test serum insulin tended ($P < 0.10$) to be correlated with PEG and RFI, but not correlated ($P > 0.25$) with FCR, DMI, or ADG. Steers with low RFI tended ($P < 0.10$) to have 11% lower insulin concentrations at the end of test compared to high RFI steers.

Table 3.1. Phenotypic correlations[a] between physiological indicator traits measured at the start of the two studies and performance and efficiency traits in growing steers

Trait[b]	ADG	DMI	FCR	PEG	RFI
IGF-I	0.07	**0.28**	**0.15**	**-0.25**	**0.18**
Insulin	-0.03	-0.01	0.07	0.01	-0.05
Leptin	-0.00	-0.04	-0.04	0.05	-0.03
Cortisol	**-0.23**	**-0.19**	**0.15**	-0.04	-0.06
Glucose	**-0.26**	**-0.24**	0.10†	-0.00	-0.03
Hematocrit[c]	**-0.26**	**-0.12**	**0.22**	-0.10†	-0.03
Exit velocity[c]	**-0.26**	**-0.31**	0.04	0.17†	-0.16
Chute score[c]	**-0.28**	**-0.28**	0.06	0.00	-0.06

[a]Correlations in bold are different from zero at $P < 0.05$.

†Correlations are different from zero at $P < 0.10$.

[b]ADG = average daily gain; DMI = dry matter intake; FCR = feed conversion ratio or feed:gain; PEG = partial efficiency of growth; RFI = residual feed intake.

[c]Study two only

Table 3.2. Phenotypic correlations[a] between physiological indicator traits measured at the end of the two studies and performance and efficiency traits in growing steers

Trait[b]	ADG	DMI	FCR	PEG	RFI
IGF-I	**0.15**	**0.16**	-0.06	0.05	0.04
Insulin	-0.01	0.07	0.10	-0.17†	0.15†
Leptin	**0.17**	0.11†	-0.11†	0.05	-0.05
Cortisol	**-0.23**	-0.14†	0.15†	-0.06	-0.00
Glucose	**-0.28**	**-0.30**	0.10	-0.04	0.03
Hematocrit[c]	**-0.40**	**-0.28**	**0.26**	-0.09	-0.03
Exit velocity[c]	-0.10	**-0.19**	-0.03	0.00	0.01
Chute score[c]	-0.08	-0.18†	-0.01	0.06	-0.09

[a]Correlations in bold are different from zero at $P < 0.05$.
†Correlations are different from zero at $P < 0.10$.
[b]ADG = average daily gain; DMI = dry matter intake; FCR = feed conversion ratio or feed:gain; PEG = partial efficiency of growth; RFI = residual feed intake.
[c]Study two only

Table 3.3. Characterization of physiological indicator traits in steers with low, medium, and high residual feed intake at the start of test

	RFI group[a]				
Trait	Low	Medium	High	SE	*P*-value
Number of steers	85	113	87		
IGF-I, ng/ml	124.4	134.4	146.6	31.5	0.10
Insulin, ng/ml	5.31	4.81	5.14	0.28	0.39
Leptin, ng/ml	4.02	2.80	3.35	1.34	0.58
Cortisol, ng/ml	30.13	28.35	29.16	6.03	0.72
Glucose, mg/dl	94.29	89.82	91.36	4.84	0.39
Hematocrit, %[c]	38.42	38.86	38.46	1.30	0.64
Exit velocity, m/s[c]	3.68	3.73	3.44	0.32	0.66
Chute score[bc]	2.00	2.36	2.05	0.16	0.20

[a]Low, medium, and high RFI steers were < 0.5 SD, ± 0.5 SD, and > 0.05 SD from the mean, respectively.
[b]1 = calm; 5 = continuous vigorous movement/excitement.
[xyz]Within a row, means without a common superscript letter differ ($P < 0.05$).
[c]Study two only.

Table 3.4. Characterization of physiological indicator traits in steers with low, medium, and high residual feed intake at the end of test

	RFI group[a]				
Trait	Low	Medium	High	SE	*P*-value
Number of steers	85	113	87		
IGF-I, ng/ml	194.5	159.1	204.7	41.3	0.24
Insulin, ng/ml	4.72	5.72	5.33	0.44	0.09
Leptin, ng/ml	3.73	3.74	3.50	1.81	0.69
Cortisol, ng/ml	25.46	25.55	25.62	6.32	0.99
Glucose, mg/dl	83.28	85.44	82.45	3.38	0.56
Hematocrit, %[c]	41.59	41.68	41.23	1.45	0.80
Exit velocity, m/s[c]	3.00	3.39	3.09	0.16	0.18
Chute score[bc]	1.40	1.48	1.25	0.12	0.29

[a]Low, medium, and high RFI steers were < 0.5 SD, ± 0.5 SD, and > 0.05 SD from the mean, respectively.
[b]1 = calm; 5 = continuous vigorous movement/excitement.
[xyz]Within a row, means without a common superscript letter differ ($P < 0.05$).
[c]Study two only.

Correlations between serum leptin at the start of test and performance and feed efficiency traits were not different from zero. Correlations between serum leptin at the end of test and PEG and RFI were not different from zero. Serum leptin at the end of test tended ($P < 0.10$) to be correlated with FCR and DMI and correlated ($P < 0.01$) with ADG. RFI groups did not differ for leptin concentrations at the start or end of test.

Serum cortisol concentrations at the start of test were not correlated ($P > 0.30$) with RFI or PEG, but were correlated ($P < 0.05$) with FCR, DMI, and ADG. Similar correlations were observed at the end of test. Serum cortisol concentrations at the end of test were not correlated ($P > 0.40$) with RFI and PEG, but tended ($P < 0.10$) to be correlated with FCR and DMI and correlated ($P < 0.01$) with ADG.

Correlations between serum glucose concentrations at the start of test and RFI and PEG were not different from zero. Feed conversion ratio tended ($P < 0.10$) to be positively correlated with serum glucose concentrations at the start of test. Serum glucose concentrations at the start of test were negatively correlated ($P < 0.001$) with DMI and ADG. End of test serum glucose concentrations were not correlated ($P > 0.11$) with FCR, PEG, or RFI. However, end of test serum glucose concentrations were negatively correlated ($P < 0.001$) with ADG and DMI.

Correlations between hematocrit at the start of test and RFI were not different from zero. However, hematocrit at the start of test tended ($P < 0.10$) to be correlated with PEG and correlated ($P < 0.05$) with FCR, DMI, and ADG. End of test hematocrit was not correlated ($P > 0.15$) with PEG or RFI. Hematocrit at the end of test was correlated ($P < 0.001$) with FCR, DMI, and ADG.

Exit velocity at the start of test was not correlated ($P > 0.10$) with RFI or FCR. Start of test exit velocity tended ($P < 0.10$) to be positively correlated with PEG and negatively correlated ($P < 0.01$) with ADG and DMI. Correlations between end of test exit velocity and RFI, PEG, FCR, and ADG were not different from zero. End of test exit velocity was negatively correlated ($P < 0.05$) with DMI.

Start of test chute score was not correlated ($P > 0.35$) with RFI, PEG, or FCR, but was negatively correlated ($P < 0.01$) with DMI and ADG. Chute score at the end of test was not correlated ($P > 0.35$) with RFI, PEG, FCR, or ADG, but tended ($P < 0.10$) to be negatively correlated with DMI.

Dry matter digestibility measured by acid insoluble ash was correlated ($P < 0.05$) with RFI and PEG (Table 3.5). Dry matter digestibility was not correlated ($P > 0.25$) with FCR, DMI, or ADG. Steers with low RFI tended ($P < 0.13$) to have 6.6% higher dry matter digestibility compared to steers with high RFI (Table 3.6).

Dorsal infrared digital thermal images were not correlated ($P > 0.25$) with performance or feed efficiency traits (Table 3.7). Cornea, eye, forehead, and nose thermal images were also not correlated ($P > 0.25$) with feed efficiency traits (Table 3.8). Eye thermal images were negatively correlated ($P < 0.05$) with ADG and DMI. Forehead thermal images were negatively correlated ($P < 0.05$) with DMI. Nose thermal images tended ($P < 0.10$) to be negatively correlated with ADG and DMI. Measurements of hair density, fiber, and curvature were not correlated with performance or feed efficiency traits (Table 3.8).

Table 3.5. Phenotypic correlations[a] between digestibility and performance and efficiency traits in growing steers[b]

Trait[c]	ADG	DMI	FCR	PEG	RFI
Digestibility[d]	-0.02	-0.16	-0.11	**0.32**	**-0.32**

[a]Correlations in bold are different from zero at $P < 0.05$.
[b]Digestibility measured in 57 random steers in year two.
[c]ADG = average daily gain; DMI = dry matter intake; FCR = feed conversion ratio or feed:gain; PEG = partial efficiency of growth; RFI = residual feed intake.
[d]Digestibilty measured by acid insoluble ash method (Van Keulen and Young, 1977).

Table 3.6. Characterization of digestibility in steers with low, medium, and high residual feed intake

	RFI group[a]				
Trait	Low	Medium	High	SE	*P*-value
Number of steers	18	20	19		
Digestibility[b], %	70.80	66.05	66.42	1.83	0.13

[a]Low, medium, and high RFI steers were < 0.5 SD, ± 0.5 SD, and > 0.05 SD from the mean, respectively.
[b]Digestibilty measured by acid insoluble ash method (Van Keulen and Young, 1977).
[xyz]Within a row, means without a common superscript letter differ ($P < 0.05$).

Table 3.7. Phenotypic correlations[a] between infrared digital thermography and performance and efficiency traits in growing steers at the start of the test

Trait[b]	ADG	DMI	FCR	PEG	RFI
Maximum Dorsal	0.05	0.08	0.03	-0.00	-0.00
Average Dorsal	-0.00	0.00	0.01	0.04	-0.03
Minimum Dorsal	-0.22	-0.02	0.22	-0.16	0.15
Cornea	-0.06	-0.04	0.10	0.04	-0.04
Eye	**-0.30**	**-0.35**	0.03	0.14	-0.20
Forehead	-0.17	**-0.28**	-0.01	-0.05	0.01
Nose	-0.25†	-0.26†	0.12	-0.01	-0.10

[a]Correlations in bold are different from zero at $P < 0.05$.
†Correlations are different from zero at $P < 0.10$.
[b]ADG = average daily gain; DMI = dry matter intake; FCR = feed conversion ratio or feed:gain; PEG = partial efficiency of growth; RFI = residual feed intake.

Table 3.8. Phenotypic correlations[a] between hair measurements and performance and efficiency traits in growing steers at the start of the test

Trait[b]	ADG	DMI	FCR	PEG	RFI
Hair density	-0.09	-0.02	0.06	-0.09	0.05
Hair fiber	-0.01	-0.00	-0.02	0.04	-0.10
Hair curvature	0.02	-0.04	-0.03	-0.01	0.03

[a]Correlations in bold are different from zero at $P < 0.05$.
†Correlations are different from zero at $P < 0.10$.
[b]ADG = average daily gain; DMI = dry matter intake; FCR = feed conversion ratio or feed:gain; PEG = partial efficiency of growth; RFI = residual feed intake.

Discussion

The use of feed efficiency traits is limited due to the necessity of measuring individual feed intake. Measuring individual intake can require additional equipment, labor, and costs. To accurately measure individual feed intake for a particular animal, Archer et al. (1997) determined that feed intake data needed to be collected for a minimum of 35-d. They also determined that individual BW data was needed for a minimum of 70-d at seven or fourteen day intervals. Weighing cattle does not seem to be the limiting factor for using RFI in selection programs. Individual pens or equipment capable of recording individual feed intake data are not as common as a scale. Therefore, identification of more efficient cattle by alternative traits, such as hormones, metabolites, temperament, or fecal indicators could reduce costs associated with testing all animals or may help to more accurately determine which animals should be subjected to feed efficiency testing.

Insulin-like growth factor-I is a potent mitogen for growth and was quantified to determine if differences in RFI were due to differences in serum IGF-I concentrations. Start of test serum IGF-I concentrations were correlated with RFI, PEG, and FCR in favorable directions. The correlations would indicate that more efficient cattle would have lower serum IGF-I concentrations. There was a tendency for steers with low RFI to have 15% lower serum IGF-I concentrations. The correlations observed between start of study IGF-I and RFI are consistent with genetic correlations observed in growing cattle (Johnston et al., 2002; Moore et al., 2005; Moore et al., 2003), although the strength of the genetic correlations in published studies was stronger than the phenotypic correlation observed in the current study. The differences in the strength of the correlation may reflect the age of the animal when the sample was collected. In the study by Moore et al. (2005), more than half of the cattle had IGF-I determined from samples collected at weaning, while the other samples were collected shortly after weaning. In the current study, the Braunvieh steers had blood samples collected closer to weaning than the Santa Gertrudis steers and the correlation between RFI and IGF-I was stronger in the Braunvieh steers. Brown et al. (2004) observed a stronger phenotypic correlation between serum IGF-I at the start of study and RFI ($r = 0.38$) and FCR ($r = 0.36$) in growing bulls than was observed in the current study. Again, the blood samples were collected closer to weaning in the bulls than in the current study. The bulls with low RFI had 25% lower IGF-I concentrations than bulls with high RFI. This might suggest that to more accurately predict RFI, FCR, or PEG using serum IGF-I concentrations the blood samples should be collected earlier in life or at weaning. Data from the Santa Gertrudis steers during the finishing phase also indicates that IGF-I at the start of test is not an indicator of RFI, FCR, or PEG when the cattle are fed a high-grain diet. In all of the studies in which IGF-I was correlated with RFI, the cattle were younger and were fed a roughage-based diet. In the current study, IGF-I at the end of study was not correlated with feed efficiency traits. Similarly, Richardson et al. (1996) did not observe significant differences between serum IGF-I between low and high RFI steers when blood samples were collected at the end of a high-roughage diet feeding period. This would further confirm that serum IGF-I concentrations are indicators of feed efficiency when sampled at a close to weaning.

In order to be an RFI indicator trait, the trait needs to be independent of ADG. Serum IGF-I at the start of test was independent of ADG, but was correlated with DMI. Moore et al. (2003) did not observe phenotypic correlations between ADG and IGF-I concentrations. Similarly, IGF-I at the start of test was not correlated with ADG, but was moderately correlated with DMI in Bonsmara bulls (Brown et al., 2004). Results indicate that serum IGF-I measured close to weaning is an indicator of RFI, PEG, and FCR. Serum IGF-I is independent of ADG, which is similar to relationships between RFI and ADG. Additional research is needed to further evaluate the appropriate time to measure IGF-I to be a more accurate indicator of RFI.

Insulin is an anabolic hormone, which promotes glucose uptake. Differences in glucose uptake, and degradation of protein or lipid could result in differences in efficiency. In the current study, insulin at the start of test was not correlated with performance or feed efficiency traits. In contrast, divergently selected high RFI cockerels had lower serum insulin concentrations in both the fasted and fed state compared to low RFI cockerels (Gabarrou et al., 2000). The lower insulin concentrations in the high RFI cockerels could result in lower uptake of glucose and increasing lipid and protein degradation. An increase in protein turnover in high RFI animals could explain some of the variation between more and less efficient animals. Protein turnover has not been directly measured in an RFI study. However, Richardson et al. (2004) observed a lower concentration of blood urea in low RFI steers compared to high RFI steers that were divergently selected for RFI. This suggests a greater rate of protein degradation in less efficient steers, as urea is a product of protein degradation. In the current study, end of test insulin concentrations tended to be correlated with RFI and PEG. There was a tendency for the high RFI steers to have higher insulin at the end of test than the low RFI steers. Similarly, divergently selected high RFI steers tended to have higher insulin concentrations than low RFI steers at the end of a feedlot test when the cattle were fed a high-grain diet (Richardson et al., 2004). Richardson et al. (2004) suggested that differences in insulin concentrations could be attributed to increased fat deposition as insulin can reduce lipolysis and stimulate lipogenesis in adipose tissue. However, if low RFI steers are more efficient due to reduced protein turnover, then the higher insulin concentrations in the divergently selected high RFI steers does not fit the hypothesis of lower protein degradation in low RFI cattle. An increase in leanness in ruminants resulted in an increased insulin sensitivity of muscles and higher glycolytic energy metabolism (McCann and Reimers, 1986; McCann et al., 1986). In the current study, the high RFI steers may have a reduced insulin sensitivity of muscle, therefore reducing the effect of insulin on muscle protein degradation. A reduction in insulin sensitivity induces an increase in basal insulin plasma concentrations, which accompanies an increase in carcass fatness (Trenkle and Topel, 1978). Insulin concentrations at the end of test were correlated ($r = 0.19$; $P < 0.05$) with final BF in the current study. Numerous studies, including the results presented in the previous chapter, have observed increased carcass fatness in high RFI cattle compared to low RFI cattle (Basarab et al., 2003; McDonagh et al., 2001; Richardson et al., 2001b). These results might indicate that insulin could be an indicator trait for RFI when the cattle have more carcass fatness, but this needs to be further evaluated.

Differences in glucose uptake by tissues could explain differences in efficiency between RFI groups. Glucose concentrations at the start of test were not correlated with RFI or PEG, but tended to be correlated with FCR. In contrast, Richardson et al. (2004) observed correlations with FCR and RFI and glucose at the start of a test in seventeen divergently selected RFI steers fed a feedlot ration. These results indicate divergently selected low RFI steers would have lower glucose concentrations compared to high RFI steers. While divergently selected high RFI cockerels had lower serum glucose concentrations compared to low RFI birds in the fasted state (Gabarrou et al., 2000). In the current study, ADG and DMI were correlated with glucose at the start of test, indicating faster growing cattle with higher intakes would have lower plasma glucose concentrations at the start of test. Conversely, Richardson et al. (2004) observed a positive correlation between ADG and start of test glucose, indicating slower growing cattle would have lower glucose concentrations. Richardson et al. (2004) also observed glucose measured three d after arrival at the test facility and ADG, DMI, FCR, and RFI were not correlated. The steers were adapted to the testing facility for three months before beginning the RFI test period. Therefore, the differences in results could be a reflection of the previous plane of nutrition or stage of maturity before glucose concentrations were measured in the different studies. End of test glucose concentrations were not correlated with feed efficiency traits measured in the current study, but were correlated with ADG and DMI. The lower plasma glucose concentrations in faster growing cattle could be due to greater use by tissue as an energy source. However, limited studies have examined glucose concentrations as an indicator trait between high and low RFI cattle. Differences in energy substrate utilization or availability could explain some of the variation in RFI, although in the current study there were no differences in plasma glucose concentrations between RFI groups.

Serum leptin concentrations at the start of test were not correlated with performance or feed efficiency traits. It might be expected that differences in leptin concentrations do not exist between high and low RFI steers at the start of the study since differences in body fat do not seem to exist or only minimal differences exist. Although, by the end of test, it might be expected that differences in leptin concentrations would exist between high and low RFI steers due to differences in body composition. In the current study, serum leptin concentrations at the end of test were not correlated with RFI or PEG, but showed a tendency to be correlated with FCR. Richardson et al. (2004) reported a moderate positive correlation between RFI and leptin concentrations at the end of the feedlot period in divergently selected steers. This indicates that low RFI (leaner) steers would have lower leptin concentrations at the end of the feeding period. Differences between results of Richardson et al.(2004) and the current study could be related to the stage of maturity and diet on body composition of the steers. In the current study, serum leptin concentrations at the end of the test were correlated with DMI and ADG, indicating that steers with higher leptin concentrations would have higher feed intakes and faster rates of gain. Richardson et al. (2004) did not observe similar correlations between end of test leptin concentrations and ADG and DMI in divergently selected RFI steers. Recent reports have found that steers with single nucleotide polymorphisms in the promoter region of the leptin gene (TT genotype) had greater leptin concentrations, higher DMI, and more backfat compared to the CC genotype steers, but did not differ in RFI or FCR (Nkrumah et al., 2005a). The use of marker-assisted selection has the potential to aid in evaluating performance and feed efficiency traits in cattle.

Serum cortisol concentrations at the start of test were not correlated with RFI or PEG, but were correlated with FCR, DMI, and ADG. It is hypothesized that the high RFI cattle might respond differently to stress compared to low RFI steers. Such observations were not observed in the current study. Additionally, correlations between RFI and hematocrit were not observed, thus indicating that differences in stress response between low and high RFI cattle were not observed. Stress responsiveness involves release of glucocorticoids (cortisol) and can result in changes in hematological profiles. At the end of test, RFI was not correlated with cortisol or hematocrit values. In contrast, Richardson et al. (2004) observed a positive correlation between cortisol and RFI after being housed in a metabolism chamber following a feedlot test period. The increase in cortisol concentrations in the high RFI steers after being handled differently for a shorter time period could indicate a difference in stress responsiveness compared to the low RFI cattle that might not be noticed after a longer period. The relationships between ADG and DMI with cortisol at the start and end of test are not unexpected. Nikolic et al.(1996) and Trenkle and Topel (1978) observed negative correlations between cortisol concentrations and ADG in growing cattle. These results suggest that cattle which are more susceptible to stress would have lower feed intakes and grow slower. Hematocrits at the start and end of test also indicate that the less stress tolerant animals would have slower rates of gain and lower feed intakes.

Previous studies have examined blood cell parameters in cattle selected for and against RFI and have found that there may be differences in blood parameters, which could affect the supply of oxygen to tissue (Richardson et al., 2004; Richardson et al., 2001a). If high RFI cattle are less efficient due to the increased demand of tissues for oxygen, it might be expected that high RFI cattle would have increased blood flow. Blood viscosity is a primary factor affecting blood circulation and viscosity is affected by red cell aggregation and hematocrit (Windberger et al., 2003). Both blood viscosity (Richardson et al., 2004) and hematocrit were lower (Richardson et al., 2002) in divergently selected low RFI steers compared to high RFI steers. However, in the current study no differences were observed between high and low RFI steers. It is possible that differences were observed in the two published studies due to differences in fatness of the animals in those studies compared to the current study. In obese humans, both blood viscosity and hematocrit have been shown to be higher (Brun et al., 2004; Wysocki et al., 1991).

Differences in excitability and behavior might contribute to biological variation in RFI. Excitability or temperament in an animal can be measured by objective and subjective techniques. Exit velocity is an effective objective measure of excitability in cattle, which measures the time it takes an animal to transverse a fixed distance when exiting a confined area (Burrow et al., 1988). Cattle identified as having excitable temperaments based on exit velocity have reduced rates of gain and carcass weights

(Petherick et al., 2002). Exit velocity has been shown to be moderately heritable (Burrow, 2001) and moderately correlated with subjective measures of temperament (Burrow and Dillon, 1997). In the current study, exit velocity and chute score were assessed as indicators of excitability. Start of test exit velocity and chute score were not correlated with RFI or FCR. Likewise, initial exit velocity and chute score were not correlated with RFI or FCR in growing Bonsmara bulls (Fox, 2004). Richardson et al. (2001a) did not observe differences in exit velocity in divergently selected high and low RFI steers when measured at four time points. Chute score at the start of test showed a tendency to be correlated with PEG in the current study. Lancaster et al. (2005a) observed correlations between initial chute score and FCR and PEG in growing Brangus heifers. Both initial exit velocity and chute score were negatively correlated with ADG and DMI, which is consistent with observations by Fox (2004). A weak correlation between DMI and initial exit velocity was observed in growing Brangus heifers (Lancaster et al., 2005a), but no relationships were observed between ADG and initial exit velocity. These results indicate that initial exit velocity and chute score are not indicators of feed efficiency traits, but may be indicators of performance.

End of test exit velocity and chute score were not correlated with feed efficiency traits. Likewise, final exit velocity was not correlated with feed efficiency traits in growing bulls (Fox, 2004) and heifers (Lancaster et al., 2005a) and final chute score was not correlated with RFI, FCR, or PEG in heifers (Lancaster et al., 2005a). End of test exit velocity and chute score showed weak correlations with DMI, but neither were correlated with ADG. A weak correlation between final exit velocity and DMI as reported in growing heifers (Lancaster et al., 2005a). Fox (2004) measured final exit velocity and observed moderate correlations with DMI and ADG in growing bulls. These results indicate that exit velocity is not an indicator of feed efficiency traits, but might be an indicator of performance traits such as ADG and DMI.

Dry matter digestibility was correlated with RFI and PEG in favorable directions to indicate that more efficient steers had higher dry matter digestiblities. Likewise, Richardson et al. (2004) observed a negative correlation between RFI and dry matter digestibility in divergently selected RFI steers fed a feedlot diet, also indicating a higher digestibility in low RFI steers. In the current study, steers with low RFI tended to have 6.6% higher dry matter digestibility compared to high RFI steers. Similarly, divergently selected low RFI steers fed a feedlot diet had a 2.2% higher dry matter digestibility compared to high RFI steers (Richardson et al., 2001a). Divergently selected low RFI bulls and heifers fed a high-roughage diet had a 1.5% higher dry matter digestibility compared to high RFI bulls and heifers (Richardson et al., 2001a). Recently, Nkrumah et al. (2005b) reported negative correlations between RFI and apparent dry matter and crude protein digestibilities in low and high RFI steers, but did not observe correlations between FCR and the digestibility measures. Likewise, in the current study dry matter digestibility was not correlated with FCR, ADG, or DMI. Richardson and Herd (2004) estimated that differences in digestibility account for 10% of the biological variation in RFI.

Differences in digestibility between low and high RFI cattle could be associated with differences in rate of passage due to differences in intake between high and low RFI steers or could be attributed to differences in gastrointestinal tract structure or microbial population. Differences in gastrointestinal structure, fermentation rate, and retention time between British and Zebu cattle were observed by Hungate et al. (1960) with Zebu cattle having higher rates of fermentation compared to British cattle. Digestibility differences between efficiency lines could be a result of diet selection preferences (Hegarty, 2004), as cattle that select diet components with higher digestibilities could be the more efficient animals. Herd et al. (2002) estimated that low RFI cattle would produce 15% less methane compared to high RFI cattle. While Nkrumah et al. (2005b) observed 28% lower methane production in low RFI steers compared to high RFI steers. Lower methane production could result in more feed energy being utilized by the animal, thus improving efficiency. Selection for lower methane production is possible as methane production has been shown to be a heritable trait in humans (Bernalier et al., 1996). This would suggest that gastrointestinal tract traits and characteristics are heritable and would allow selection to improve efficiency in cattle.

Channon et al. (2004) reported differences in site of starch digestion between high and low RFI steers. Fecal dry matter was negatively correlated with RFI in divergently selected RFI cattle indicating a higher percentage of starch digestion occurred in the rumen and small intestine. Fecal dry matter can be used as an indicator of hindgut fermentation with a higher dry matter content to indicate a reduced hindgut fermentation and more efficient digestion in the rumen and small intestine. In the same study, fecal pH was negatively correlated with RFI, also indicating more efficient cattle had higher rumen and small intestine starch digestion. A lower fecal pH would reflect higher acidity as a result of fermentation in the large intestine. Site of digestion could also contribute to differences in efficiency as seen in the study by Channon et al.

Digital thermal images were not correlated with feed efficiency traits in the current study. In contrast, Schaefer et al. (2005) found that cows with low RFI had 9% lower average dorsal temperatures compared to cows with high RFI. These results suggest differences in efficiency lines could be attributed to thermoregulation. Hens with lower RFI had smaller nude body areas, from which they could lose energy, compared to high RFI hens (Luiting et al., 1994). Additionally, the low RFI hens were better feathered compared to the high RFI hens. These factors could have an effect on thermal regulation. However, Gabarrou et al. (1997) observed no differences in low and high RFI selected cockerels for basal heat production. In the current study, hair density, curvature, and fiber were not different between high and low RFI steers, which is in contrast to the study by Luiting et al. (1994) where differences in feathers were observed between RFI lines. The results from the current study suggest that thermoregulation does not differ between high and low RFI steers, although additional research is warranted.

Conclusion

The results from this study indicate that RFI has the potential to allow producers to select for more efficient cattle without increasing mature size of the cowherd that may occur if selection programs used other feed efficiency traits. However, measuring feed intake in cattle is labor intensive and expensive. Therefore, identification of physiological indicators that are predictive of RFI may have potential to be used as screening tests to reduce the number of animals that would have to be measured. Moreover, hormones that are correlated with RFI may have utility as physiological markers of RFI to improve the accuracy of identifying animals with superior genetic merit for RFI. Serum IGF-I concentrations were correlated with RFI, but not ADG in this study suggesting that IGF-I may be predictive of RFI. Measurement of IGF-I may facilitate early detection and (or) more accurate selection of animals that are superior for RFI.

CHAPTER IV

RELATIONSHIPS BETWEEN FEED EFFICIENCY AND CARCASS TRAITS IN FINSHING STEERS

Introduction

A number of studies have demonstrated that genetic variation in RFI exists in growing cattle (Arthur et al., 2001b, Arthur et al., 1996). However, few studies have been conducted to determine if RFI measured in growing calves is comparable with RFI measured in finishing calves. In Charolais-crossbred steers, Crews et al. (2003) found that RFI measured during the growing phase while fed a barley-silage diet was positively correlated genetically (r_g = 0.55) to RFI measured during the subsequent finishing phase while fed a barley-grain diet. Arthur et al. (2001c) evaluated FCR and RFI in bulls immediately postweaning and again in the same bulls at one year of age. The genetic and phenotypic correlations between bulls measured at the two ages were stronger for RFI than FCR. These studies suggest that although RFI measured in growing and finishing steers were favorably associated, the two traits may not be genetically equivalent. Additional studies are needed to examine the relationships between RFI measured on roughage- vs grain-based diets.

Differences in body composition may also contribute to variation in RFI. Positive, but low genetic correlations between RFI and ultrasound estimates of carcass fatness have been reported (Arthur et al., 2001; Herd & Bishop, 2000), suggesting that cattle with lower RFI are leaner. However, Crews et al. (2003) reported a negative genetic correlation between RFI and carcass backfat thickness. Positive phenotypic correlations have been reported between RFI and ultrasound estimates of backfat thickness (Carstens et al., 2002) and empty body fat (Basarab et al., 2003), but the magnitude of these relationships were small. Few studies have examined the relationships between RFI and carcass quality traits. McDonagh et al. (2001) examined carcass quality traits in steers produced from a single generation of divergent selection for low and high RFI. In this study, selection for RFI had no effect on marbling scores, meat or fat color, or LD muscle shear force. However, steers from the low RFI parents had a lower index of myofibril fragmentation in LD muscle and higher levels of calpastatin activity compared to steers from the high RFI parents. These later findings suggest the possibility that long-term selection for low RFI may be associated with a reduction in the rate of postmortem protein degradation, which could potentially have a negative impact on tenderness. Additional studies are needed to examine relationships between RFI and carcass composition and quality.

Materials and methods

Animals and management. The steers used in this study were part of study two discussed in chapter II. Briefly, one hundred twenty sire-identified Santa Gertrudis steers from the King Ranch (Kingsville, TX) were used. Steers were fed a high-roughage diet for 77 d consisting of (as-fed basis) 54% alfalfa, 21.5% cottonseed hulls, and 15.5% dry rolled corn. Analyzed metabolizable energy was 2.1 Mcal/kg and crude protein was 11.2%.

The high-roughage diet was followed by a 28-d transition period to a high-grain diet, which consisted of dry rolled corn, cottonseed meal, chopped alfalfa hay, coastal hay, molasses, and premix (3.0 Mcal/kg ME; 10.1% CP) (Table 4.1). Steers were fed for 80-d on the high-grain diet during the finishing phase. Steers were approximately thirteen to fifteen mo of age and weighed 429.5 ± 42.63 kg. The diet was fed twice per d in sufficient amounts to allow ad libitum intake. Individual feed intake data was recorded daily and feed refusals weighed weekly for each steer. Steers had ad libitum access to fresh drinking water. Anabolic implants were not administered to steers during the study.

During the study, individual feed ingredients were sampled every 14-d and stored frozen. At the end of the study, individual feed ingredients were composited and sent to Dairy One Inc., Forage Testing Lab (Ithaca, NY) for chemical analysis (CNCPS option) (Table 4.1). Estimates of TDN were derived from chemical analyses results using equations from Weiss et al. (1992), and estimates of ME, NE_m, and NE_g determined according to NRC (1996).

Growth, ultrasound, and carcass data. Steers were weighed at 14-d intervals. Ultrasound measurements of 12^{th} rib fat thickness (FT), Longissimus muscle area (LEA), and percentage intramuscular fat (IMF) were obtained 35 d prior to the initiation of the study and on d-70 of the study using an Aloka SSD-500V real-time ultrasound unit (Walpole, MA) equipped with a 17-cm, 3.5-MHz linear array transducer.

Table 4.1. Ingredient and nutrient composition of the finishing diet

Diet	Amount
Ingredients (As-fed basis):	
Chopped alfalfa	5.0
Coastal hay	5.0
Dry rolled corn	76.5
Cottonseed meal	7.5
Molasses	4.0
Premix[a]	2.0
Nutrients (Dry matter basis):	
Dry matter, %	89.1
Crude protein, %	10.2
Metabolizable energy, Mcal/kg	3.0
Net energy for maintenance, Mcal/kg	2.00
Net energy for growth, Mcal/kg	1.37
Acid detergent fiber, %	7.54
Neutral detergent fiber, %	15.9
Calcium, %	0.44
Phosphorus, %	0.39
Ash, %	3.15

[a]Premix contained 1.66 g/kg monensin, 0.55 g/kg tylosin, 8.84% CP, 15.3% Ca, 675 mg/kg Cu, 1050 mg/kg Mn, 2850 mg/kg Zn, 15 mg/kg Se, 34.5 mg/kg I, 7.5 mg/kg Co, 132,300 IU/kg vitamin A, and 3308 IU/kg vitamin E.

Following the 80-d test period, steers were harvested at a common endpoint of 1.0 cm BF determined by ultrasound measurements. Steers were transported to Sam Kane Beef Processors, Inc. (Corpus Christi, TX) to be harvested. After a 48-h chill, carcass characteristics (skeletal and muscle maturity, FT thickness, longissimus muscle area (LEA), kidney, pelvic and heart fat (KPH), and marbling score) were measured to determine yield and quality grades by trained technicians. The 6-12th rib sections were removed from the left carcass, vacuum packaged and transported to Rosenthal Meat Science Center (College Station, TX). Two steaks were obtained from the 12th rib section for one and fourteen d aging periods to determine Warner-Bratzler shear force (WBSF) (AMSA, 1995). The 9-11th rib sections were dissected into separable fat, lean and bone tissue, and analysis of moisture, protein and lipid content of carcass were conducted. Protein was determined using a Leco analyzer and fat content determined by Soxhlet procedures (AOAC, 1990).

Animal care and use. All procedures were approved by the University Laboratory Animal Care Committee of Texas A&M.

Derivation statistical analyses. During the 77-d high-roughage phase, one steer died and three animals' data were removed due partial castration. At the end of the high-grain diet, one steer was omitted due to illness based on examination of weekly BW and feed intake patterns. Growth traits were calculated for each individual steer. Growth rates of individual steers were modeled by linear regression of BW on days on test using PROC REG of SAS (SAS, Inst., Cary, NC). The regression coefficients were used to derive initial and final BW, and mid-test $BW^{0.75}$ (MBW). Moisture analyses of feed ingredients were used to compute average daily DMI from feed intake data.

Residual feed intake (RFI) was calculated as the difference between actual DMI and expected DMI from a phenotypic regression model using PROC GLM of SAS of actual DMI on ADG and MBW (Arthur et al., 2001b). Standard deviations above and below the mean RFI were used to group steers into low (< 0.5 SD), medium (± 0.5), and high (> 0.5 SD) RFI. To evaluate the importance of carcass ultrasound traits in the prediction of DMI, stepwise regression analysis was conducted using PROC REG of SAS to determine the order in which carcass ultrasound traits should be added to the base model. Using the order derived from stepwise regression analysis, carcass traits were progressively included in linear models, and the change in the coefficient of determination used to evaluate the relative importance of their inclusion. Based on these results, an additional RFI trait was computed (RFI_c), where final ultrasound FT was included in the adjusted model to compute expected DMI that also accounted for variation in carcass traits. Residual feed intake adjusted for carcass traits (RFI_c) for each steer was calculated as the actual DMI minus expected DMI from the adjusted model. Feed conversion ratio was calculated as the ratio of DMI to ADG. Partial efficiency of growth was computed as the ratio of ADG to the difference in actual DMI and expected DMI for maintenance (Arthur et al., 2001b). Expected DMI for maintenance was calculated as $0.077 \times MBW \div NE_m$ concentration of the diet.

Least squares procedures using PROC MIXED of SAS was used to examine the effects of RFI_p group on performance, efficiency, and carcass data with a model that included the random effects of herd and interaction of herd and RFI group. Differences in RFI_p group were determined by F-tests using Type III sums of squares. The PDIFF option of SAS was used for mean separation and differences between RFI groups. Partial correlation coefficients among traits were determined using PROC CORR of SAS with the partial correlation option used to adjust for random effects of herd.

Results

Steers in this study had an overall ADG of 1.03 kg/d (SD = 0.24), DMI of 9.07 kg/d (SD = 1.70), FCR of 9.13 kg of DMI/kg of gain (SD = 1.96), and PEG of 0.21 ADG/DMI for growth (SD = 0.06) (Table 4.2). Reasons for the unexpected low performance of steers during the finishing phase were not evident, but could be related to time of year. Residual feed $intake_p$ averaged 0.00 kg/d (SD = 1.02) and ranged from an efficient –2.12 to an inefficient 2.40 kg/d. This represents a difference of 4.52 kg of feed per day.

Differences in performance and feed efficiency traits are presented in Table 4.2, and partial correlations between performance and feed efficiency traits are presented in Table 4.3. Finishing steers with low RFI_p did not differ ($P > 0.70$) in initial or final BW, MBW, or ADG compared to steers with medium or high RFI_p. However, steers with low RFI_p consumed 14 and 22% less ($P < 0.001$) feed than steers with medium and high RFI_p, respectivley. The low RFI_p steers were more efficient ($P < 0.001$) as measured by RFI, FCR, and PEG compared to both the medium and high RFI_p steers. Steers with low

Table 4.2. Characterization of performance and feed efficiency traits in finishing steers with low, medium, and high residual feed intake

			RFI group[a]				
Trait	Mean[b]	SD[c]	Low	Medium	High	SE	*P*-value
Number of steers			37	42	36		
Initial BW, kg	431.4	42.7	431.0	431.0	432.1	8.23	0.99
Final BW, kg	513.9	51.2	513.1	515.7	513.0	8.86	0.97
Mid-test metabolic BW, kg^{75}	101.3	7.44	101.2	101.4	101.2	1.37	0.99
ADG, kg/d	1.03	0.24	1.02	1.05	1.01	0.04	0.70
DMI, kg/d	9.07	1.70	7.90[x]	9.16[y]	10.17[z]	0.24	0.0005
Residual feed intake, kg/d	0.00	1.02	-1.14[x]	-0.01[y]	1.18[y]	0.07	<0.0001
Partial efficiency of growth[d]	0.21	0.06	0.27[x]	0.20[y]	0.16[z]	0.01	<0.0001
Feed conversion ratio, kg of DMI/kg of gain	9.13	1.96	8.08[x]	8.90[y]	10.48[z]	0.29	0.001
Residual feed intake adjusted for back fat, kg/d	0.00	0.95	-0.95[x]	-0.05[y]	1.04[z]	0.09	<0.0001

[a]Steers with low, medium, and high RFI were <0.05, ±0.05, and >0.05 SD from the mean RFI, respectively.
[b]Overall trait mean.
[c]Overall trait standard deviation.
[d]ADG/DMI for growth.
[xyz]Means with different superscripts in the same row differ ($P < 0.05$).

Table 4.3. Phenotypic correlations[a] between performance and feed efficiency traits in finishing steers

Trait[b]	ADG	DMI	FCR	PEG	RFI_p	RFI_c
MBW	**0.45**	**0.69**	0.11	**-0.36**	0.02	0.02
ADG		**0.69**	**-0.63**	-0.03	0.01	0.02
DMI			0.07	**-0.65**	**0.60**	**0.57**
FCR				**-0.64**	**0.54**	**0.50**
PEG					**-0.79**	**-0.71**
RFI_p						**0.93**

[a]Correlations in bold are different from zero at $P < 0.05$.
†Correlations are different from zero at $P < 0.10$.
[b]MBW = mid-test $BW^{.75}$; ADG = average daily gain; DMI = dry matter intake; FCR = feed conversion ratio; PEG = partial efficiency of growth; RFIp = residual feed intake base model; RFI_c = adjusted RFI for back fat.

RFI and FCR values and high PEG values have the more desirable phenotypes. Residual feed intake$_p$ was correlated (*P* < 0.001) with FCR and PEG, but was not correlated (*P* > 0.10) with ADG, MBW, initial or final BW. Dry matter intake was strongly correlated (*P* < 0.001) with ADG, initial and final BW, MBW, PEG, and RFI$_p$, but not correlated with FCR. Feed conversion ratio was correlated (*P* < 0.001) with ADG, initial BW, and PEG, but not correlated with MBW or final BW. Partial efficiency of growth was correlated (*P* < 0.001) with initial and final BW, and MBW, but not correlated with ADG.

Correlations between RFI$_p$ and initial ultrasound FT and IMF were not different from zero (Table 4.4). However, weak correlations (*P* < 0.05) between RFI$_p$ and initial ultrasound LEA were observed. Steers with low RFI$_p$ had 8% larger (*P* < 0.05) initial LEA compared to steers with high RFI$_p$ (Table 4.5). Partial efficiency of growth was correlated (*P* < 0.05) with initial ultrasound FT, but not correlated with initial ultrasound LEA or IMF. Correlations between FCR and initial ultrasound measurements were not different from zero. Average daily gain and DMI were not correlated with initial ultrasound LEA or IMF, but DMI tended (*P* < 0.10) to be correlated with FT.

Correlations between RFI$_p$ and final ultrasound LEA and IMF were not different from zero. However, a moderate correlation (*P* < 0.001) between RFI$_p$ and final ultrasound FT was observed. Steers with low RFI$_p$ (*P* < 0.05) had 18 and 22% less FT compared to steers with medium and high RFI$_p$, respectively. Steers with low RFI$_p$ also tended (*P* < 0.10) to have less final IMF compared to medium and high RFI$_p$ steers. Partial

Table 4.4. Phenotypic correlations[a] between carcass ultrasound measurements and performance and efficiency traits in finishing steers

Trait[b]	ADG	DMI	FCR	PEG	RFI_p	RFI_c
Initial longissimus area	0.08	0.14	0.03	-0.03	**-0.22**	**-0.20**
Initial 12th rib fat thickness	-0.01	0.17†	0.09	**-0.19**	0.15	0.04
Final intramuscular fat	0.02	0.07	0.01	-0.11	0.07	0.04
Final longissimus area	**0.33**	**0.44**	-0.01	**-0.21**	0.10	0.11
Final 12th rib fat thickness	**0.38**	**0.62**	0.10	**-0.46**	**0.31**	0.02
Final intramuscular fat	0.09	0.09	-0.08	-0.09	0.07	0.06

[a]Correlations in bold are different from zero at $P < 0.05$.
†Correlations are different from zero at $P < 0.10$.
[b]ADG = average daily gain; DMI = dry matter intake; FCR = feed conversion ratio or feed:gain; PEG = partial efficiency of growth; RFI_p = residual feed intake base model; RFI_c = adjusted RFI for back fat.

Table 4.5. Characterization of carcass ultrasound traits in finishing steers with low, medium, and high residual feed intake

	RFI group[a]				
Trait	Low	Medium	High	SE	*P*-value
Number of steers	37	42	36		
Initial longissimus area, cm^2	63.20^{x}	60.33^{xy}	58.65^{y}	1.29	0.04
Initial 12^{th} rib fat thickness, cm	0.29	0.32	0.36	0.03	0.19
Final intramuscular fat, %	1.71	1.94	1.91	0.14	0.36
Final longissimus area, cm^2	79.31	81.86	79.47	1.73	0.43
Final 12^{th} rib fat thickness, cm	0.76^{x}	0.93^{y}	0.97^{y}	0.05	0.03
Final intramuscular fat, %	2.70	3.16	3.04	0.12	0.06

[a]Low, medium, and high RFI steers were < 0.5 SD, ± 0.5 SD, and > 0.05 SD from the mean, respectively.

[xyz]Within a row, means without a common superscript letter differ ($P < 0.05$).

efficiency of growth was correlated (P < 0.05) with final ultrasound LEA and FT. Correlations between FCR and final ultrasound measurements were not different from zero. Average daily gain and DMI were correlated (P < 0.001) with final ultrasound LEA and FT, but not correlated with IMF.

The significant correlation between final ultrasound FT and RFI_p, suggests that RFI_p should be adjusted for estimates of carcass fatness. Inclusion of final ultrasound FT in an adjusted model used to calculate RFI_c accounted for more of the variation in DMI (R^2 = 0.69; RSME = 0.96) compared to the base model (R^2 = 0.64; RMSE = 1.02) (Table 4.6). Inclusion of final ultrasound LEA or IMF did not account for additional variation in DMI, so these carcass ultrasound traits were excluded from the linear regression model used to calculate RFI_c. The Spearman rank correlation between RFI_p and RFI_c was 0.93, indicating that RFI_p and RFI_c are highly related. Both RFI traits were similarly correlated with the performance and efficiency traits. As expected RFI_c was not correlated with final ultrasound FT, which was used to calculated DMI, and was not correlated with final ultrasound LEA or IMF.

Correlations between RFI_p and carcass cooler traits of hot carcass weight, dressing percentage, LEA, KPH, marbling, and quality grade were not different from zero (Table 4.7). However, correlations (P < 0.01) between RFI_p and carcass FT and yield grade were observed. This resulted in steers with low RFI_p having 23-24% less FT and 14-17% lower yield grades compared to medium and high RFI_p steers (Table 4.8). Although, no significant correlations were observed between RFI_p and marbling, differences between RFI_p groups were observed. Steers with low RFI_p had lower (P <

Table 4.6. Amount of variation explained in feed intake models by inclusion of carcass traits

Model	R^2
Base model (BM)[a]	64.11
BM + final 12th rib fat thickness	68.60
BM + final longissimus area	64.34
BM + final intramuscular fat	64.47

[a]DMI = $ß_0$ + $ß_1$MBW + $ß_2$ADG + error.

Table 4.7. Phenotypic correlations[a] between carcass traits obtained at slaughter, and performance and feed efficiency traits in finishing steers

Trait[b]	ADG	DMI	FCR	PEG	RFI_p	RFI_c
Carcass cooler traits						
Hot carcass weight	**0.56**	**0.72**	-0.03	**-0.34**	0.04	0.04
Dressing percent	**-0.22**	**-0.25**	0.02	-0.01	0.09	0.08
Longissimus area	0.15	0.10	-0.09	0.01	-0.09	-0.02
12th rib fat thickness	**0.34**	**0.55**	0.06	**-0.42**	**0.30**	0.15
KPH	-0.02	-0.06	-0.11	-0.02	0.07	0.04
Marbling score	-0.04	0.11	0.17†	**-0.30**	0.13	0.09
Yield grade	**0.37**	**0.58**	0.04	**-0.42**	**0.28**	0.14
Quality grade	0.01	0.16†	0.17†	**-0.36**	0.13	0.10
Tenderness traits						
Day-1 WBSF	-0.15	**-0.22**	-0.05	**0.23**	0.04	0.09
Day-14 WBSF	-0.04	-0.10	-0.09	0.09	0.07	0.12
9-11th rib composition						
Protein	-0.16†	**-0.27**	-0.02	**0.29**	-0.13	-0.02
Lipid	**0.30**	**0.42**	0.01	**-0.40**	**0.22**	0.08
Ash	**-0.27**	**-0.37**	0.00	**0.32**	-0.17†	-0.03
Dissectible rib composition[c]						
Subcutaneous fat	**0.33**	**0.48**	0.04	**-0.36**	**0.25**	0.12
Seam fat	**0.32**	**0.50**	0.01	**-0.41**	**0.28**	0.15
Channel fat	0.03	0.09	-0.00	-0.14	0.12	0.11
Longissimus dorsi	**-0.38**	**-0.39**	0.15	**0.24**	-0.16†	-0.04
Other lean	-0.14	**-0.32**	-0.09	**0.28**	**-0.19**	-0.13
Bone	**-0.29**	**-0.53**	-0.12	**0.51**	**-0.38**	**-0.23**

[a]Correlations in bold are different from zero at $P < 0.05$.
†Correlations are different from zero at $P < 0.10$.
[b]ADG = average daily gain; DMI = dry matter intake; FCR = feed conversion ratio or feed:gain; PEG = partial efficiency of growth; RFI_p = residual feed intake base model; RFI_c = adjusted RFI for back fat; KPH = kidney, pelvic and heart fat; WBSF = Warner-Bratzler shear force.
[c]Each trait is expressed as a percent of rib weight.

Table 4.8. Characterization of carcass traits obtained at slaughter in finishing steers with low, medium, and high residual feed intake[a]

Trait	Low	Medium	High	SEM	*P*-value
Number of steers/group	37	42	36	--	--
Carcass cooler traits					
Hot carcass weight, kg	317.0	322.8	318.9	5.70	0.75
Dressing Percentage	62.0	62.8	62.5	0.39	0.35
Longissimus area, cm^2	77.4	76.1	76.6	1.21	0.73
12^{th} rib fat thickness, cm	0.96[x]	1.24[y]	1.27[y]	0.08	0.03
KPH[b]	2.02	2.36	2.18	0.12	0.19
Marbling[c]	450.1[x]	502.7[y]	494.7[y]	13.5	0.05
Yield grade	2.68[x]	3.21[y]	3.11[y]	0.12	0.02
Quality grade[d]	414.6	432.6	429.7	5.51	0.09
Tenderness traits					
Day-1 WBSF	2.90	2.70	3.00	0.14	0.21
Day-14 WBSF	2.22	2.14	2.34	0.08	0.26
9-11th rib composition					
Protein, %	15.1	14.2	14.5	0.36	0.20
Lipid, %	31.0[x]	35.5[y]	34.4[y]	1.03	0.03
Ash, %	0.70	0.65	0.66	0.01	0.09
Dissectible rib composition[e]					
Subcutaneous fat, %	9.31	9.67	10.5	0.43	0.21
Seam fat, %	13.1[x]	16.8[y]	15.9[y]	0.59	0.005
Channel fat, %	4.38	4.90	4.75	0.27	0.27
LD, %[f]	21.1	19.8	19.9	0.44	0.08
Other lean, %	32.5	30.9	31.3	0.55	0.14
Bone, %	19.3[x]	17.4[y]	17.1[y]	0.55	0.02

[a]Steers identified as low, medium, and high NFI were < 0.5, ± 0.5, > 0.5 SD from the mean RFI .
[b]Kidney, pelvic, and heart fat.
[c]400 = Small; 500 = Modest.
[d]400 = Choice
[e]Each trait is expressed as a percent of rib weight
[f]Longissmus dorsi muscle.
[xy]Means with unlike superscripts differ (P < 0.05).

0.05) marbling scores compared to steers with medium or high RFI_p. Correlations between RFI_c and carcass cooler traits were not different from zero. Partial efficiency of growth was negatively correlated ($P < 0.01$) with hot carcass weight, FT, marbling, and yield and quality grades, but was not correlated with dressing percentage, LEA, or KPH. Feed conversion ratio tended ($P < 0.10$) to be correlated with marbling and quality grade, but not the other carcass cooler traits. The correlations of RFI_p and PEG with FT and YG were confirmed by chemical analysis of 9-11th rib sections and dissectible rib composition. The fat content of the 9-11th rib sections was correlated ($P < 0.05$) with RFI_p and PEG, but not correlated with FCR. Likewise, subcutaneous and seam fat dissected from the ribs were correlated ($P < 0.01$) with RFI_p and PEG. Steers with low RFI_P had less ($P < 0.05$) 9-11th rib fat and less dissected rib seam fat than steers with medium or high RFI_p. Although carcass LEA was not correlated with performance or efficiency traits, 9-11th rib protein content and LD muscle and other lean from the rib dissection were correlated ($P < 0.01$) with PEG. Dissected LD muscle tended ($P < 0.10$) to be correlated with RFI_p and other lean tissue was correlated ($P < 0.05$) with RFI_p. Correlations of RFI_c with 9-11th rib chemical composition and rib dissection composition were not different from zero. However, correlations ($P < 0.05$) of RFI_p, RFI_c, and PEG with bone tissue were observed, but correlations of FCR and bone tissue were not observed. Steers with low RFI_p had 12% higher ($P < 0.05$) bone as a percent of rib weight compared to steers with medium and high RFI_p.

Average daily gain and DMI were correlated ($P < 0.05$) with hot carcass weight, dressing percentage, FT, and yield grade. Dry matter intake also tended ($P < 0.10$) to be correlated with quality grade. Dry matter intake and ADG correlated with FT and yield grade were confirmed by the correlations of DMI and ADG with 9-11th rib chemical composition, and dissectible rib subcutaneous and seam fat. Rib protein and LD muscle were also correlated with ADG and DMI. Average daily gain and DMI were correlated (P < 0.01) with bone tissue.

Correlations of RFI_p with d 1 and 14 WBSF were not different from zero. Relationships of RFI_c and FCR with d 1 and 14 WBSF were not different from zero. Partial efficiency of growth was positively correlated (P < 0.05) with d 1 WBSF. Dry matter intake was negatively correlated (P < 0.05) with d 1 WBSF.

Correlations between growing and finishing phase performance and feed efficiency traits were examined in these steers. The same steers reported in this study were evaluated for performance and efficiency traits prior to the finishing phase when the steers were fed a high-roughage diet. The results from the growing phase are presented in chapter II in a combined data set. Average daily gain was moderately correlated (P < 0.01) during the two phases (Table 4.9). Dry matter intake was strongly correlated (P < 0.0001) during the two phases. Of the feed efficiency traits measured, RFI_p had the strongest correlation (P < 0.01) between the two phases, followed by PEG and then FCR.

Table 4.9. Phenotypic correlations[a] between performance and efficiency traits measured at two stages of production

Trait[b]	Current Study	Arthur et al., 2001	Archer et al., 2002
Sex	steers	bulls	heifers/cows
ADG	**0.27**	0.02	**0.28**
DMI	**0.52**	**0.61**	**0.51**
FCR	**0.22**	0.06	0.10
PEG	**0.29**	---	---
RFI	**0.47**	**0.43**	**0.40**

[a]Correlations in bold are different from zero at $P < 0.05$.
[b]ADG = average daily gain; DMI = dry matter intake; FCR = feed conversion ratio or feed:gain; PEG = partial efficiency of growth; RFI = residual feed intake.

Discussion

As expected, steers with low RFI_p did not differ in initial or final BW, MBW, or ADG. In general, RFI has been shown to be independent of growth and body size, unlike FCR (Arthur et al., 2001b). However, there was a strong correlation between RFI_p and FCR similar to phenotypic correlations reported by Arthur et al. (2001b) and Nkrumah et al. (2004). The correlation between RFI_p and PEG was stronger than the correlation with FCR in the current study as well as previous studies (Arthur et al., 2001b; Nkrumah et al., 2004). Selection for FCR would likely result in increasing growth rates and mature size as FCR is not independent of growth and mature size (Koots et al., 1994). Selection programs using only PEG could result in minimal responses on growth rate. While, selection pressure against DMI would improve feed efficiency as measured by RFI_p and PEG, but would also result in a reduction in growth rate and mature size. Selection programs using for ADG could result in increases in DMI and an improvement in FCR. Ideally, improvements in beef production should attempt to maintain growth rates and mature size, while reducing feed inputs. Such improvements would be economically beneficial to beef producers as well as reduce negative impacts to the environment.

From the three feed efficiency traits examined, both RFI_p and PEG attempt to partition feed intake into growth and maintenance components. Both traits are independent of ADG and correlated with DMI such that more favorable phenotypes would consume significantly less feed. Previous studies have reported that PEG was weakly or not correlated with ADG and MBW in growing cattle, but strongly correlated with DMI (Arthur et al., 2001b; Lancaster et al., 2005b; Nkrumah et al., 2004). The differences in the correlations may reflect differences in how DMI for maintenance was calculated between the various studies. Depending on the method used to calculated RFI it too may not be independent of growth rate and mature size (Arthur et al., 2001b; Liu et al., 2000).

The correlations between RFI_p and initial ultrasound LEA might indicate that the more efficient cattle had larger LEA at the start of the study. This is inconsistent with Basarb et al. (2003), who did not observe significant correlations in steers between initial ultrasound LEA and RFI over a 120-d performance feedlot period. Initial LEA was not correlated with RFI in Bonsmara bulls fed a high-roughage diet (Fox, 2004). The inconsistency may stem from the fact that the initial ultrasound measurements were collected 35-d prior to the start of the high-grain feeding in this study, therefore not accurately reflecting carcass composition of the steers at the start of the study. Correlations between PEG and initial ultrasound FT suggest that the more efficient steers were leaner at the start of the study, but the correlations between FT and RFI_p were not significant enough to suggest the same findings.

Correlations between final LEA and PEG are inconsistent with previous studies in which final LEA and PEG were not correlated in growing steers and bulls (Nkrumah et al., 2004) and in growing heifers (Lancaster et al., 2005a). Correlations observed between ADG and DMI with final ultrasound LEA and FT are similar to reports in steers and bulls (Nkrumah et al., 2004; Schenkel et al., 2004). These results indicate that cattle with faster growth rates and higher intakes would have larger LEA and more FT compared to the slower growing cattle that consume less fed. Final ultrasound FT was correlated in favorable directions with PEG and RFI_p. Likewise, final FT was correlated with RFI and PEG in steers and bulls (Lancaster et al., 2005b; Nkrumah et al., 2004). Steers and bulls with low RFI had 16% less FT compared to steers and bulls with high RFI (Nkrumah et al., 2004). In the current study, steers with low RFI_p had 22% less FT compared to high RFI_p steers. The tendency for low RFI_p steers in this study to have less IMF could lead to a reduction in marbling. Richardson et al. (2001b) reported no differences in IMF between high and low RFI steers at slaughter. However, the low RFI steers had numerically less IMF. In Bonsmara bulls, RFI tended to be correlated with ultrasound final IMF and low RFI bulls had less IMF compared to high RFI bulls (Fox, 2004). Fox suggested that low RFI bulls might have slower rates of lipid accretion compared with high RFI bulls. These findings indicate an unfavorable response associated with RFI.

The significant correlation of FT with RFI_p warranted examination of final ultrasound traits in the linear regression model used to calculate DMI. Arthur et al. (2003) observed an increase in the amount of variation explained by the model with the inclusion of FT, but the addition of other carcass ultrasound traits did not explain any more variation. Calculation of an additional RFI_c value for each steer, including final ultrasound FT, was warranted from the results generated by stepwise regression. Adjusting the base RFI model was deemed successful by the lack of significant correlations between RFI and ultrasound carcass traits. Basarab et al. (2003) also calculated adjusted RFI, which included carcass traits determined after harvest. Adjusted RFI was independent of most carcass ultrasound and cooler traits. As they pointed out, this type of adjustment to the RFI model is not practical, as it requires sacrifice of the animals. Adjustments in the RFI model, including carcass traits determined after harvest, would limit practical use of adjusted RFI in bull development programs. Residual feed intake adjusted for ultrasound traits can also be independent of carcass cooler traits and carcass ultrasound measurements. In the current study, final ultrasound FT was included in the base RFI model, resulting in no correlation between RFI_c and carcass traits determined after harvest. Similarly, Basarab et al. (2003) included gain in ultrasound FT and gain in marbling to the base RFI model and found no significant correlations between adjusted RFI for ultrasound traits and carcass traits determined after harvest.

Hot carcass weight was correlated with PEG and was a result of correlations between PEG and BW measurements. This is evident by results from Nkrumah et al. (2004), in which cold carcass weight was not correlated with PEG in growing steers and bulls, nor was PEG correlated with MBW. Hot carcass weight, dressing percentage, and carcass FT were correlated with ADG and DMI, similar to observations in growing steers and bulls reported by Nkrumah et al. (2004). These results indicate that cattle with faster growth rates and higher intakes will have heavier hot carcass weights and more FT. Partial efficiency of growth and RFI_p showed significant correlations with carcass FT, indicating that more efficient cattle were leaner. Numerous studies have found differences in carcass fatness between low and high RFI cattle (Nkrumah et al., 2004; Richardson et al., 2001b). Results presented from 9-11th rib chemical composition also showed significant correlations with PEG and RFI_p, which confirms the differences in fatness in low and high RFI_p steers. Additionally, correlations were observed with subcutaneous and seam fat dissected from the ribs with RFI_p and PEG. Richardson et al. (2001b) observed no differences in dissected subcutaneous or intramuscular fat between low and high RFI steers, but total dissected fat was increased in high RFI steers.

Feed conversion ratio and PEG were related to marbling score in the current study. However, Nkrumah et al. (2004) did not observe significant relationships, though the direction and magnitude were similar. In the current study, the reduction in marbling score in the low RFI_p steers is an undesirable response that could be associated with RFI. Using adjusted RFI models, like RFI_c, can eliminate the undesirable effects on carcass traits. When steers were grouped into low, medium, and high RFI_c, marbling score and final carcass ultrasound IMF were not different among the groups. Fox (2004) also used an adjusted RFI model that included both change in ultrasound FT and final IMF, which eliminated correlations between RFI adjusted and carcass ultrasound traits. Such adjusted models deserve further investigations.

Carcass yield grade was related to RFI_p and PEG. Steers with low RFI_p also had lower yield grades indicating a more desirable phenotype. Likewise, in steers fed a barley-grain diet PEG, RFI and FCR were correlated with carcass yield grade (Nkrumah et al., 2004). Such correlations with yield grade are likely related to less carcass fatness. Less carcass fatness could be regarded as a favorable improvement for the consumer. Although the reduction in carcass fatness could be beneficial to consumers, changes in other carcass traits, such as tenderness and marbling, would not be desired.

For the breeding sector of the industry, the reduction in carcass fatness must not adversely affect reproduction. Several studies have observed a reduction in fatness, but no adverse affects on scrotal circumference, sperm motility, semen consistency, sperm abnormalities, and overall breeding soundness were observed between bulls differing in RFI (Fox, 2004; Lancaster et al., 2005b; Schenkel et al., 2004).

Correlations between PEG, RFI_p, and RFI_c with bone dissected from the rib tissue were observed. The correlations indicate that more efficient cattle would have a higher bone percentage compared to the less efficient cattle. Richardson et al. (2001b) observed no difference in weight of bones between high and low divergently selected RFI steers. However, steers with low RFI had 4% more bone as a percent of live weight compared to steers with high RFI. Both ADG and DMI were negatively correlated with bone dissected from the rib tissue, indicating that faster growing cattle and cattle with higher DMI also had less bone tissue.

Data from the dissected ribs seems to summarize the traits associated with faster growing cattle and the more efficient cattle. Faster growing cattle with higher intakes will have more fat, less lean, and less bone as a percent of their weight compared to slower growing cattle with lower feed intakes. While more efficient cattle, based on RFI_p or PEG, would have more lean, less fat, and more bone as a percent of their live weight compared to less efficient cattle. Together, it might seem that slower growing cattle are the more efficient cattle, but that is not true. Residual feed intake and PEG are independent of growth and mature size.

Another concern in selecting for improved RFI is the effect on meat tenderness. McDonagh et al. (2001) reported no differences in d-1 or -14 shear force between divergently selected first generation low and high RFI steers. Likewise, d-1 or -14 WBSF were not different between low, medium, or high RFI_p steers in the current study. Partial efficiency of growth was weakly related to d-1 WBSF, indicating that more efficient cattle as measured by PEG might have reduced tenderness. Divergently selected first generation low RFI steers had 13% higher calpastatin in LD muscle tissue compared to divergently selected high RFI steers (McDonagh et al., 2001). Calpastatin is a potent inhibitor of calpain activity and has been previously linked with toughness following 14 d of post mortem aging (Whipple et al., 1990). This could indicate that continuous selection for RFI might increase toughness.

Residual feed intake had the highest correlation between growing and finishing phases feed efficiency traits, suggesting that RFI may be the more appropriate trait to assess feed efficiency across various production phases from the three efficiency traits measured in this study. Crews et al. (2003) observed a positive genetic correlation between RFI measured in steers fed roughage- and grain-based diets. Likewise, Arthur et al. (2001c) observed positive genetic and phenotypic correlations between RFI measured in growing bulls at two different ages fed the same roughage-diet. Phenotypic correlations between FCR measured at two ages were not correlated in these bulls. Stronger correlations were observed for RFI measured at two stages of production in heifers and later as cows than for FCR (Archer et al., 2002; Arthur et al., 1999). Similar to the observations in this study, DMI was strongly correlated at the two ages, but ADG was not correlated. However, in the current study ADG was weakly correlated between the two phases. The results indicate that RFI was moderately correlated between the two phases, and that diet and (or) stage of maturity may influence genetic ranking.

Conclusion

The results presented in this study only attempt to explain 5-10% of the variation associated with RFI (Herd et al., 2004). Other sources of variation including activity level, feeding and temperament behavior, digestion and heat increment of feeding, and other metabolic processes need to be further characterized to gain additional understanding in the variation associated with RFI. Results in this study indicate that RFI_p is independent of growth rate and mature size, but highly related to DMI. Favorable phenotypes of RFI have the potential to improve efficiency in beef cattle. Similar relationships between performance traits and PEG, indicate that PEG might be an alternative feed efficiency trait. More efficient steers as measured by PEG and RFI_p were leaner, with minimal responses to other carcass traits. These results suggest that RFI_p and PEG offer opportunities to improve feed efficiency, while maintaining carcass quality. Additionally, if RFI is adjusted for variation in carcass composition traits, such as back fat, then the potential for unfavorable responses in composition could be minimized. Of the feed efficiency traits examined, RFI_p was the trait most highly related between growing steers fed a high-roughage diet and finishing steers fed a high-grain diet. However, these results indicate that cattle with genetic potential for improved feed utilization on a roughage-based diet may rank differently when feed efficiency is evaluated on a high-grain diet.

CHAPTER V

RELATIONSHIPS BETWEEN FEED EFFICIENCY AND PHYSIOLOGICAL INDICATOR TRAITS IN FINISHING STEERS AND CONCLUSIONS

Introduction

Selection for improved feed efficiency has concentrated on selecting for output traits. Any past attempts to improve genetic merit of feed efficiency has concentrated on feed conversion ratio (FCR). However, FCR is negatively correlated with growth rate and mature size in cattle (Koots et al., 1994). An alternative measure of feed efficiency is needed that is independent of growth rate and mature size. A relatively new feed efficiency trait, residual feed intake (RFI), is independent of body size and growth rate (Archer et al., 1999). To measure RFI, individual feed intake and body weight are needed. However, measuring individual feed intake is expensive and labor intensive. Identification of indicator traits would improve accuracy of selecting more efficient cattle or identify cattle that should be subjected to RFI testing.

Numerous studies have observed positive correlations between RFI and serum IGF-I concentrations in steers and bulls fed a roughage-based diet (Brown et al., 2004; Johnston et al., 2002; Moore et al., 2005). However, the use of serum IGF-I as an indicator trait for RFI in finishing cattle has not been evaluated. Richardson et al. (2004) reported correlations between RFI and physiological indicator traits at the start and end of the feedlot test period in divergently selected RFI steers. Serum glucose was correlated with RFI in divergently selected RFI steers ($r = 0.40$), but was also correlated with ADG ($r = 0.57$), such that lower glucose concentrations would result in more efficient cattle with lower rates of gain (Richardson et al., 2004). However, RFI is independent of ADG and the indicator trait should be independent of growth rate. This indicates that serum glucose would not be an appropriate indicator trait for RFI. At the end of the test, RFI was positively correlated with serum insulin and leptin concentrations. Both serum insulin and leptin concentrations were not correlated with ADG, DMI, or FCR. However, an indicator trait for RFI when cattle are consuming a high-grain diet has not been identified. Therefore, the objectives were to examine the relationships between performance and feed efficiency traits and physiological indicator traits in cattle fed a high-grain diet.

Materials and methods

The experimental animals and design used in this study were described in the Chapter II and IV. Briefly, study two used one hundred-twenty Santa Gertrudis steers from the King Ranch (Kingsville, TX). Steers were individually fed for 77-d on a high-roughage diet. Individual feed intake and body weights were recorded for each steer and used to calculate the performance and feed efficiency traits described in Chapter II. At the end of the high-roughage diet, steers were transition to a high-grain diet over a 28-d period. Steers were then fed a high-grain diet (described in Chapter IV) for 80-d. Individual feed intake and body weights were recorded for each steer and used to calculated performance and feed efficiency traits described in Chapter II.

Blood collection and assays. Blood samples were collected from the jugular vein of each steer 28 d prior to the start of the high-grain diet and d 70 of the test period. Serum was harvested by centrifugation and aliquots frozen at -20ºC for later analysis. Insulin-like growth factor-I concentrations were determined by radioimmunoassay (RIA) procedures after removal of binding proteins (Strauch et al., 2003). Leptin concentrations in serum were determined at the University of Missouri using a double-antibody RIA (Delavaud et al., 2000). Insulin concentrations in serum were determined at the University of Missouri using a specific, double-antibody, equilibrium RIA as described by Elsasser et al. (1986) with modifications. Serum cortisol concentrations were determined by using a single antibody RIA procedure adapted from Willard et al. (1995). Serum glucose concentrations were determined using an YSI Automatic Analyzer (Yellow Springs Instruments, Co., Yellow Springs, OH). Whole blood was collected to determine hematocrits.

Measurement of temperament. Temperament was assessed in each steer using both a subjective and objective method. Chute score (1 = calm; 5 = continuous vigorous movement/excitement) was assigned to each steer by a single observer while confined, but not restrained in a squeeze chute (Voisinet et al., 1997) 35 d prior to the start of the high-grain diet and on d 70 of the test. Exit velocity was measured as the rate (m/s) at which a steer exited a squeeze chute and transversed a distance of 1.83 m 35 d prior to the start to the high-grain diet and on d 70 of the high-grain diet (Burrow et al., 1988).

Fecal sample collections and pH. Fecal samples were collected from all steers by rectal palpation on d 42 and 56. Samples immediately had pH measured and samples were frozen for DM analysis. Four grams of fresh feces were mixed with 4 ml of deionized water and pH was measured with a portable pH meter (Beckman Instruments, Fullerton, CA) (Channon et al., 2004). Fecal dry matter was determined by recording fecal weight before and after being dried in an oven for 100°C for 48 h.

Animal care and use. All procedures were approved by the University Laboratory Animal Care Committee of Texas A&M.

Derivation statistical anlysis. During the 77-d high-roughage phase, one steer died and three animals' data were removed due partial castration, At the end of the high-grain diet, one steer was omitted due to illness based on examination of weekly BW and feed intake patterns. Growth traits were calculated for each individual steer. Growth rates of individual steers were modeled by linear regression of BW on days on test using PROC REG of SAS (SAS, Inst., Cary, NC). The regression coefficients were used to derive initial and final BW, and mid-test $BW^{0.75}$ (MBW). Moisture analyses of feed ingredients were used to compute average daily DMI from feed intake data.

Residual feed intake (RFI) was calculated as the difference between actual DMI and expected DMI from a phenotypic regression model using PROC GLM of SAS of actual DMI on ADG and MBW (Arthur et al., 2001b). Standard deviations above and below the mean RFI were used to group steers into low (< 0.5 SD), medium (± 0.5), and high (> 0.5 SD) RFI. Feed conversion ratio was calculated as the ratio of DMI to ADG. Partial efficiency of growth was computed as the ratio of ADG to the difference in actual DMI and expected DMI for maintenance (Arthur et al., 2001b). Expected DMI for maintenance was calculated as $0.077 \times MBW \div NE_m$ concentration of the diet.

Least squares procedures using PROC MIXED of SAS were used to examine the effects of RFI group on performance, efficiency, and physiological indicator trait data with a model that included the random effects of herd and interaction of herd and RFI group. Differences in RFI group were determined by F-tests using Type III sums of squares. The PDIFF option of SAS was used for mean separation and differences between RFI groups. Partial correlation coefficients among traits were determined using PROC CORR of SAS with the partial correlation option used to adjust for random effects of herd.

Results

Performance and feed efficiency data have been presented and discussed in chapter IV. Briefly, steers in this study had an overall ADG of 1.03 kg/d (SD = 0.24), DMI of 9.07 kg/d (SD = 1.70), FCR 9.13 kg of DMI/kg of gain (SD = 1.96), and PEG of 0.21 ADG/DMI for growth (SD = 0.06) (Table 4.2). Residual feed intake averaged 0.00

kg/d (SD = 1.02) and ranged from an efficient –2.12 to an inefficient 2.40 kg/d. This represents 4.52 kg of feed per d difference between the least and most efficient steers.

Differences in performance and feed efficiency traits are presented in Table 4.2 and partial correlations between performance and feed efficiency traits are presented in Table 4.3. As expected, steers with low RFI did not differ in initial or final BW or MBW. Steers with low RFI consumed 14 and 22% less feed compared to medium or high RFI steers, respectively. This resulted in steers with low RFI having a lower FCR compared to medium or high RFI steers. Steers with low RFI were also more efficient as measured by PEG compared to medium and high RFI steers.

Partial correlations between performance, feed efficiency traits and physiological indicator traits are presented in Table 5.1 and differences in the physiological indicator traits between RFI groups are presented in Table 5.2. Serum IGF-I concentrations at the initiation of the finishing phase and feed efficiency traits were not different from zero. However, IGF-I at the initiation of the finishing phase was positively correlated ($P < 0.05$) with ADG and tended ($P < 0.10$) to be positively correlated with DMI. Serum IGF-I at the end of the phase was negatively correlated ($P < 0.001$) with FCR and ADG and tended ($P < 0.10$) to be negatively correlated with RFI.

Table 5.1. Phenotypic correlations[a] between physiological indicator traits and performance and efficiency traits in finishing steers

Trait[b]	ADG	DMI	FCR	PEG	RFI
Initiation of Phase					
IGF-I	**0.23**	0.18†	-0.13	-0.01	-0.12
Insulin	-0.14	-0.01	0.14	-0.11	0.15†
Leptin	0.06	**0.21**	0.11	**-0.21**	0.08
Cortisol	-0.01	-0.10	-0.08	0.11	-0.06
Glucose	0.13	0.13	-0.04	-0.04	0.11
Hematocrit	-0.13	**-0.20**	-0.04	0.08	-0.11
Exit velocity	0.03	**-0.21**	**-0.24**	**0.19**	-0.11
Chute score	0.00	-0.11	-0.12	0.10	-0.02
End of Phase					
IGF-I	**0.28**	0.04	**-0.33**	0.14	-0.18†
Insulin	**0.21**	**0.36**	0.04	**-0.25**	0.18†
Leptin	**0.49**	**0.56**	-0.09	**-0.37**	**0.25**
Cortisol	0.18†	0.05	-0.13	0.07	-0.02
Glucose	0.16†	0.02	**-0.19**	0.03	0.10
Hematocrit	0.18†	0.09	-0.16†	-0.07	0.07
Exit velocity	**-0.24**	**-0.38**	-0.08	**0.20**	-0.06
Chute score	0.08	0.02	-0.06	0.03	0.05

[a]Correlations in bold are different from zero at $P < 0.05$.
†Correlations are different from zero at $P < 0.10$.
[b]ADG = average daily gain; DMI = dry matter intake; FCR = feed conversion ratio or feed:gain ratio; PEG = partial efficiency of gain; RFI = residual feed intake.

Table 5.2. Characterization of physiological indicator traits in steers with low, medium, and high residual feed intake

	RFI group[a]				
Trait	Low	Medium	High	SE	*P*-value
Number of steers	37	42	36		
Initiation of Phase					
IGF-I, ng/ml	114.9	116.9	100.5	6.70	0.14
Insulin, ng/ml	4.80	5.31	5.60	0.42	0.30
Leptin, ng/ml	6.80	7.54	7.40	0.31	0.24
Cortisol, ng/ml	16.15	14.61	14.97	1.02	0.54
Glucose, mg/dl	79.33	78.45	81.06	1.91	0.56
Hematocrit, %	43.56	44.92	43.32	1.23	0.43
Exit velocity, m/s	3.22	3.33	2.96	0.18	0.35
Chute score[b]	1.59	1.30	1.38	0.18	0.48
End of Phase					
IGF-I, ng/ml	93.13	92.82	83.39	4.15	0.20
Insulin, ng/ml	6.15	8.36	8.66	0.74	0.08
Leptin, ng/ml	12.08	14.07	14.30	0.67	0.08
Cortisol, ng/ml	12.14	12.44	12.21	0.83	0.96
Glucose, mg/dl	79.27	79.58	80.40	2.73	0.94
Hematocrit, %	40.43	41.71	40.85	0.68	0.40
Exit velocity, m/s	2.64	2.54	2.49	0.14	0.74
Chute score[b]	2.15	2.07	2.18	0.08	0.58

[a]Low, medium, and high RFI steers were < 0.5 SD, ± 0.5 SD, and > 0.05 SD from the mean, respectively.
[b]1 = calm; 5 = continuous vigorous movement/excitement.
[xyz]Within a row, means without a common superscript letter differ ($P < 0.05$).

Initiation of the finishing phase serum insulin concentrations tended ($P < 0.10$) to be positively correlated with RFI, but not correlated ($P > 0.15$) with FCR, PEG, DMI, or ADG. Differences ($P > 0.30$) were not observed between RFI groups for serum insulin concentrations at the initiation of the finishing phase. End of finishing phase serum insulin concentrations tended ($P < 0.10$) to be positively correlated with RFI and were negatively correlated ($P < 0.05$) with PEG, but not correlated ($P > 0.70$) with FCR. There was a tendency ($P < 0.10$) for low RFI steers to have 29% lower serum insulin concentrations at the end of the finishing phase compared to high RFI steers. End of the finishing phase serum insulin concentrations were positively correlated ($P < 0.05$) with DMI and ADG.

Correlations between serum leptin concentrations at the initiation of the finishing phase and RFI, PEG, and ADG were not different from zero. However, serum leptin concentrations at the initiation of the finishing phase were correlated ($P < 0.05$) with PEG and DMI. Serum leptin concentrations at the end of the finishing phase were correlated ($P < 0.05$) with RFI, PEG, DMI, and ADG, but were not correlated ($P > 0.35$) with FCR. Steers with low RFI tended ($P < 0.10$) to have 16% lower serum leptin concentrations at the end of the finishing phase compared to steers with high RFI.

Correlations between serum cortisol concentrations at the initiation of the finishing phase and performance and feed efficiency traits were not different from zero. Serum cortisol concentrations at the end of the finishing phase were not correlated ($P > 0.15$) with RFI, PEG, FCR, or DMI, but tended ($P < 0.10$) to be correlated with ADG. Differences were not observed ($P > 0.50$) between RFI groups for initial and final serum cortisol concentrations.

Serum glucose concentrations at the initiation of the finishing phase were not correlated (*P* > 0.15) with performance or feed efficiency traits. At the end of finishing phase, serum glucose concentrations were not correlated (*P* > 0.30) with RFI, PEG, or DMI, but were negatively correlated (*P* < 0.05) with FCR and tended (*P* < 0.10) to be positively correlated with ADG. Differences were not observed (*P* > 0.50) between RFI groups for initial and final serum glucose concentrations.

Correlations between hematocrit at the initiation of the finishing phase and RFI, FCR, PEG, and ADG were not different from zero. However, hematocrit at the initiation of the finishing phase was negatively correlated (*P* < 0.05) with DMI. At the end of the finishing phase, hematocrit was not correlated (*P* > 0.35) with RFI, PEG, or DMI. Final hematocrit tended (*P* < 0.10) to be correlated with FCR and ADG. No significant differences were observed (*P* > 0.40) between RFI groups for initial and final hematocrit values.

Exit velocity at the initiation of the finishing phase was not correlated (*P* > 0.20) with RFI or ADG, but was correlated with (*P* < 0.05) PEG, FCR, and DMI. Final exit velocity was not correlated (*P* > 0. 50) with RFI or FCR. However, final exit velocity was correlated (*P* < 0.05) with PEG, DMI, and ADG. Steers in the low, medium, and high RFI groups did not differ (*P* > 0.35) in initial and final exit velocity. Correlations between initial chute score and performance and feed efficiency traits were not different from zero. Similarly, correlations between final chute score and performance and feed efficiency traits were also not different from zero.

Fecal dry matter and pH on d 42 were not correlated (*P* > 0.10) with performance or feed efficiency traits (Table 5.3). Differences between RFI groups were not observed

($P > 0.35$) for fecal dry matter or pH on d 42 (Table 5.4). Fecal dry matter on d 56 was correlated ($P < 0.001$) with RFI, PEG, and DMI, but not correlated ($P > 0.10$) with FCR or ADG. Fecal pH on d 56 was not correlated ($P > 0.50$) with performance or feed efficiency traits. Differences were not observed ($P > 0.15$) between RFI groups for fecal dry matter or pH on d 56.

Discussion

Adoption of RFI into selection programs is limited due to measuring individual feed intake. Measuring individual feed intake is costly and labor intensive. However, the use of an indicator trait to predict RFI could reduce costs associated with testing all animals or may help to more accurately determine which animals should be subjected to feed efficiency testing.

Serum IGF-I concentrations at the initiation of the finishing phase were not correlated with feed efficiency traits. This is inconsistent with reports by Moore et al. (2005) where IGF-I was correlated with RFI. The difference between the current study and the study by Moore et al. is the age of the cattle when the blood sample was collected and type of diet fed. In the current study, serum IGF-I was measured in the steers six to eight mo after weaning. The steers in the study by Moore et al. had IGF-I determined from samples collected at weaning and RFI determined on a high-roughage diet. Brown et al. (2004) reported correlations between RFI and serum IGF-I in growing bulls fed a high-roughage diet. These results indicate that IGF-I may be an indicator trait for RFI when measured early in life, but not an indicator of RFI in older cattle consuming a high-grain diet. Initial serum IGF-I concentrations were correlated with ADG and tended to be

Table 5.3. Phenotypic correlations[a] between fecal indicator traits and performance and efficiency traits in finishing steers

Trait[b]	ADG	DMI	FCR	PEG	RFI
Fecal dry matter d 42	0.13	0.16	0.02	-0.02	0.03
Fecal dry matter d 56	0.16	**0.35**	0.11	**-0.38**	**0.25**
Fecal pH d 42	-0.03	-0.15	-0.09	0.12	-0.16
Fecal pH d 56	0.07	0.05	-0.06	-0.00	-0.06

[a]Correlations in bold are different from zero at $P < 0.05$.
[b]ADG = average daily gain; DMI = dry matter intake; FCR = feed conversion ratio or feed:gain ratio; PEG = partial efficiency of gain; RFI = residual feed intake.

Table 5.4. Characterization of fecal indicator traits in steers with low, medium, and high residual feed intake

	RFI group[a]				
Trait	Low	Medium	High	SE	*P*-value
Number of steers	37	42	36		
Fecal dry matter d 42	22.49	22.35	23.04	0.74	0.74
Fecal dry matter d 56	21.01	22.11	23.48	0.80	0.15
Fecal pH d 42	6.45	6.42	6.33	0.06	0.36
Fecal pH d 56	6.70	6.63	6.60	0.06	0.48

[a]Low, medium, and high RFI steers were < 0.5 SD, ± 0.5 SD, and > 0.05 SD from the mean, respectively.
[xyz]Within a row, means without a common superscript letter differ ($P < 0.05$).

correlated with DMI. This is contrast to reports by Brown et al. (2004) where initial serum IGF-I concentrations were independent of ADG. For a trait to be an indicator of RFI, it also needs to be independent of ADG. This further indicates that serum IGF-I at the initiation of the study is not a potential indicator trait for RFI.

End of the finishing phase serum IGF-I concentrations tended to be negatively correlated with RFI and negatively correlated with FCR. These results indicate that less efficient cattle would have higher IGF-I concentrations. Tomas et al. (1998) found that by infusing broiler chickens with IGF-I that there was an improvement in FCR compared to non-infused broilers. The improvement in FCR in broilers was attributed to increasing nitrogen retention, growth rates and reducing carcass fatness when serum IGF-I concentrations were higher. However, in the current study the higher IGF-I concentrations at the end of the study were associated with high RFI steers that were fatter and less efficient. The higher serum IGF-I concentrations in the high RFI steers at the end of the study did not result in leaner carcasses or improvements in nitrogen retention. Richardson et al. (1996) reported evidence to indicate that high RFI steers have higher rates of protein degradation compared to low RFI steers. Likewise, in divergently selected RFI steers blood urea concentrations were positively correlated with RFI (Richardson et al., 2004) also indicating a higher rate of protein degradation. In growing cattle, low RFI is associated with lower serum IGF-I concentrations (Brown et al., 2004; Moore et al., 2003) and reduced carcass fatness (Arthur et al., 1997; Basarab et al., 2003). Moore et al. (2005) reported positive correlations between serum IGF-I and carcass estimates of fatness in growing cattle, also indicating that low RFI is associated with reduced fatness. However, IGF-I is considered an anabolic hormone and has been reported to be higher in more efficient cattle as measured by FCR (Stick et al., 1998). This would suggest that other sources of biological variation are contributing to the differences in RFI.

Serum insulin concentrations tended to positively correlated with RFI at the initiation of the finishing phase. This would suggest that low RFI steers would have lower insulin concentrations compared to high RFI steers. Steers with high RFI had numerically higher insulin concentrations at the initiation of the phase. Serum insulin at the end of the phase also tended to be positively correlated with RFI and high RFI steers tended to have 41% higher serum insulin concentrations compared to low RFI steers. Richardson et al. (2004) also observed positive correlations between RFI and serum insulin at the end of the feedlot phase in divergently selected RFI steers. The divergently selected high RFI steers tended to have 36% higher serum insulin concentrations at the end of the feedlot phase. However, the higher serum insulin concentrations in the current study and the study by Richardson et al. (2004) does not fit the hypothesis associated with protein turnover. Normally, insulin is associated with increased energy requirements by muscle by increasing amino acid transport and protein synthesis, and decreasing muscle degradation (Hocquette et al., 1998). However, it is hypothesized that high RFI steers are less efficient due to increased protein turnover. Richardson et al. (2004) observed positive correlations between RFI and total plasma protein and urea in divergently selected RFI steers, indicating an increase in protein degradation in high RFI steers. Therefore, the higher serum insulin concentrations in high RFI steers must not function to reduce protein degradation. It may be that high RFI steers are fatter and have a reduced insulin sensitivity similar to findings in obese sheep and heifers (McCann and

Reimers, 1986; McCann et al., 1986). Obesity in humans is also associated with reduced insulin sensitivity, hyperinsulinemia, and high blood viscosity (Brun et al., 2004).

Serum insulin concentrations at the initiation of the finishing phase were not correlated with FCR, PEG, DMI or ADG. However, at the end of the finishing phase PEG was negatively correlated with serum insulin concentrations. The negative correlation between IGF-I and PEG would suggest that less efficient cattle would have lower serum insulin concentrations similar to the finding reported for RFI. The same pattern between indicators of RFI and PEG is desired as both appear to be more appropriate feed efficiency traits compared to FCR. Dry matter intake and ADG were positively correlated with insulin at the end of the finishing phase. Likewise, Lapierre et al. (2000) observed increases in insulin concentrations in steers when fed at higher intakes compared to low intake steers. In contrast, Richardson et al. (2004) did not observe correlations with ADG or DMI and serum insulin at the end of the feedlot phase in divergently selected RFI steers.

Serum glucose concentrations at the initiation of the finishing phase were not correlated with RFI or PEG, but were correlated with FCR and tended to be correlated with DMI. This suggests that more efficient cattle as measured by FCR had lower glucose concentrations and cattle with higher DMI also had lower glucose concentrations. Richardson et al. (2004) observed moderate positive correlations between start of the feedlot phase glucose and RFI to indicate that more efficient cattle had lower glucose concentrations. Feed conversion ratio was negatively correlated with serum glucose at the start of feedlot test, which is in contrast to the findings of the current study. End of finishing phase serum glucose concentrations were not correlated with RFI or PEG, but were negatively correlated with FCR and tended to be correlated with ADG. Richardson et al. (2004) did not report end of test correlations for glucose. However, they did observe positive correlations between start of test glucose and ADG, to indicate that faster growing cattle had higher glucose concentrations, which is similar to the finding in the current study with end of test glucose concentrations. Likewise, Hersom et al. (2004) observed higher glucose concentrations in faster growing steers compared to steers with slower growth rates.

Serum leptin concentrations at the initiation of the finishing phase were correlated with PEG and DMI. The correlations with leptin and PEG and DMI indicated that more efficient cattle with lower DMI would have lower leptin concentrations at the start of the phase. The more efficient cattle, as measured by PEG, were also leaner as were the cattle with lower intakes. Serum leptin concentrations at the initiation of the finishing phase were correlated (r = 0.44; $P < 0.001$) with backfat at the start of the finishing phase (data not presented). End of finishing phase serum leptin concentrations were correlated with RFI and PEG, indicating that more efficient steers had lower serum leptin concentrations. Steers with low RFI tended to have 16% lower serum leptin concentrations compared to high RFI steers. Final backfat was also correlated with RFI and PEG, and final backfat was correlated (r = 0.50; $P < 0.001$) with leptin at the end of the finishing phase (data not presented). Likewise, serum leptin concentrations were positively correlated with RFI in two other studies (Richardson and Herd, 2004; Richardson et al., 2004). The higher serum leptin concentrations in the high RFI steers was not unexpected since leptin is produced by adipocytes and is involved in the regulation of feed intake and energy metabolism (Houseknecht et al., 1998). Leptin synthesis is also stimulated by insulin and glucose as well as changes in energy intake and growth and development can alter leptin concentrations (Macajova et al., 2004). Final leptin and insulin concentrations were moderately correlated (data not presented) in the current study. Additionally, Macajova et al. (2004) reported that obesity is associated with disturbance in the somatotrophic axis, such that growth hormone and IGF-I binding proteins are decreased in obese patients. Recently, Nkrumah et al. (2005a) reported a single nucleotide polymorphism in the promoter region of the leptin gene which was associated with ADG and DMI, but not RFI or FCR. The use of marker-assisted selection has potential to aid in evaluating performance and efficiency traits in cattle.

Hematocrit at the initiation of the finishing phase was not correlated with the three feed efficiency traits. However, hematocrit at the initiation of the phase was correlated with DMI. End of finishing phase hematocrit tended to be negatively correlated with FCR and ADG. Hematocrit was measured as an indicator of blood viscosity (Windberger et al., 2003). It is hypothesized that high RFI cattle have higher tissue oxygen requirements and have higher blood viscosity. Several studies have reported differences in blood cell parameters between high and low RFI cattle (Richardson et al., 2002; Richardson et al., 1996; Richardson et al., 2001a). Hematocrit has been reported to be related to RFI in growing cattle (Richardson et al., 2002) and hematocrit can contribute to differences in blood viscosity. Differences in blood viscosity can also be affected by carcass fatness. Obesity in humans is associated with higher blood viscosity, and hematocrit as well as reduction in insulin sensitivity (Brun et al., 2004; Wysocki et al., 1991).

Serum cortisol concentrations at the initiation of the finishing phase were not correlated with performance or feed efficiency traits. At the end of the finishing phase, serum cortisol tended to be correlated with ADG. Although, correlations between cortisol and feed efficiency traits do not exist in the current study, it is hypothesized that differences in efficiency could be attributed to differences in stress responsiveness or excitability. At the end of the finishing phase, cortisol concentrations tended to be correlated with ADG, which is similar to reports by Nikolic et al. (1996) and Trenkle and Topel (1978) in growing cattle. These results indicate that cortisol is an indicator of performance, but not feed efficiency.

Subjective and objective scores can measure differences in excitability. For subjective scores, chute score was examined, while exit velocity was used to objectively determine excitability. Exit velocity has been reported to be moderately correlated with objective measures of temperament, ADG, and carcass weights in cattle (Burrow and Dillon, 1997; Petherick et al., 2002). Cattle with more excitable temperaments (Voisinet et al., 1997) and faster exit velocity (Bindon, 2002) have been reported to produce less tender beef than cattle with calm temperaments and slower exit velocity.

Initial exit velocity was not correlated with RFI, but was correlated with PEG and FCR, such that more efficient cattle would have faster exit velocities. Such findings contradict the hypothesis that more efficient cattle are more stress tolerant. Lancaster et al. (2005a) and Fox (2004) did not observe correlations between exit velocity and feed efficiency traits in growing heifers and bulls. Initial exit velocity was negatively correlated with DMI in the current study and is consistent with observations by Lancaster et al. (2005) and Fox (2004). Initial chute score was not correlated with performance or feed efficiency traits similar to Fox (2004), although Lancaster et al. (2005) did report correlations with RFI, PEG, and FCR. This indicated that more efficient cattle had lower chute scores and were less excitable in the squeeze chute. End of test exit velocity was positively correlated with PEG to indicate more efficient cattle had faster exit velocities. Again, this is contradictory to the hypothesis and to observations by Lancaster et al. (2005). Final exit velocity was also correlated with DMI and ADG to indicate that calmer cattle would grow faster and consume more. Similarly, Lancaster et al (2005) and Fox (2004) reported negative correlations between final exit velocity and performance traits. Final chute score was not correlated with performance and feed efficiency traits, consistent with observations by Lancaster et al. (2005) in growing heifers. These results indicate that temperament traits may be more predictive of performance than of feed efficiency.

Efficiency of digestion is estimated to account for 5% of the biological variation in RFI. It is hypothesized that differences in starch digestion between low and high RFI cattle can be detected by examining fecal pH and DM. Barajas and Zinn (1998) observed a significant negative correlation between fecal pH and fecal starch content in growing steers fed corn diets. Additionally, they observed that higher fecal pH and lower fecal starch content were associated with higher ruminal starch digestion. Orskov (1986) reported that increasing amounts of starch to the large intestine could result in low fecal pH and lower fecal DM. Channon et al.(2004) observed negative correlations between fecal dry matter and RFI, indicating that more efficient cattle would have higher fecal dry matter contents. The higher fecal dry matter content is an indicator of reduced hindgut fermentation and more efficient starch digestion in the rumen and small intestine. They also observed negative correlations between fecal dry matter and DMI, indicating more efficient starch digestion by cattle with lower DMI. Additionally, fecal pH can be a reflection of the site of starch digestion, small intestine versus large intestine. The lower fecal pH reflected the higher concentration of acid resulting from greater hindgut fermentation.

In the current study, significant correlations were not observed between d 42 fecal dry matter or pH and performance and feed efficiency traits. Significant correlations were also not observed between d 56 fecal pH with performance and feed efficiency traits. However, correlations between d 56 fecal dry matter and RFI, PEG, and DMI were observed. The correlations observed in the current study with fecal dry matter and RFI, PEG, and DMI indicated that more efficient cattle would have lower starch digestion in the rumen and small intestine and that cattle with higher DMI would have higher starch digestion in the rumen and small intestine. Reasons for the inconsistency between fecal DM in this study and Channon et al (2004) are unclear. Although, numerically, fecal pH was lower for steers with high RFI indicating that there may have been more hindgut fermentation of starch compared to steers with low RFI. Additional research is warranted to further examine the site of starch digestion as a source of biological variation in RFI.

Conclusion

Results from this study indicate that RFI has the potential to improve feed efficiency in beef cattle and to reduce costs for beef producers without increasing mature size of the cowherd that may occur if selection programs used other feed efficiency traits. However, the labor and expense associated with measuring individual feed intake is high. Identification of the more efficient cattle by using physiological indicator traits appropriate for various stages of production could aid in identifying more efficient cattle that should be subjected to testing. Unlike growing cattle, serum IGF-I does not appear to be an indicator trait in finishing cattle. In the current study, a physiological indicator trait for finishing phase RFI was not observed, therefore additional research is warranted to further evaluate other potential physiological indicator traits.

Overall conclusions

Growing and finishing steers with low RFI consumed 19-22% less feed than growing and finishing steers with high RFI, but did not differ in ADG. Steers with low RFI were also more efficient as measured by FCR and PEG. Steers with low RFI had less FT compared to steers with high RFI. Initial serum IGF-I was correlated with RFI in growing steers indicating that IGF-I might be a potential indicator trait for RFI in growing cattle. Additionally, RFI was correlated with digestibility to indicate more efficient cattle had higher dry matter digestibility. Results indicate that RFI has potential to allow producers to select more efficient animals without increasing growth rate.

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VITA

Name:	Erin Gwen Brown
Address:	Stephen F. Austin State University P.O. Box 13000, SFA Station Nacogdoches, Texas 75962
Email Address:	browneg@sfasu.edu
Education:	B.S., Animal Science, Texas A&M University, 1999 M.S., Animal Science, Michigan State University, 2002 Ph.D., Nutrition, Texas A&M University, 2005