BIOLOGICAL SOURCES OF VARIATION IN RESIDUAL FEED INTAKE IN BEEF CATTLE

A Dissertation

by

PHILLIP ALLAN LANCASTER

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

May 2008

Major Subject: Animal Science

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Approved by:

Chair of Committee,	Gordon E. Carstens
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ABSTRACT

Biological Sources of Variation in Residual Feed Intake in Beef Cattle. (May 2008)

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Chair of Advisory Committee: Dr. Gordon E. Carstens

Objectives of this study were to characterize residual feed intake (RFI) in growing calves and to examine relationships with growth, carcass composition, physiological indicators, energy metabolism and reproduction. To accomplish these objectives, multiple experiments were conducted. In all experiments, RFI was calculated as the difference between actual DMI and expected DMI from linear regression of DMI on mid-test metabolic BW and ADG. To examine the relationships between RFI and rate and composition of growth, and reproduction an experiment was conducted with postweaning Brangus heifers (N = 348). Measures of carcass composition (longissimus muscle area, LMA; and 12th rib fat thickness, BF) were obtained by ultrasound at the start and end of each experiment. To determine if serum IGF-I concentration is associated with RFI, two experiments were conducted with Angus bulls and heifers (N = 95) divergently selected for serum IGF-I concentration. To evaluate relationships with energy metabolism, calves with low and high RFI were selected for determination of heart rate as an indicator trait for energy expenditure (4 experiments) and liver mitochondrial function (3 experiments).

Residual feed intake was not correlated with ADG, but was positively correlated with gain in BF such that the more efficient calves were leaner. Calves from the low IGF-I selection line had lower RFI suggesting that RFI and IGF-I are related and that IGF-I could be used as an indicator trait to aid in selection for improved RFI in Angus cattle. Calves with low RFI had lower energy expenditure and greater mitochondrial acceptor control ratios than calves with high RFI suggesting improved regulation of energy metabolism. A similar percentage of heifers with low RFI attained puberty as those with high RFI by the end of the experiment. Results from this study indicate that producers can utilize RFI to select for improved feed efficiency with minimal impact on growth, carcass composition and reproduction.

DEDICATION

I would like to dedicate this dissertation to my wife, Sarah, who has helped on many of my projects and for her love and support during my frustration. I would also like to dedicate this dissertation to my mother and father who instilled in me the confidence to complete anything that I put my mind to.

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I would like to thank the staff at NPC for all of their help in completing this research: Kerry Dean and Kenton Krueger. These people have made the organization of conducting a research study much easier. Furthermore, I would like to thank Lisa Slay, Pat Chen, Jennie Lyons and Jennifer Michal for all of their help in processing and analyzing samples.

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CHAPTER I

INTRODUCTION AND LITERATURE REVIEW

Overview

The principal goal of livestock production is to meet consumer demand for meat, milk, eggs and wool in an economically and environmentally sustainable manner. Feed costs comprise a significant proportion of the variable expenses involved with livestock production. In a world of increasing population, the availability and competition for feed resources will reduce that available for livestock production. Thus, increasing the efficiency with which animals use available feed would aid producers in sustaining a viable business and maintaining low food costs for the consumer. Improvement in feed efficiency would provide greater benefit to beef production due to larger amounts of feed required to sustain the breeding herd compared to other species.

Previous studies have evaluated feed conversion ratio (**FCR**; feed:gain), the typical measure of feed efficiency, as a trait to select for improved feed efficiency (Mrode et al., 1990; Herd and Bishop, 2000; Arthur et al., 2001b; Nkrumah et al., 2004). These studies demonstrated that FCR is related to the component traits of DMI and ADG, and mature body size such that selection for improved FCR would increase ADG and mature body size. This would be undesirable for cow/calf enterprises because increased mature body size would increase maintenance requirements of the cow herd

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This dissertation follows the style of Journal of Animal Science.

without necessarily improving overall production efficiency (Herd and Bishop, 2000). Furthermore, given that FCR is related to ADG and mature body size, selection for increased ADG and adjusted yearling weights should improve FCR without the need to measure feed intake (Mrode et al., 1990). However, several studies have reported that selection for improved growth rate in beef cattle resulted in progeny that were similar (Herd et al., 1990, 1991; Lymbery and Tudor, 1994) or less efficient (Rust et al., 1995) than progeny for control herds or parents selected for low growth rate. In addition, MacNeil et al. (1991) concluded that efficient genetic improvement in FCR required measurement of feed intake as well as ADG.

Several other feed efficiency traits have also been examined: Kleiber ratio, partial efficiency of growth and relative growth rate. These feed efficiency traits are also related to growth rate (Arthur et al., 2001b; Nkrumah et al., 2004) suggesting that selection for improved efficiency would result in increased cow mature size and feed requirements for maintenance of the cow herd. Residual feed intake (**RFI**) was proposed by Koch et al. (1963) as an alternative feed efficiency trait to measure the variation in feed intake beyond requirements for growth rate and body size. Despite adjusting for growth and body size, significant variation in feed intake exists among animals such that animals of similar body size and growth rate do not necessarily consume similar amounts of feed. Therefore, animals that consume less feed than expected based on growth rate and body size are considered to be more efficient (low RFI). Several studies have demonstrated that sufficient genetic variation (h^2 = 0.3 to 0.4) exists in residual feed intake of beef cattle to merit genetic selection (Archer et al., 1999; Arthur et al.,

2001a; Herd and Bishop, 2000). Several studies (Herd and Bishop, 2000; Arthur et al., 2001a; Schenkel et al., 2004; Nkrumah et al., 2007) have reported that RFI is not phenotypically or genetically related to growth rate or body size, as is FCR, but is positively related to feed intake. However, Arthur et al. (2001b) reported a weak positive genetic correlation between RFI and body size (0.32), and Archer et al. (2002) reported a weak negative genetic correlation between RFI and body size (-0.21). Arthur et al. (2001b) and Archer et al. (2002) reported strong positive genetic correlations (0.79 and 0.71, respectively) between RFI and feed intake.

Residual feed intake is a moderately heritable trait that is, in general, independent of growth and body size, but positively related to feed intake. Therefore, selection for RFI to improve feed efficiency (low RFI) will reduce feed inputs with minimal impact on growth and body size.

Relationships between RFI and Other Economically Relevant Traits

In addition to relationships with growth and cow mature size, it is important to understand the impact of selection for improved feed efficiency on other economically relevant traits such as carcass composition and reproduction. Several studies have demonstrated weak positive correlations between RFI and carcass fatness traits in growing cattle fed roughage-based diets (0.14 to 0.17; Arthur et al., 2001a; Schenkel et al., 2004; Brown, 2005), whereas, slightly stronger positive correlations between RFI and carcass 12^{th} rib fat thickness have been reported in finishing steers fed a grain-based diet (0.23 to 0.30; Nkrumah et al., 2004, 2007; Brown, 2005). In addition, Basarab et al. (2003) reported similar positive correlations of RFI with gain in 12^{th} rib fat thickness

(0.22) and gain in empty body fat (0.26) in finishing steers. However, these same studies reported no relationship between RFI and longissimus muscle area. Collectively, these studies provide strong evidence that more efficient calves are slightly leaner, although, this relationship is weak. Thus, selection for improved RFI should result in minimal changes in carcass composition with a slight improvement in lean meat yield.

Reproductive efficiency is an important economical trait for cow/calf producers that affects retention of females in the herd, calving interval and lifetime productivity of the beef cow. The rate of fat and protein deposition has been implicated in the onset of puberty in gilts (Gaughan et al., 1997). Buskirk et al. (1995) reported that heifers fed to gain weight at a faster rate gained more 12^{th} rib fat thickness and had an increased percentage of heifers pubertal before the breeding season (70.9 vs. 61.3%) than heifers fed for a slower rate of gain. Furthermore, Hall et al. (1995) reported that heifers fed for a faster rate of gain had greater 12^{th} rib fat thickness at puberty and attained puberty at a younger age than those fed for a slower rate of gain (386 vs. 415 d, respectively). Owens et al. (1993) stated that the age when growth rate begins to slow is often associated with puberty. This point also corresponds to approximately 50% of mature weight and the time where rate of fat deposition begins to increase relative to the rate of protein deposition. These results suggest that selection for low RFI may have a negative impact on age of puberty due to indirect selection for decreased fat composition, which would reduce the productivity of the cow-calf operation. Arthur et al. (2005) reported that females selected for low RFI (1.5 generations) had less 12^{th} rib fat thickness and calved 5 d later during the calving season compared to females selected for high RFI. Similarly,

Basarab et al. (2007) reported that dams of progeny with low RFI calved 4 d later during the calving season compared to dams of progeny with high RFI. Given that the age of dam by progeny RFI group interaction was not significant in this study, these results suggest that the later calving day occurred as first calf heifers and may have been a result of later attainment of puberty. However, Arthur et al. (2005) and Basarab et al. (2007) reported similar pregnancy and calving rates in females divergently selected for RFI or in dams of progeny with low or high RFI, respectively.

Several studies (Smith et al., 1989; Morris et al., 1992; Vargas et al., 1998; Martinez-Velazquez et al., 2003) have demonstrated negative relationships between scrotal circumference in bulls and age at puberty of heifer progeny. These results suggest that selection for improved RFI in bulls could affect reproductive traits in heifers if a relationship exists between RFI and scrotal circumference. However, several studies have reported no correlation between RFI and scrotal circumference in bulls (Arthur et al., 2001a; Fox et al., 2004; Schenkel et al., 2004).

Identification of Physiological Indicators

Identification of physiological traits that are predictive of RFI would facilitate early detection, and enhance accuracy of selection of animals with improved feed efficiency. Insulin-like growth factor-I (**IGF-I**) is a hormone released by the liver and peripheral tissues in response to growth hormone. Insulin-like growth factor-I can act in an endocrine, autocrine or paracrine manner. The actions of IGF-I affect glucose and amino acid metabolism, and protein accretion (Jones and Clemmons, 1995) by increasing protein synthesis relative to protein degradation (Lobley, 1992) suggesting

that IGF-I influences growth, carcass composition and feed efficiency. Therefore, IGF-I may be useful as an indicator trait to identify animals that have superior growth, carcass composition and feed efficiency.

Davis and Simmen (1997) and Moore et al. (2003) reported negative genetic correlations of circulating IGF-I with weaning weight and postweaning gain in growing Angus beef cattle. Negative genetic correlations between IGF-I and BW at the end of a postweaning test have been reported (Davis and Simmen, 1997; Moore et al., 2005). However, Davis and Simmen (2006) reported positive genetic correlations of IGF-I with end of test BW and ADG during the test in Angus cattle; while Brown (2005) reported positive phenotypic correlations of IGF-I with postweaning ADG in Santa Gertrudis steers. Davis and Simmen (2000) reported weak negative genetic correlations between postweaning IGF-I and 12^{th} rib fat thickness, whereas, Johnston et al. (2001), Davis et al. (2003) and Moore et al. (2005) reported weak positive genetic correlations. Davis and Simmen (2000) and Davis et al. (2003) reported weak positive genetic correlations between postweaning IGF-I and longissimus muscle area, whereas, Moore et al. (2005) reported a moderate negative genetic correlation. However, Moore et al. (2005) did report a weak positive genetic correlation between weaning IGF-I and longissimus muscle area, suggesting that time of sampling for IGF-I may influence the relationship.

Several studies have reported positive genetic (Johnston et al., 2002, $r_g = 0.56$; Moore et al., 2005, $r_g = 0.57$) and phenotypic (Brown et al., 2004, $r_p = 0.38$) correlations between postweaning IGF-I concentration and RFI in *Bos taurus* cattle fed a roughage-based diet. However, Wolcott et al. (2006) reported a strong negative genetic correlation

(-0.80) between post-weaning serum IGF-I concentration and RFI in *Bos indicus* cattle implanted and fed a grain-based diet. Anonymous (2007) reported a weak positive genetic correlation (0.17) in cattle fed a roughage-based diet and a weak negative genetic correlation (-0.22) in cattle fed a grain-based diet between serum IGF-I concentration and RFI. Similarly, Brown (2005) reported a weak positive phenotypic correlation (0.18) when fed a roughage-based diet and a weak negative phenotypic correlation (-0.12) when fed a grain-based diet between postweaning serum IGF-I concentration in *Bos taurus* x *Bos indicus* crossbred cattle.

In addition to diet and breed, stage of maturity may influence the relationship between IGF-I concentration and RFI. Moore et al. (2005) evaluated the relationship between postweaning serum IGF-I concentration and RFI in *Bos taurus* cattle with a final BW of 359 kg, whereas, Wolcott et al. (2006) utilized *Bos indicus* cattle with an initial BW of 400 kg suggesting that the cattle of Wolcott et al. (2006) were at a greater stage of maturity. Moore et al. (2005) reported a positive correlation between postweaning serum IGF-I concentration and RFI, whereas, Wolcott et al. (2006) reported a negative correlation. These studies suggest that the positive association between IGF-I concentration and RFI exhibited in younger calves depositing more lean tissue is diminished in older cattle depositing more fat or a greater percentage of fat.

Wolcott et al. (2006) reported that the relationship between IGF-I concentration and RFI became more negative as IGF-I was sampled later in the finishing period for Brahman steers (r_g = -0.12, 0.03 and -0.54 for postweaning, initial and final IGF-I concentration, respectively), but for the tropical composite steers the relationship

became more positive even though the correlation coefficient was always negative. Brown (2005) also reported that this relationship became more negative as IGF-I was measured later in the growing (r_p = 0.18 and 0.04 for initial and final IGF-I concentration with RFI on a roughage diet, respectively) and finishing (r_p = -0.12 and -0.18 for initial and final IGF-I concentration with RFI on a grain diet, respectively) period for Santa Gertrudis steers.

Collectively, these data demonstrate that the relationship of IGF-I concentration with performance, feed efficiency and ultrasound composition traits is complex and may be influenced by diet, stage of maturity at the time animals are performance tested, time relative to weaning for IGF-I sampling, and possibly, breed and implant regimen. This indicates a substantial lack of knowledge about animal variation in circulating IGF-I levels and the affect on growth and feed efficiency. In addition, the multitude of factors influencing the relationship between IGF-I and RFI creates substantial complexity to the use of IGF-I as a physiological indicator.

These conflicting results may be due to IGF-I binding proteins (**IGFBP**) that are affecting the actions and (or) concentrations of circulating IGF-I differently at different stages of growth. Six IGFBP have been characterized: IGFBP 1 to 6 (Jones and Clemmons, 1995; Hossner et al., 1997). The IGFBPs are increased by IGF-I and function to modulate the actions of IGF-I. Insulin-like growth factor binding proteins act as carrier proteins in plasma and regulate efflux of IGF-I from the vascular space, increase the half-life of IGF-I, provide a means of tissue and cellular specificity for IGF-I actions, and directly modulate the interaction of IGF-I with its receptor. The IGFBPs

have several actions in common and each individual binding protein has specific actions inherent to that protein (Jones and Clemmons, 1995). Insulin-like growth factor binding proteins 1, 2, 3 and 4 inhibit the intracellular actions of IGF-I by reducing IGF-I affinity for its receptor. Specific proteases cleave IGFBP 2, 3, 4 and 5 to reduce their affinity for IGF-I releasing IGF-I at the cell surface to interact with its receptor. Furthermore, IGFBP 1, 3 and 5 can bind to integrin receptors on the cell surface and can mediate intracellular actions dependently and independently of IGF-I. Insulin-like growth factor-I binding protein-2 has been reported to be phenotypically negatively correlated with body weight (Pagan et al., 2003) and positively associated with growth rate (Connor et al., 2000) in Angus cattle. These results suggest that IGFBP-2 may be a candidate protein to consider as an indicator trait for RFI in conjunction with IGF-I.

Sources of Biological Variation

The goal of ongoing research is not just to develop the practical methods of selection for improved feed efficiency independent of growth, carcass composition and reproduction, but also to understand the biological basis for variation in feed efficiency. A better understanding of the biological mechanisms associated with the variation in feed efficiency could lead to candidate genes and ultimately gene markers to aid in selection of animals with improved RFI. Richardson and Herd (2004) and Herd et al. (2004) discussed the possible mechanisms contributing to the variation in RFI (Figure 1.1). These researchers concluded that variation in feed digestion, activity, heat increment of feeding and composition of gain contributed 10-15, 5-10, 10 and 5% of the variation in RFI, respectively. However, there remains 65% of the variation unexplained.

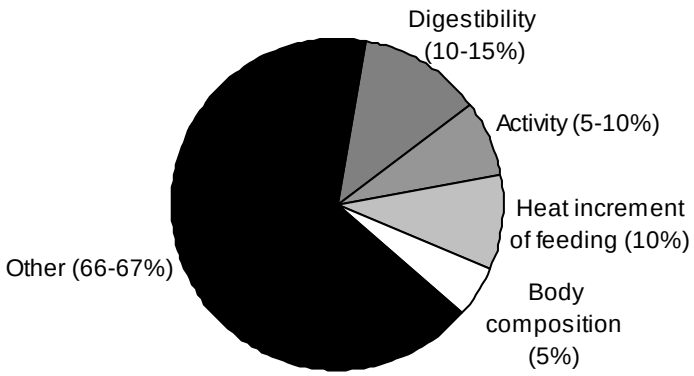

Figure 1.1. Contribution of various biological mechanisms to the variation in residual feed intake. Adapted from Herd et al. (2004) and Richardson and Herd (2004).

These authors speculated that the remaining 65% of the variation in RFI may be related to mechanisms involved in energy expenditure such as protein turnover, cellular ion pumping and mitochondrial proton leak, all of which affect energy balance of the whole animal. Rolfe and Brown (1997) concluded from a review of the research that 20% of mitochondrial oxygen consumption is related to proton leak. Furthermore, these authors concluded that protein synthesis and Na^+-K^+-ATPase account for 28 and 19-28% of ATP driven mitochondrial oxygen consumption, respectively. These data suggest that proton leak, protein turnover and ion pumping contribute significantly to energy expenditure and may be candidate mechanisms contributing to variation in feed efficiency. Richardson and Herd (2004) proposed that protein turnover, tissue metabolism and stress collectively account for 37% of the variation in RFI. Furthermore, Knott et al. (2007) reported a positive correlation between cortisol response to an adrenocorticotropin hormone challenge and RFI (0.65) suggesting that more efficient rams were less responsive to stress and would spend less energy maintaining homeostasis.

The first law of thermodynamics states that energy can not be created or destroyed. Thus, the gross energy consumed must be equal to the energy lost plus the energy retained in the body. This can be summarized by the energy balance equation: gross energy intake = fecal + urine + gaseous + heat + retained energy (NRC, 1996). Several researchers have found significant inter-animal variation in energy expenditures of cattle does exist (Wedegaertner et al., 1981; Carstens et al., 1987; Hotovy et al., 1991).

Calves with high RFI (less efficient) on average consume 15 to 20% more gross energy compared to calves with low RFI (more efficient), even though growth and body weight are similar (Basarab et al., 2003; Nkrumah et al., 2004; Kolath et al., 2006a; White, 2004; Brown, 2005). The greater proportion of energy lost by the less efficient animal could be attributed to undigested intake energy and (or) to increased losses of gaseous energy, urinary energy or heat energy. Recent research has demonstrated negative correlations ($r = -0.33$ and -0.32 for Nkrumah et al., 2006 and Brown, 2005, respectively) between RFI and feed dry matter digestibility, such that calves with high RFI phenotypes had lower digestibilities than calves with low RFI. Nkrumah et al. (2006) reported that calves with low RFI had lower methane production (gaseous energy loss) per day and as a percent of gross energy intake than calves with high RFI. Hegarty et al. (2007) also reported lower daily methane production for calves with low RFI, but similar methane production as percent of DMI. However, methane production per kg of ADG was numerically in favor of calves with low RFI in this study.

Metabolizable energy can be lost as heat or retained in body tissues. The energy lost as heat can be influenced by the amount of metabolizable energy intake (Ferrell and Jenkins, 1998) due to more energy required to metabolize the absorbed nutrients or by an inefficiency in the conversion of nutrients to muscle and fat. Luiting et al. (1991) reported an average of 21% greater heat loss in poultry with high RFI than those with low RFI when poultry with high RFI consumed an average of 15% greater DMI. In addition, Basarab et al. (2003) reported that calves with high RFI had 10% greater heat loss than calves with low RFI when calves with high RFI consumed 11% greater

metabolizable energy. In contrast, Nkrumah et al. (2006) reported 27% greater heat loss for calves with high RFI when calves with high RFI consumed 10% less metabolizable energy than calves with low RFI. White (2004) reported similar heat loss between calves with low or high RFI when metabolizable energy intake was similar. Gabarrou et al. (1997) reported greater diet-induced thermogenesis of cockerels with high RFI compared to those with low RFI. These data suggest that the increased heat production of calves with high RFI may be partially explained by the increased feed intake of this RFI phenotype substantiating the results of Herd et al. (2004) which indicated 10% of the variation in RFI could be attributed to variation in heat increment of feeding.

The amount of retained energy in growing cattle can be affected by the rate as well as tissue composition of growth (Old and Garrett, 1987; Owens et al., 1995). Energy retention increases as the proportion of fat in growth increases due to greater energy concentration of fat than lean tissue (8.3 vs. 1.2 kcal/g of fresh tissue; Owens et al., 1995). Furthermore, fat deposition is 1.6 times more efficient than protein deposition due to less energy losses from protein turnover. As previously described, a positive relationship exists between RFI and rate of fat deposition suggesting greater retained energy for calves with high RFI. In fact, Basarab et al. (2003) reported 14% greater retained energy for steers with high RFI compared to steers with low RFI. However, steers with high RFI also consumed 11% greater metabolizable energy indicating that the proportion of metabolizable energy retained was most likely similar (0.300 and 0.307 for steers with low and high RFI, respectively). Furthermore, Castro Bulle et al. (2007) reported that steers with high RFI had 32% greater retained energy with only 14%

greater metabolizable energy intake resulting in a numerically greater proportion of retained metabolizable energy compared to steers with low RFI (0.330 vs. 0.284, respectively). These data suggest that the efficiency of ME use for growth is similar between RFI phenotypes. In addition, Castro Bulle et al. (2007) reported that calves with high RFI had numerically greater metabolizable energy for maintenance requirements compared to calves with low RFI. Gabarrou et al. (1997) reported numerically greater heat loss of cockerels with high RFI compared to cockerels with low RFI when feed deprived. These data suggest that calves with high RFI may have increased maintenance energy requirements, which may be influenced by visceral organ mass.

Visceral organ mass can significantly affect the energy balance of the whole animal by increasing maintenance energy requirements. Visceral tissues account for 6 to 10% of live weight, but 40 to 50% of whole body oxygen consumption (Burrin et al., 1990). Burrin et al. (1990) demonstrated that weight of liver, kidney, stomach and small intestine respond to level of energy intake. The proportion of organ weight per unit of empty-body weight increased in sheep fed ad libitum, whereas, weights of these organs decreased in sheep fed at maintenance intake. Metabolic activity and oxygen consumption of liver, rumen epithelium and jejunum did not change per gram of tissue weight (Burrin et al., 1990), but the overall oxygen consumption by the liver and portal-drained viscera was greater for sheep fed ad libitum. In addition, blood flow through the portal and hepatic veins differed between treatments such that sheep fed at maintenance had 25 and 41% lower blood flow than sheep fed ad libitum. Studies evaluating weight of liver and gastrointestinal tract between low and high RFI cattle have been conflicting.

Basarab et al. (2003) reported that stomach and intestine, and liver were heavier in high RFI cattle (48.7 vs. 45.1 and 6.6 vs. 6.1 kg, respectively). In contrast, Richardson et al. (2001) reported that internal organ and gastrointestinal tract weights were similar in steer progeny of parents divergently selected for RFI. In addition, White (2004) reported similar liver and gastrointestinal tract weights in Branvieh crossbred calves differing in RFI phenotype. Ribeiro et al. (2007) reported similar liver weights between calves with low and high RFI, but calves with high RFI had greater gastrointestinal tract weights compared to calves with low RFI. These data suggest that numerically increased maintenance energy requirements of calves with high RFI (Castro Bulle et al., 2007) may be due to increased visceral organ mass.

Several processes contribute to energy expenditure in the liver and gastrointestinal tract, but those with the largest contributions include ion pumping (16 to 55 and 28 to 60%, respectively) and protein synthesis (15 to 24 and 20 to 23%, respectively; McBride and Kelly, 1990). Furthermore, urea synthesis contributes 7.1% to the oxygen consumption of the liver. Overall, the liver and gastrointestinal tract account for 20% of whole-body oxygen consumption each, demonstrating that maintenance of these tissues contributes greatly to whole body heat production. Even though metabolism of these tissues is important to energy expenditure, no studies have evaluated metabolism of these tissues in calves with low and high RFI. However, Ojano-Dirain et al. (2005) reported greater protein carbonyl content of duodenal mitochondria of broilers with high FCR compared to broilers with low FCR, suggesting greater oxidative damage to proteins of the small intestine, thus greater protein turnover.

Protein turnover is the balance of relative rates of protein synthesis and protein degradation. Increased protein turnover results in greater energy required for re-synthesis of the peptide bond, thus, decreased efficiency in conversion of nutrients to muscle and fat. Variation in protein turnover could contribute to the variation in RFI. McDonagh et al. (2001) reported greater calpastatin levels and less myofibril fragmentation in postmortem muscle tissue of calves with low RFI than those with high RFI. These data suggest that if greater levels of calpastatin are present in the growing animal, protein turnover could be significantly decreased in calves with low RFI. Furthermore, the positive relationship between serum IGF-I concentration and RFI suggests a lower protein turnover in calves with low RFI due to the intracellular action of IGF-I to increase protein degradation and synthesis. Oksbjerg et al. (2004) reported that mice over expressing IGF-I in skeletal muscle had larger muscle mass than control mice. In addition, exogenous administration of growth hormone increases the rate of protein turnover in cattle and sheep (Lobley, 1992) by increasing the rate of protein synthesis and protein degradation (Pell and Bates, 1987). These effects are most likely through the actions of IGF-I. However, Richardson et al. (2004) reported no correlation between RFI and urinary 3-methylhistidine, creatinine or 3-methylhistidine:creatinine ratio, which are measures of skeletal muscle protein turnover, in Angus steers divergently selected for RFI. Similarly, Castro Bulle et al. (2007) reported similar rates of skeletal muscle protein degradation, synthesis and accretion between calves with low and high RFI. These data suggest that RFI is not influenced by skeletal muscle protein turnover;

however, no studies have evaluated rates of protein turnover in other tissues or the whole body.

Differences in heat production have their basis in the cellular oxygen consumption of the animal. Realizing that 80 to 90% of cellular oxygen consumption and energy production occur through the electron transport chain and oxidative phosphorylation of the mitochondria, a small variation in mitochondrial function could significantly alter energy balance (Harper et al., 2002). Cellular respiration consists of oxygen being reduced to water by the shuttling of electrons through the electron transport chain which is coupled to the pumping of protons creating a proton gradient. Protons move down their gradient through ATP synthase driving ATP synthesis (Nelson and Cox, 2000). Mechanisms that control the cellular respiration rate have been extensively studied and several reviews have been published (Bohnensack et al., 1982; McMillin and Pauly, 1988; Brown, 1992). The cellular phosphorylation potential (ATP:ADP + Pi) is the primary indicator of cellular energy status. Bohnensack et al. (1982) demonstrated that as the extramitochondrial ATP:ADP ratio decreased, the volume of oxygen consumed increased. The synthesizing processes of the cell increase cytosolic ADP, which increases flux of ADP into mitochondria, thus increasing ADP for ATP synthesis. Brown (1992) suggested that ATP synthesis, utilization and transport exerted the majority (84%) of the control of mitochondrial ATP synthesis. However, these same mechanisms had only 49% of the control over the mitochondrial respiration rate. Other mechanisms such as substrate supply, adenine nucleotide translocase, cytochrome c oxidase and proton leak also have control over respiration rate.

Brown et al. (1990) suggested the cellular substrate supply (pyruvate or fatty acids) had approximately 15 to 30% of the control over the respiration rate. However, large concentrations of substrates were required to invoke a change in respiration rate suggesting that control of respiration is small. The adenine nucleotide translocase (**ANT**) shuttles ATP out into the cytosol and ADP into the mitochondria (McMillin and Pauly, 1988). Several studies have implicated ANT as a rate-controlling step that limits the supply of ADP for ATP synthesis, thereby respiration rate (McMillin and Pauly, 1988). In fact, Groen et al. (1982) demonstrated that increasing doses of carboxyatractyloside, an irreversible inhibitor of ANT, significantly decreased oxygen consumption. However, evidence has shown that concentrations of free cytosolic ADP would not be saturating to the translocase, therefore not limiting the flux through the mitochondrial membrane (McMillin and Pauly, 1988). In addition, studies have demonstrated that equilibrium exists between cytosolic phosphorylation potential and the reactions of the mitochondrial inner membrane space necessary for net ATP synthesis suggesting that ANT must also be at equilibrium. Assuming that ANT is not limiting ADP flux, then oxidative phosphorylation should operate near equilibrium except for cytochrome c oxidase. Cytochrome c oxidase catalyzes the conversion of oxygen to water (removal of electrons from the transport chain), thus, its activity can limit the flux of electrons through the transport chain, thereby, respiration rate. Groen et al. (1982) demonstrated that cytochrome c oxidase has approximately 17% of the control over respiration rate. Furthermore, Brown (1992) suggested that in most cells the concentration of oxygen was not limiting to cytochrome c oxidase.

Mitochondria have tight control over the flux of molecules and atoms crossing the inner membrane such that a proton gradient can be established to drive ATP synthesis. However, a proportion of protons do return down their gradient by a path other than ATP synthase. This proton leak has been shown to have significant control (~80%) over the respiration rate (Groen et al., 1982; Bohnensack et al., 1982). The greater proton leak reduces the proton motive force and the number of protons flowing through the ATP synthase, thus a greater respiration rate is required to maintain the cytosolic phosphorylation potential and energy for anabolic reactions (Erlanson-Albertsson, 2003).

Therefore, phosphorylation potential and proton leak each have some control over respiration rate; however, the level of control seems to be dependent upon the cellular demand for energy (Bohnensack et al., 1982; Groen et al., 1982; Brown, 1992). As anabolic reactions in the cell increase, the phosphorylation potential decreases and the rate of ATP synthesis increases allowing a greater proportion of protons to move down the gradient via the synthase. At this point (state 3 respiration), cellular energy demand has control over the respiration rate as well as ATP synthesis rate. When ATP utilization is low, the activity of the ATP synthase is low, however, the flux of electrons through the respiratory chain continues at a slower rate. At this point (state 4 respiration), the control of the proton leak increases and cellular respiration is uncoupled from ATP synthesis dissipating the energy as heat. Brown (1992) suggested that the proton leak accounts for 20 to 30% of the basal respiration rate in liver of rats. Rolfe and coworkers (1996, 1999) have demonstrated that proton leak accounts for 15 to 20%

of the basal metabolic rate in rats. Uncoupling proteins (**UCP**) have been cited as major avenues decreasing the proton motive force without creating useful energy (Erlanson-Albertsson, 2003). There are currently five known uncoupling proteins: UCP1, UCP2, UCP3, UCP4, and UCP5, but UCP 1, 2 and 3 will be the focus of this discussion.

Uncoupling protein 1 is found in brown adipocytes and provides the mechanism for non-shivering thermogenesis in mammalian young (Sell et al., 2004). Uncoupling protein 1 allows movement of protons down the gradient creating heat to maintain the body temperature of the newborn (Carstens, 1998; Erlanson-Albertsson, 2003). Several researchers have hypothesized that UCP1 could regulate energy balance in animals, but UCP1 is only expressed in brown adipose tissue, which is lost a few weeks after birth (Carstens, 1998). However, UCP2 and UCP3 are 56 and 57% homologous to UCP1, respectively, in their amino acid sequence and are expressed in several tissues of adult animals suggesting that they are responsible for maintaining energy balance (Erlanson-Albertsson, 2003; Ricquier, 2005). Therefore, one would expect the properties of UCP2 and UCP3 to be similar to UCP1. However, unlike UCP1, there is no evidence that UCP2 and UCP3 can move unbound protons into the mitochondria (Brand and Esteves, 2005; Ricquier, 2005). Circumstantial evidence has proposed that UCP2 and UCP3 uncouple respiration by transporting a fatty acid anion out of the mitochondria, which can be protonated and move back into the mitochondria freely, thus causing proton movement into the mitochondria (Brand and Esteves, 2005), although, there is no substantial evidence to support this theory.

Some evidence has shown possible involvement of UCP2 and UCP3 in proton leak. In fact, studies have demonstrated that the rate of ATP synthesis was fourfold greater in UCP3 ablated mice and that over expression of UCP3 resulted in mice that consumed more food but weighed less than their wild type litter mates (Erlanson-Albertsson, 2003), but this was due to a pharmacological level of expression of UCP3 in those mice (Ricquier, 2005). Despite these studies, there is no direct evidence that UCP2 or UCP3 is responsible for changing the energy balance of the whole animal as is UPC1 (Adams, 2000; Harper et al., 2002; Erlanson-Albertsson 2003; Brand and Esteves, 2005; Ricquier, 2005). This is most likely due to UCP2 and UCP3 being expressed at much lower concentrations than UCP1: UCP2 and UCP3 are present at 0.01 and 0.1% of membrane protein, respectively, compared to 10% for UCP1 (Brand and Esteves, 2005).

The most pronounced evidence against a role for UCP2 or UCP3 in maintaining energy balance is the significant increase in UCP2 and UCP3 expression during fasting: not a situation in which energy wasting would be desirable. Two separate studies have shown that a significant increase in UCP3 expression occurs in muscle during fasting, but there is no change in proton leak (Harper et al., 2002). Several studies have not been able to show a correlation between metabolic rate and UCP2 or UCP3 expression (Adams, 2000; Harper et al., 2002; Brand and Esteves, 2005). However, artificial expression of UCP1 into white adipose tissue and skeletal muscle of mice caused a significant increase in energy expenditure at physiological levels of expression (Ricquier, 2005). This evidence demonstrates clearly that UCP2 and UCP3 do not function to uncouple respiration as does UCP1. Bottje et al. (2002) and Iqbal et al.

(2004) reported that broilers with high FCR have greater reactive oxygen species production and protein carbonyl content of skeletal muscle mitochondria, indicating greater oxidative stress. Given the role of UCP3 to mediate reactive oxygen species production and the 70% homology between UCP3 and the avian UCP (Brand and Esteves, 2005), these data suggest greater expression of avian UCP in broilers that are more efficient. However, Kolath et al. (2006b) reported similar levels of expression of UCP3 in skeletal muscle of calves with low and high RFI.

Even though UCP mediated uncoupling does not contribute to energy expenditure, there is sufficient evidence that proton leak does. Harper et al. (2002) stated that 26% of resting energy expenditure in liver was due to proton leak dependent oxygen consumption, while this contribution was 52% in skeletal muscle. At the whole body level, 15 to 20% of resting energy expenditure is due to proton leak (Rolfe and Brown, 1997). Furthermore, differences in energy balance of animals have been attributed to differences in mitochondrial respiration rate. Bottje et al. (2002) demonstrated differences in the respiratory control ratio, a measure of respiratory chain coupling, of skeletal muscle mitochondria between broilers varying in feed conversion ratio. Birds exhibiting a low FCR were found to have greater respiratory chain coupling than those exhibiting a high FCR. Likewise, Golden et al. (2004) and Kolath et al. (2006a) demonstrated that cattle exhibiting low RFI (more efficient) had higher respiratory control ratios than those exhibiting high RFI (less efficient) in skeletal muscle. Other research has also implicated mitochondrial respiration efficiency in performance differences. Brown et al. (1988) found a positive correlation between respiratory control

ratio of liver mitochondria and dam milk production index in Holstein cows suggesting that increased mitochondrial coupling allowed more energy for milk production. However, in beef breeds, ATP synthesis rate was either not correlated or had a negative correlation with growth rate suggesting that mitochondrial efficiency has negligible effect on growth rate in cattle (Brown et al., 1988).

Conclusion

Collectively, these results indicate a lack of knowledge regarding the biological mechanisms involved in accounting for inter-animal variation in feed efficiency. Few studies have evaluated the energy metabolism (heat production and mitochondrial function) of low and high RFI phenotypes, even though differences in energy intake and similar composition of gain suggest differences in heat production. In addition, genetic variation in serum IGF-I concentrations may influence composition of growth and feed efficiency, but this relationship is complex and further investigation is necessary to determine the value of IGF-I as an indicator trait for RFI. Although differences in fat composition exist between low and high RFI calves, the response to selection for improved RFI on female reproduction has not been evaluated. Therefore, the objectives of this dissertation were to characterize RFI in growing calves and examine relationships with carcass composition, serum IGF-I concentration, energy metabolism and reproduction.

CHAPTER II

CHARACTERIZATION OF FEED EFFICIENCY TRAITS IN BRANGUS HEIFERS AND RELATIONSHIPS WITH PERFORMANCE AND ULTRASOUND CARCASS COMPOSITION TRAITS

Introduction

Cost of feed is the largest variable expense associated with producing beef. Approximately 65% of total feed requirements are used to maintain the breeding herd (Arthur et al., 2004). Thus, a large improvement in profitability could be realized by reducing the amount of feed required per unit of production (i.e. improved feed efficiency). Feed conversion ratio is the typical trait measured, but feed conversion ratio is strongly negatively correlated with growth and mature size such that selection against feed conversion ratio would result in increased mature size and feed requirements for maintenance (Herd and Bishop, 2000). In addition, another measure of feed efficiency, partial efficiency of growth, has been characterized in growing calves. Nkrumah et al. (2004) reported a weak positive correlation between partial efficiency of growth and growth, even though this relationship is weak, selection for improved partial efficiency of growth may result in a correlated response in mature body size.

Residual feed intake is the deviation between actual feed intake and expected feed intake calculated by linear regression of feed intake on growth and body size. Koch et al. (1963) suggested that residual feed intake would be an improved measure of feed efficiency due to independence from growth traits. In addition, Arthur et al. (1997,

2001a) and Schenkel et al. (2004) have demonstrated that residual feed intake is a moderately heritable trait (~ 0.40). Furthermore, Herd and Bishop (2000) demonstrated adequate potential for selection against residual feed intake to improve feed conversion ratio and efficiency of maintenance energy expenditure without increasing mature size. Furthermore, several studies have evaluated relationships between residual feed intake and carcass composition traits in growing calves (Arthur et al., 2001a; Carstens et al., 2002; Nkrumah et al., 2004). These studies demonstrated that residual feed intake is weakly correlated (0.14 to 0.25) with measures of 12^{th} rib fat thickness, but not with longissimus muscle area or intramuscular fat.

However, few studies have evaluated relationships between multiple measures of feed efficiency and carcass composition in replacement heifers. Thus, the objectives of this study were to characterize feed efficiency traits and examine phenotypic correlations with performance and ultrasound carcass composition traits in growing Brangus heifers.

Materials and Methods

Animals and Management

A total of 468 purebred Brangus heifers from Camp Cooley ranch were used in this study. Four postweaning tests were conducted in 4 consecutive years at the O. D. Butler Jr. Animal Science Teaching Research and Extension Center in College Station, TX to measure performance and feed efficiency of heifers. Upon arrival, heifers were blocked by BW, randomly assigned to 20 pens (6 heifers per pen) and adapted to the test diet for 24 d. Heifers were fed ad libitum twice daily and individual feed intakes

measured weekly for 70 d using Calan gate feeders. Heifers were weighed at 7-d intervals and real-time ultrasound measurements of 12th rib fat thickness (**BF**), longissimus muscle area (**LMA**) and percent intramuscular fat (**IM**) obtained at the start and end of each test by a Ultrasound Guidelines Council field certified technician using an Aloka 500-V instrument with a 17-cm 3.5 MHz transducer (Corometrics Medical Systems, Inc., Wallingford, CT, USA). Images were collected and analyzed by the Beef Image Analysis Pro software (Designer Genes Inc., Harrison, AR) or sent to the National Centralized Ultrasound Processing laboratory (Ames, IA).

Diet ingredient samples were collected weekly and composited by weight at the end of each test. Moisture analysis was conducted by drying in a forced air oven for 48 h at 105^{O}C (AOAC, 1995), and chemical analysis conducted by an independent laboratory (Cumberland Valley Analytical Services, Inc., Hagerstown, MD). Metabolizable and net energy concentrations of the test diets were computed from the chemical analysis using the Cornell Net Carbohydrate and Protein System (Version 5.0, Cornell University, Ithaca, NY). Ingredient and chemical composition of the diet fed to heifers is presented in tables 2.1 and 2.2, respectively.

Computations

Growth rates of individual heifers were modeled by linear regression of BW on day of test using the general linear model of SAS (SAS Inst., Cary, NC). These regression coefficients were used to compute initial and final BW and ADG. Metabolic BW (**MBW**; mid-test BW$^{.75}$) was then computed as the average of initial and final BW

raised to the 0.75 power. Moisture analyses of diet ingredient samples were used to compute average daily DMI from feed intake data.

A total of four feed efficiency traits were computed for each heifer. Residual feed intake (**RFIp**) was computed as actual DMI minus expected DMI to meet growth and maintenance energy requirements (Koch et al., 1963). Expected DMI was derived from linear regression of DMI on MBW and ADG using the mixed procedure of SAS with test and test by independent variable interactions as random effects and the variance component option used for the var-(co)variance matrix structure (St. Pierre, 2001). Feed conversion ratio (FCR) was computed as the ratio of daily DMI to ADG. Partial efficiency of growth (**PEG**) was computed as the ratio of ADG to DMI used for growth (actual DMI minus expected DMI for maintenance). Expected DMI to meet maintenance requirements was calculated as MBW multiplied by 0.077 Mcal NEm/$kg^{.75}$ then divided by NEm concentration of the test diets.

To determine if individual-animal variation in carcass composition (ultrasound traits) affected the derivation of expected DMI, a two-step approach was used. First, stepwise regression analysis was performed using the regression procedure of SAS to determine the order in which ultrasound carcass composition traits should be included in the base model that included MBW and ADG. Using the order derived from stepwise regression analysis, ultrasound traits were then sequentially added to the base regression model, and the resulting change in coefficient of determination used to determine their relative importance to derivation of expected DMI. The coefficient of determination was

Table 2.1. Ingredient composition of the diet fed to Brangus heifers in each of the four tests

Item	Value, as-fed %
Chopped alfalfa	35.00
Pelleted alfalfa	15.00
Dry rolled corn	20.95
Cottonseed hulls	21.50
Molasses	7.00
Salt	0.40
Vitamin E[1]	0.14
Trace mineral[2]	0.02

[1]Vitamin E contained 44,000 IU/kg of product.

[2]Trace mineral contained minimum 19.0% Zn, 7.0% Mn, 4.5% Cu, 4,000 ppm Fe, 2,300 ppm I, 1,000 ppm Se and 500 ppm Co.

Table 2.2. Chemical composition of diets fed to Brangus heifers in the four tests

Item	Test 1	Test 2	Test 3	Test 4
DM, %	87.49	89.36	88.05	86.81
CP, % DM	12.57	13.16	12.48	12.58
NDF, % DM	43.04	43.75	44.97	45.87
ME, Mcal/kg DM[1]	2.03	2.00	1.93	1.96

[1]Metabolizable energy content computed using Cornell Net Carbohydrate and Protein System.

computed using four models:

(2.1) $Y_j = \beta_0 + \beta_1 MBW_j + \beta_2 ADG_j + \beta_x X_j + e_j$

where Y_j = DMI of the *j*th heifer, X_j = ultrasound composition trait(s) for the *j*th heifer, β_0 = regression intercept, β_1 = partial regression coefficient on MBW, β_2 = partial regression coefficient on ADG, β_x = partial regression coefficient on ultrasound composition trait X, e_j = random test and uncontrolled error for the *j*th heifer,

(2.2) $Y_{ij} = \beta_0 + \beta_1 MBW_{ij} + \beta_2 ADG_{ij} + \beta_3 T_i + \beta_x X_{ij} + e_{ij}$

where Y_{ij} = DMI of the *j*th heifer in the *i*th test, T_i = fixed effect of the *i*th test, X_{ij} = ultrasound composition trait(s) for the *j*th heifer in the *i*th test, β_0 = regression intercept, β_1 = partial regression coefficient on MBW, β_2 = partial regression coefficient on ADG, β_3 = partial regression coefficient on test, β_x = partial regression coefficient on ultrasound composition trait X, e_{ij} = random uncontrolled error and error associated with fixed interactions of independent variables and test for the *j*th heifer in the *i*th test,

(2.3) $Y_{ij} = \beta_0 + \beta_1 MBW_{ij} + \beta_2 ADG_{ij} + \beta_3 \tau_i + \beta_4 MBW_j * \tau_i + \beta_5 ADG_j * \tau_i + \beta_{x1} X_{ij} + \beta_{x2} X_j * \tau_i + e_{ij}$

where Y_{ij} = DMI of the *j*th heifer in the *i*th test, τ_i = random effect of the *i*th test, X_{ij} = ultrasound composition trait(s) for the *j*th heifer in the *i*th test, β_0 = regression intercept, β_1 = partial regression coefficient on MBW, β_2 = partial regression coefficient on ADG, β_3 = partial regression coefficient on random test, β_4 = partial regression coefficient on random interaction of

MBW and test, β_5 = partial regression coefficient on random interaction of ADG and test, β_{x1} = partial regression coefficient on ultrasound composition trait X, β_{x2} = partial regression coefficient on the random interaction of ultrasound composition trait X and test, e_{ij} = uncontrolled error for the *j*th heifer in the *i*th test,

(2.4) $Y_j^* = Y_{ij} - [\beta_3\tau_i + \beta_4 MBW_j*\tau_i + \beta_5 ADG_j*\tau_i + \beta_{x2}X_j*\tau_i]$,

$Y_j^* = \beta_0 + \beta_1 MBW_j + \beta_2 ADG_j + \beta_{x1}X_j + e_j$

where Y_j^* = DMI of the *j*th heifer without the effect of the *i*th test, Y_{ij} = DMI of the *j*th heifer in the *i*th test, τ_i = random effect of the *i*th test, X_j = ultrasound composition trait(s) for the *j*th heifer, β_0 = regression intercept, β_1 = partial regression coefficient on MBW, β_2 = partial regression coefficient on ADG, β_3 = partial regression coefficient on random test, β_4 = partial regression coefficient on random interaction of MBW and test, β_5 = partial regression coefficient on random interaction of ADG and test, β_{x1} = partial regression coefficient on ultrasound composition trait X, β_{x2} = partial regression coefficient on the random interaction of ultrasound composition trait X and test, e_{ij} = uncontrolled error for the *j*th heifer in the *i*th test.

Results from these analyses were used to compute an additional RFI trait (**RFIc**), in which expected DMI was adjusted for variation in ultrasound estimates of carcass composition as well as MBW and ADG.

Statistical Analysis

All performance, feed efficiency and ultrasound carcass composition traits were adjusted to remove the random effect of test using the MIXED procedure of SAS. Phenotypic correlation coefficients among adjusted performance, feed efficiency and ultrasound carcass composition traits were generated using the CORR procedure of SAS. To further characterize RFI, heifers were classified into low, medium and high RFI groups that were < 0.5, ± 0.5 and > 0.5 SD, respectively, from the mean RFIp of 0.00 ± 0.71 kg/d, and the MIXED procedure of SAS used to examine fixed effect of RFIp group on performance, feed efficiency and ultrasound composition traits. Comparisons of least square means between RFIp groups were performed using Tukey's post hoc test.

Results and Discussion

Summary statistics are presented in Table 2.3 for the four performance tests. The initial age of the heifers averaged 231 ± 12 d across the four tests and ranged from 226 d in test 1 to 236 d in test 2. The average performance and DMI were slightly numerically lower for heifers in test 1 than in the other tests. However, the variation in ADG (CV = 13 to 17%), DMI (CV = 9 to 12%) and FCR (CV = 10 to 15%) were similar across the four tests. Few studies have measured feed intake and efficiency in heifers, but Arthur et al. (2003) reported similar means and SD for DMI (9.2 ± 1.2 kg/d) and ADG (1.19 ± 0.19 kg/d) in Angus heifers fed a roughage-based diet. In addition, Arthur et al. (2001a) reported overall means and SD of 1.26 ± 0.24 kg/d, 9.65 ± 1.33 kg/d, 7.79 ± 1.35 and 0.00 ± 0.74 kg/d for ADG, DMI, FCR and RFI, respectively, of Angus bulls and heifers fed a roughage-based diet. The overall means and phenotypic standard deviations of the

test-adjusted variables (Table 2.4) were within the range of the variables across the four tests.

The amount of explained variation in DMI by the base regression on MBW and ADG using the four models is presented in Table 2.5. The base regression explained 42.6% of the variation in DMI without including the effect of test (model 2.1). This is lower than what would be expected based on the four individual tests (R^2 ranged from 0.433 to 0.572). However, including test as a fixed effect into model 2 only slightly increased the R^2 (0.442). Previous authors have included test as a class variable (fixed or random effect unknown; Arthur et al., 2001a, 2003; Schenkel et al., 2004) or as a fixed effect (Arthur et al., 2001b). However, these authors did not report the effect that this had on the amount of explained variation in DMI. Arthur et al. (2003) reported an R^2 of 0.687 in growing heifers when using a model that included test. St. Pierre (2001) indicated that ignoring the effect of test and test by independent variable interactions when performing regression across multiple tests would lead to biased estimates of regression coefficients. This would then result in a biased estimate of the residual variance (SD of RFI). In addition, test is fundamentally a random variable because inference is to be made about future tests. In our study, including test and test by independent variable (MBW and ADG) interactions as random effects into model 2.3 resulted in an improved R^2compared to model 1 or 2 (0.555 vs. 0.426 and 0.442, respectively) suggesting that including random interactions of test and independent variables was important to explain variation in DMI across the four tests. The R^2 for

Table 2.3. Summary statistics (± SD) of performance, feed efficiency and ultrasound composition traits of Brangus heifers in the four tests

Trait[1]	Test 1	Test 2	Test 3	Test 4
No. animals	114	115	119	120
Initial age, d	225.8 ± 9.1	236.0 ± 10.7	235.6 ± 14.6	228.3 ± 11.7
Initial BW, kg	285.1 ± 28.0	268.5 ± 23.8	267.8 ± 25.8	264.4 ± 26.9
Final BW, kg	345.8 ± 31.2	342.9 ± 28.9	337.7 ± 29.0	339.7 ± 30.0
ADG, kg/d	0.90 ± 0.15	1.06 ± 0.16	1.00 ± 0.13	1.08 ± 0.17
DMI, kg/d	9.10 ± 1.11	9.47 ± 1.04	9.92 ± 1.06	9.53 ± 0.88
FCR, feed/gain	10.26 ± 1.54	9.04 ± 1.31	10.02 ± 1.00	9.01 ± 1.21
PEG[2]	0.22 ± 0.04	0.24 ± 0.04	0.21 ± 0.03	0.24 ± 0.04
RFIp, kg/d	0.00 ± 0.75	0.00 ± 0.68	0.00 ± 0.70	0.00 ± 0.66
Initial BF, cm	0.44 ± 0.15	0.38 ± 0.15	0.37 ± 0.09	0.43 ± 0.13
Initial LMA, cm^2	57.58 ± 7.15	62.67 ± 7.27	52.76 ± 7.16	52.39 ± 7.64
Final BF, cm	0.65 ± 0.17	0.68 ± 0.18	0.66 ± 0.17	0.66 ± 0.19
Final LMA, cm^2	70.96 ± 7.94	79.42 ± 7.40	62.51 ± 7.18	63.48 ± 8.55

[1]FCR = feed conversion ratio; PEG = partial efficiency of growth; RFIp = residual feed intake from base model; BF = 12th rib fat thickness; LMA = longissimus muscle area.

[2]PEG is ADG / DMI for growth.

Table 2.4. Overall summary statistics of test-adjusted performance, feed efficiency and ultrasound composition traits of Brangus heifers

Trait[1]	Mean	SD	Minimum	Maximum
Initial age, d	231.4	11.7	197.0	259.0
Initial BW, kg	271.4	26.1	211.1	337.9
Final BW, kg	341.5	29.7	273.5	421.3
ADG, kg/d	1.01	0.15	0.59	1.53
DMI, kg/d	9.51	1.02	6.94	12.68
FCR, feed/gain	9.55	1.27	6.71	15.72
PEG, ADG/DMI for growth	0.23	0.04	0.12	0.37
RFIp, kg/d	0.00	0.71	-2.01	2.20
RFIc, kg/d	0.00	0.68	-1.90	2.01
Final BF, cm	0.66	0.18	0.20	1.17
Final LMA, cm^2	69.09	7.76	46.39	89.67

[1]FCR = feed conversion ratio; RFIp = residual feed intake from base model; RFIc = residual feed intake from composition adjusted model; BF = 12^{th} rib fat thickness; LMA = longissimus muscle area.

Table 2.5. Percentage of variation explained (R^2) by different models to predict DMI

	Model Number[1]			
Regression[2]	(2.1) $F1+e_1$	(2.2) $F2+e_2$	(2.3) $F1+R+e_3$	(2.4) $F1-R+e_3$
Base model (BM; ADG and MBW)	0.426	0.442	0.555	0.534
BM + gain in BF	0.477	0.493	0.597	0.576
BM + final LMA	0.446	0.452	0.566	0.541
BM + gain in BF + final LMA	0.508	0.512	0.602	0.578

[1]F1 =fixed effects of indicated variables; F2 = fixed effects of indicated variables + fixed effect of test; R = random effects of test and test by independent variable interactions; e_1 = random test and uncontrolled error; e_2 = random uncontrolled error and error associated with fixed interactions of test and independent variables; e_3 = random uncontrolled error.

[2]MBW = mid-test $BW^{0.75}$; BF = 12^{th} rib fat thickness; LMA = longissimus muscle area.

model 2.3 was similar to that of the individual tests giving a reasonable description of the variation in DMI explained by the independent variables. However, removing the random effects of test and test by independent variable interactions from actual DMI to obtain DMI adjusted for test (model 2.4) resulted in an R^2 of 0.534, which is more similar to the average ($R^2 = 0.529$) of the individual tests than the R^2 of model 2.3. Therefore, based on our analysis, we conclude that model 2.3 provides the best estimate of RFI (uncontrolled error) when calculated across multiple tests compared to models 2.1 and 2.2, and that adjusting DMI for test, as in model 2.4, best describes the variation in DMI explained by the independent variables, MBW and ADG, compared to models 2.1, 2.2 and 2.3.

Results from stepwise regression analysis determined the order of inclusion of ultrasound carcass composition traits to be: gain in BF, then final LMA. Final BF and gain in LMA were not selected as significant variables by the regression procedure. Gain in BF explained the largest amount of additional variation (5 percentage units). Arthur et al. (2003) and Basarab et al. (2003) also reported that inclusion of carcass fat traits in a linear regression model accounted for more of the variation in DMI (R^2 increase ranges from 2 to 4 percentage units). The inclusion of final LMA had minimal effect on the amount of explained variation in DMI (0.2 percentage units) above gain in BF according to model 2.4. Thus, the final regression to compute carcass adjusted RFI (RFIc) from expected DMI included gain in BF, in addition to MBW and ADG as fixed effects, and test and test by independent variable interactions as random effects.

Phenotypic correlations among growth and feed efficiency traits are presented in Table 2.6. Dry matter intake was strongly correlated with ADG (0.57) and final BW (0.49), which is consistent with phenotypic correlations previously reported in growing steers (Nkrumah et al., 2004), bulls and heifers (Arthur et al., 2001a) and bulls (Fox et al., 2004; Schenkel et al., 2004). Feed conversion ratio was weakly correlated with DMI (0.15), and as expected, strong phenotypic correlations were found between FCR and ADG (-0.71). Recent studies have also reported strong phenotypic and genetic correlations between FCR and ADG (< -0.50; Arthur et al., 2001b, c; Schenkel et al., 2004). In this study, PEG was strongly correlated with DMI (-0.55) and weakly correlated with ADG (0.25). Similarly, Arthur et al. (2001b) and Nkrumah et al. (2004) reported strong correlations of PEG with DMI and weak correlations with ADG. Residual feed intake from the base model and RFIc were strongly correlated with DMI (0.70 and 0.67, respectively), but independent of ADG and final BW such that heifers with low RFIp consumed 15% less ($P < 0.01$) DMI than heifers with high RFIp, even though ADG and final BW were similar (Table 2.7). This is not unexpected as use of linear regression to compute RFI forces it to be phenotypically independent of the component traits. In general, RFIp has been found to be both phenotypically and genetically independent of growth and body size in growing bulls (Arthur et al., 2001c; Fox et al., 2004; Schenkel et al., 2004) and bulls and heifers (Arthur et al., 2001a). These results suggest that selection for improved FCR or PEG would result in increased cow mature size and feed requirements for maintenance, but selection for improved RFI would have minimal impact on cow mature size.

Table 2.6. Phenotypic correlations among performance and feed efficiency traits in Brangus heifers

Trait[1]	ADG	DMI	FCR	PEG	RFIp	RFIc
FBW	0.49*	0.65*	-0.04	-0.01	0.00	0.00
ADG		0.57*	-0.71*	0.25*	-0.01	0.00
DMI			0.15*	-0.55*	0.70*	0.67*
FCR				-0.77*	0.59*	0.56*
PEG					-0.79*	-0.75*
RFIp						0.97*

[1]FCR = feed conversion ratio; PEG = partial efficiency of growth; RFIp = residual feed intake from base model; RFIc = residual feed intake from composition adjusted model; FBW = final BW.

*Correlations are different from zero at $P < 0.05$.

Table 2.7. Performance, feed efficiency and ultrasound composition traits of heifers with low (< 0.5 SD), medium (± 0.5 SD) and high (> 0.5 SD) RFI

Trait[1]	Low RFI	Med RFI	High RFI	SE	*P*-value
No. animals	150	176	142		
Initial BW, kg	272.4	271.0	271.0	3.1	0.87
Final BW, kg	342.8	340.7	341.2	3.5	0.81
ADG, kg/d	1.01	1.01	1.01	0.02	0.86
DMI, kg/d	8.76^{x}	9.48^{y}	10.34^{z}	0.09	0.01
FCR, feed/gain	8.75^{x}	9.52^{y}	10.42^{z}	0.13	0.01
PEG, ADG/DMI for growth	0.271^{x}	0.224^{y}	0.189^{z}	0.003	0.01
RFIp, kg/d	-0.78^{x}	-0.01^{y}	0.83^{z}	0.04	0.01
RFIc, kg/d	-0.73^{x}	-0.01^{y}	0.76^{z}	0.04	0.01
Initial composition traits					
12^{th} rib fat thickness, cm	0.42	0.40	0.39	0.02	0.08
Longissimus muscle area, cm^2	57.53^{x}	56.30^{xy}	55.15^{y}	0.85	0.02
Intramuscular fat, %	2.88	2.97	3.03	0.07	0.09
Final composition traits					
12^{th} rib fat thickness, cm	0.65	0.66	0.68	0.02	0.45
Longissimus muscle area, cm^2	69.77	68.88	68.65	0.92	0.43
Intramuscular fat, %	3.38	3.49	3.50	0.08	0.15
Gain in composition traits					
12^{th} rib fat thickness, cm	0.23^{x}	0.25^{x}	0.29^{y}	0.01	0.01
Longissimus muscle area, cm^2	12.19	12.55	13.47	0.78	0.24
Intramuscular fat, %	0.50	0.53	0.49	0.06	0.77

[1]FCR = feed conversion ratio; PEG = partial efficiency of growth; RFIp = residual feed intake from base model; RFIc = residual feed intake from composition adjusted model.

[xyz]Means in the same row with unlike superscripts are different at $P < 0.05$.

Residual feed intake from the base model and RFIc were strongly correlated with FCR (0.59 and 0.56, respectively) and PEG (-0.79 and -0.75, respectively) such that heifers with low RFIp had 16% lower ($P < 0.05$) FCR and 43% higher ($P < 0.05$) PEG compared to heifers with high RFIp. Similarly, Arthur et al. (2001b) and Nkrumah et al. (2004) reported strong phenotypic correlations of RFIp with FCR (0.57 and 0.62, respectively) and PEG (-0.65 and -0.89, respectively) in growing bulls and steers, respectively. These data indicate stronger relationships of RFI with PEG than with FCR, which is not unexpected given that both RFI and PEG attempt to partition feed intake into maintenance and growth requirements, whereas, FCR does not. Furthermore, these data indicate that selection for improved RFI or PEG will result in an improvement in gross feed efficiency (FCR).

Pearson (0.97) and Spearman rank (0.96) correlation coefficients between RFIp and RFIc were strong. Other studies have reported weaker rank correlations (range 0.87 to 0.92) between RFI computed from base and carcass adjusted models (Basarab et al., 2003; Lancaster et al., 2005). As described previously, relationships of DMI, FCR, and PEG with RFIc were similar to those with RFIp, suggesting that selection for improved RFIc would result in similar corresponding changes in feed intake and efficiency as selection for improved RFIp. These data suggest that inclusion of carcass composition traits in the regression model to derive expected DMI will not have additional benefit above the base regression model.

Longissimus muscle area and BF traits were weakly to moderately correlated with ADG and DMI (Table 2.8). Nkrumah et al. (2004) and Schenkel et al. (2004) also

reported weak to moderate correlations of BF and LMA with ADG and DMI in finishing steers and growing bulls, respectively. Final BF was weakly correlated with FCR, PEG and RFIp such that more efficient heifers were leaner. In addition, gain in BF was weakly correlated with PEG (-0.16) and RFIp (0.22) such that heifers with low RFIp gained 21% less ($P < 0.05$) BF during the test than heifers with high RFIp. Recent studies have reported weak positive correlations between RFI and carcass fat traits in growing bulls (Arthur et al., 2001a; Fox et al., 2004; Schenkel et al., 2004) and steers (Basarab et al., 2003; Nkrumah et al., 2004), as well as, between FCR and carcass fat traits (Nkrumah et al., 2004; Schenkel et al., 2004). Gain in BF was not correlated with RFIc, which is expected given that inclusion of gain in BF in a linear regression model forces RFIc to be independent of its component traits. In addition, final BF was not correlated with RFIc, which agrees with the results of Basarab et al. (2003) who reported that inclusion of change in carcass fat traits during the test in an adjusted model to compute expected DMI resulted in a lack of correlation between final carcass fat traits and RFIc.

Final LMA and gain in LMA were weakly correlated with FCR such that more efficient heifers had less final LMA, but gained more LMA during the test. Final LMA and gain in LMA were not correlated with PEG, RFIp or RFIc. Previous studies have reported non-significant correlations between final LMA and RFIp (-0.10 to 0.09; Arthur et al., 2001a, 2003; Carstens et al., 2002; Nkrumah et al., 2004; Schenkel et al., 2004). In addition, Basarab et al. (2003) reported a lack of correlation between gain in ultrasound LMA and RFIp in finishing steers. In this study, heifers with low RFIp had similar final

Table 2.8. Phenotypic correlations between feed efficiency and ultrasound composition traits in Brangus heifers

Trait[1]	ADG	DMI	FCR	PEG	RFIp	RFIc
Final BF	-0.03	0.23*	0.21*	-0.17*	0.12*	-0.03
Gain in BF	0.23*	0.35*	0.00	-0.16*	0.22*	0.00
Final LMA	0.01	0.18*	0.13*	-0.03	-0.05	-0.07
Gain in LMA	0.17*	0.12*	-0.09*	0.00	0.05	0.01
Final IM	-0.11*	-0.02	0.10*	-0.10*	0.08	0.06
Gain in IM	-0.01	-0.05	-0.04	0.05	-0.04	-0.04

[1]FCR = feed conversion ratio; PEG = partial efficiency of growth; RFIp = residual feed intake from the base model; RFIc = residual feed intake from the composition adjusted model; BF = 12th rib fat thickness; LMA = longissimus muscle area; IM = intramuscular fat.

*Correlations are different from zero at $P < 0.05$.

LMA and gain in LMA during the test compared to heifers with high RFIp; however, heifers with low RFIp had larger ($P < 0.05$) initial LMA (57.53 vs. 55.15 cm^2) than heifers with high RFIp. Brown (2005) also reported greater initial ultrasound LMA in finishing steers with low RFIp than steers with high RFIp (63.20 vs. 58.65 cm^2, respectively), but similar final LMA.

Final IM was weakly correlated with FCR (0.10) and PEG (-0.10), but not RFIp or RFIc such that more efficient heifers had less IM, whereas, gain in IM was not correlated with any of the feed efficiency traits. Nkrumah et al. (2004) reported a weak correlation of final ultrasound marbling score with PEG (-0.19), but not FCR or RFIp in growing steers. Similarly, Schenkel et al. (2004) reported no correlation of final ultrasound IM with FCR or RFIp in growing bulls. In contrast, Basarab et al. (2003) and Nkrumah et al. (2007) reported positive correlations between carcass marbling score and RFIp in growing steers.

Implications

Identifying a feed efficiency trait that facilitates reductions in feed inputs without impacting growth or other value-determining traits (e.g., carcass composition) has the capability to improve profitability of beef production systems. Compared to the other feed efficiency traits examined, RFI has considerable potential for use in selection programs as it is less impacted by differences in growth. In addition, RFI can easily be computed to be independent of carcass composition traits; however, this appears to provide little benefit to accurate selection for improved RFI. Furthermore, due to its

strong relationship with FCR, RFI can be used as a selection tool to improve gross feed efficiency without influencing cow mature size.

CHAPTER III

EFFECTS OF DIVERGENT SELECTION FOR SERUM IGF-I CONCENTRATION ON PERFORMANCE, FEED EFFICIENCY AND ULTRASOUND CARCASS COMPOSITION TRAITS IN ANGUS BULLS AND HEIFERS

Introduction

Feed efficiency is an important trait to consider in developing selection programs to identify cattle that are more economically and environmentally sustainable to produce. Considerable genetic variation is known to exist in efficiency of feed utilization (Herd and Bishop, 2000), but the expense of measuring feed intake in cattle has limited the implementation of selection programs that target this trait. Moreover, the traditional measure of feed efficiency (feed conversion ratio; FCR) is inversely related to growth and mature size, such that selection for improved FCR leads to larger mature cow size (Archer et al., 1999). Residual feed intake (RFI) is an alternative measure of efficiency that facilitates selection for improved feed efficiency in cattle independent of growth traits and mature size.

Identification of physiological indicators that are predictive of RFI would facilitate early detection, and enhance accuracy of selection of animals with improved feed efficiency. The endocrine actions of insulin-like growth factor-I (IGF-I**)** affect glucose and amino acid metabolism, protein accretion and linear growth (Jones and Clemmons, 1995) suggesting a role for IGF-I in nutrient utilization. Research from

Australia has demonstrated that serum concentrations of IGF-I are genetically correlated with RFI in pigs (Bunter et al., 2002) and cattle (Moore et al., 2005). Moore et al. (2005) reported a strong genetic correlation (0.57) between RFI and serum IGF-I in bulls and heifers. Likewise, Brown et al. (2004) reported positive phenotypic correlations of serum IGF-I with RFI (0.38) and FCR (0.36) in growing bulls.

Since 1989, Davis and coworkers have conducted a divergent selection study based on postweaning serum IGF-I concentrations in Angus cattle. Following 5 yr of selection, Davis and Simmen (1997) reported a negative genetic correlation (-0.30 to -0.50) between serum IGF-I concentration and postweaning gain. However, more recent analysis (Davis and Simmen, 2006) revealed that IGF-I was positively correlated (0.10 to 0.30) with growth traits following 10 yr of divergent selection. These researchers have not evaluated feed efficiency traits in calves selected for low or high serum IGF-I concentration. Therefore, the primary objective of this study was to examine the effects of divergent selection for serum IGF-I on performance and feed efficiency traits in Angus calves. The central hypothesis tested was that calves from the low IGF-I selection line would have improved RFI compared to calves from the high IGF-I selection line.

Materials and Methods

Animals and Management

Angus bull and heifer progeny from parents divergently selected for serum IGF-I concentration for approximately 13 yr at the Eastern Agricultural Research Station (**EARS**, The Ohio State University) were used in this study. Selection procedures are reported elsewhere (Davis and Simmen, 1997). Calves used in this experiment were

weaned on October 6, 2004 and October 5, 2005 and shipped to the O.D. Butler, Jr. Animal Science Complex at Texas A&M University on February 10, 2005 and January 11, 2006 for studies 1 and 2, respectively. In study 1, upon weaning calves were adapted to a grain-based diet (30% shelled corn, 25% crimped oats, 10% ground corn cobs, 10% dehydrated alfalfa, 10% wheat middlings, 10% soybean meal, 3% molasses and 2% minerals on as-fed basis) at the EARS for 55 d and growth traits measured for 70 d; bulls were allowed ad libitum access to the diet, whereas, heifers were limit fed to gain approximately 0.75 kg/d. Upon arrival at Texas A&M University, bulls (low line n = 9; high line n = 8; initial BW = 367.1 ± 22.9 kg) and heifers (low line n = 9; high line n = 13; initial BW = 286.4 ± 28.6 kg) were blocked by gender and BW, randomly assigned to pens (6 calves per pen), and adapted to a roughage-based diet (ME = 1.95 Mcal/kg DM) for 24 d. In study 2, upon weaning calves were fed fescue hay ad libitum and offered a supplement (80% soybean hulls: 20% shelled corn) at 2.7 $kg \cdot head^{-1} \cdot d^{-1}$ for 98 days prior to being shipped to Texas A&M University. Upon arrival, bulls (low line n = 15; high line n = 12; initial BW = 297.5 ± 34.4 kg) and heifers (low line n = 9; high line n = 20; initial BW = 256.0 ± 25.1 kg) were blocked by gender and BW, randomly assigned to pens (6 calves per pen), and adapted to a grain-based diet (ME = 2.85 Mcal/kg DM) for 32 d. Individual intakes were measured using Calan gate feeders and BW measured at 7-d intervals for 77 and 70 d in studies 1 and 2, respectively. Ultrasound measures of 12^{th} rib fat thickness (BF) and longissimus muscle area (LMA) were obtained at the start and end of each study by a Ultrasound Guidelines Council field certified technician using an Aloka 500-V instrument with a 17-cm 3.5 MHz

transducer (Corometrics Medical Systems, Inc., Wallingford, CT, USA). Images were analyzed using the Beef Image Analysis Pro software (Designer Genes Inc., Harrison, AR) in study 1, and sent to the National Centralized Ultrasound Processing laboratory (Ames, IA) for analysis in study 2. In addition, hip height was measured at the start and end of each study.

Diet ingredient samples were collected weekly throughout each study and composited by weight for chemical analyses. Moisture analysis was conducted by drying in a forced-air oven for 48 h at 105^{O}C (AOAC, 1995). Chemical analysis was conducted by an independent laboratory (Cumberland Valley Analytical Services, Inc., Hagerstown, MD), and ME concentrations of the experimental diets computed using the Cornell Net Carbohydrate and Protein System (Version 5.0, Cornell University, Ithaca, NY). Ingredient and chemical composition of the experimental diets are presented in Table 3.1.

Growth rates of individual calves were modeled by linear regression of BW against day of study using the general linear model of SAS (SAS Inst., Cary, NC). Regression coefficients were used to compute initial and final BW, ADG and metabolic BW (MBW; mid-test BW$^{.75}$). Moisture analysis of diet ingredient samples was used to determine average daily DMI from as-fed feed intake data. Residual feed intake was computed within study as the difference between actual DMI and that predicted from the regression of DMI on MBW and ADG using the following model:

(3.1) $DMI = ß_0 + ß_1MBW + ß_2ADG + ß_3gender + ß_4gender*MBW + ß_5gender*ADG + €,$

Table 3.1. Ingredient and chemical composition of diets fed to bulls and heifers in studies 1 and 2

Item	Study 1	Study 2
Ingredient, % as fed		
Chopped alfalfa hay	35.00	12.80
Pelleted alfalfa hay	15.00	3.20
Cracked corn	20.87	74.83
Cottonseed hulls	21.50	2.13
Molasses	7.00	4.27
Salt	0.40	1.00
Urea	--	1.17
Vitamin E[1]	0.14	0.34
Vitamin ADE[2]	0.08	0.20
Trace mineral[3]	0.02	0.05
Chemical analysis		
DM, % AF	88.26	88.85
CP, % DM	13.41	13.14
NDF, % DM	47.25	17.46
ADF, % DM	37.74	11.19
ME, Mcal/kg DM	1.95	2.85

[1]Vitamin E contained 44,000 IU/kg of product.

[2]Vitamin ADE contained 2,200,000 IU vitamin A/kg, 440,000 IU vitamin D/kg and 8,800 IU vitamin E/kg of product.

[3]Trace mineral contained a minimum of 19.0% Zn, 7.0% Mn, 4.5% CU, 4,000 ppm Fe, 2,300 ppm I, 1,000 ppm Se and 500 ppm Co.

where $ß_0$ = y-intercept, $ß_1$ = partial regression coefficient of MBW, $ß_2$ = partial regression coefficient of ADG, $ß_3$ = partial regression coefficient of gender, $ß_4$ = partial regression coefficient of gender by MBW interaction, $ß_5$ = partial regression coefficient of gender by ADG interaction, € = error term.

Blood Collection and Assays

To determine serum IGF-I concentrations at weaning, blood samples were collected via blood spot cards at 2 wk postweaning in study 1, and at weaning in study 2, and IGF-I determined using an enzyme-linked immunosorbent assay (Primegro Inc., Adelaide, SA). At the start and end of each feed-intake measurement period, blood samples were collected via jugular venipuncture using evacuated serum tubes (Becton, Dickson and Company, Franklin Lakes, NJ), and serum harvested after centrifugation (3,000 x *g* at 4^{O}C for 20 min), after blood samples were allowed to clot overnight at 4^{O}C. Serum samples were stored at -20^{O}C for later analysis of IGF-I concentrations in duplicate using enzyme immunoassay procedures (IDS, Inc., Fountain Hills, AZ).

Statistical Analysis

Due to differences in pre-study management, and the diets fed during the studies, each study was analyzed independently. The effects of IGF-I selection line and gender on performance, feed efficiency and ultrasound carcass composition traits were evaluated using the mixed procedure of SAS (SAS Inst., Cary, NC). The model included fixed effects of IGF-I selection line, gender and the interaction term. Least square means were computed for IGF-I selection line within gender groups and pairwise comparisons made using Tukey's *W* procedure. Phenotypic correlations among performance, feed

efficiency and ultrasound carcass composition traits and serum IGF-I concentrations were computed using the correlation procedure of SAS with the partial option used to adjust for the fixed effects of gender and IGF-I selection line. Additionally, regression analysis was used to evaluate the effect gender on the relationship between RFI and serum IGF-I. A full model that included the effects of gender, selection line and gender by selection line interaction as class variables, serum IGF-I concentration as a covariate, and all interactions. Non-significant interaction terms were removed and the final reduced model included gender, selection line, serum IGF-I and gender by serum IGF-I interaction.

Results

As expected, serum concentrations of IGF-I were affected by selection line (Table 3.2). At weaning, calves from the high IGF-I selection line had 31 and 40% higher ($P < 0.05$) IGF-I concentrations than calves from the low selection line in studies 1 and 2, respectively. There was a gender by selection line interaction ($P < 0.05$) for IGF-I concentrations at the start of study 1. High selection line bulls had 36% higher ($P < 0.05$) IGF-I concentrations than low selection line bulls, whereas, heifers from divergent selection lines had similar serum IGF-I concentrations at the start of study 1. At the end of study 1, and at the start and end of study 2, IGF-I concentrations were 16 to 23% higher ($P < 0.05$) in calves from the high selection line compared to those from the low selection line.

In study 1, IGF-I selection line had little influence on ultrasound carcass composition (Table 3.3). Calves from the high IGF-I selection line had numerically

Table 3.2. Effects of gender and IGF-I selection line on serum IGF-I concentrations in studies 1 and 2

	Heifers		Bulls			*P*-value[1]		
Trait[2]	High	Low	High	Low	SE	L	G	L*G
Study 1								
No. animals	13	9	8	9				
Weaning IGF-I, ng/mL	234.3	156.3	274.3	232.8	25.5	0.02	0.02	0.44
Initial IGF-I, ng/mL	184.8^{x}	150.8^{x}	328.3^{y}	241.6^{z}	13.4	0.01	0.01	0.04
Final IGF-I, ng/mL	165.0	133.5	260.0	211.5	13.1	0.01	0.01	0.49
Study 2								
No. animals	20	9	12	15				
Weaning IGF-I, ng/mL	127.2	93.0	191.0	134.0	16.7	0.01	0.01	0.42
Initial IGF-I, ng/mL	158.7	117.3	251.1	234.5	13.4	0.01	0.01	0.27
Final IGF-I, ng/mL	147.4	125.5	294.8	254.9	13.6	0.01	0.01	0.43

[1]*P*–value for the effects of IGF-I selection line (L), gender (G) and the interaction term.

[2]IGF-I = insulin-like growth factor-I.

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

Table 3.3. Effects of gender and IGF-I selection line on ultrasound composition traits in studies 1 and 2

	Heifers		Bulls			*P*-value[1]		
Trait[2]	High	Low	High	Low	SE	L	G	L*G
Study 1								
Final LMA, cm^2	65.60	65.84	73.78	75.44	2.53	0.69	0.01	0.76
Final BF, cm	1.05	0.91	0.78	0.75	0.07	0.17	0.01	0.37
LMA gain, cm^2	18.52	16.66	12.96	12.08	2.63	0.58	0.04	0.84
BF gain, cm	0.56	0.49	0.18	0.17	0.05	0.35	0.01	0.47
Study 2								
Final LMA, cm^2	60.60	58.77	73.05	72.89	2.14	0.58	0.01	0.64
Final BF, cm	0.84	0.71	0.64	0.54	0.06	0.02	0.01	0.76
LMA gain, cm^2	17.12	19.92	25.26	25.24	1.81	0.36	0.01	0.35
BF gain, cm	0.42	0.32	0.31	0.21	0.05	0.02	0.01	0.98

[1]*P*-value for the effects of IGF-I selection line (L), gender (G) and the interaction term.

[2]LMA = longissimus muscle area; BF = 12^{th} rib fat thickness.

greater ($P = 0.17$) final BF (0.92 vs. 0.83 ± 0.07 cm) than calves from the low IGF-I selection line. In study 2, calves from the high IGF-I selection line had greater ($P < 0.05$) final BF (0.74 vs. 0.63 ± 0.06 cm) and gain in BF (0.37 vs. 0.27 ± 0.05 cm) than calves from the low IGF-I selection line. Final LMA and gain in LMA were similar between IGF-I selection lines in studies 1 and 2.

In study 1, calves from the low IGF-I selection line had similar initial BW, ADG, and final HH, but tended ($P = 0.06$) to have larger final BW compared to calves from the high IGF-I selection line (Table 3.4). Although IGF-I selection lines had similar FCR and DMI, calves from the low IGF-I selection line tended ($P = 0.09$) to have lower RFI (-0.26 vs. 0.24 kg/d) than calves from the high IGF-I selection line. In study 2, IGF-I selection line had no effect on growth traits, DMI, FCR or RFI. However, there was a tendency ($P = 0.15$) for an IGF-I selection line by gender interaction for RFI. Bulls from the low IGF-I selection line had numerically lower RFI compared to bulls from the high IGF-I selection line, whereas, RFI was similar between IGF-I selection lines in heifers.

Phenotypic correlations among serum IGF-I concentrations at the various sampling times are presented in Table 3.5. Weaning IGF-I concentrations were not correlated with either initial or final IGF-I concentration, but initial IGF-I concentration was positively correlated with final IGF-I concentration (0.44 and 0.25 in study 1 and 2, respectively). The lack of correlation of weaning with initial or final IGF-I concentration may be due to different procedures for determining serum IGF-I concentration: weaning samples were collected using a blood spot card and analyzed using an enzyme-linked immunosorbent assay by Primegro Inc., whereas, initial and final blood samples were

Table 3.4. Effects of gender and IGF-I selection line on performance and feed efficiency traits in studies 1 and 2

	Heifers		Bulls			*P*-value[1]		
Trait[2]	High	Low	High	Low	SE	L	G	L*G
Study 1								
Initial BW, kg	282.3	292.3	359.2	374.2	9.3	0.15	0.01	0.77
Final BW, kg	354.3	368.3	457.1	479.6	10.3	0.06	0.01	0.66
Final HH, cm	119.3	119.4	121.3	124.0	1.08	0.16	0.01	0.19
ADG, kg/d	0.93	0.99	1.27	1.37	0.06	0.21	0.01	0.71
DMI, kg/d	11.07	11.28	11.92	11.87	0.53	0.87	0.15	0.79
FCR, feed/gain	11.99	11.55	9.41	8.82	0.47	0.24	0.01	0.86
RFI, kg/d	0.15	-0.22	0.33	-0.30	0.31	0.09	0.86	0.66
Study 2								
Initial BW, kg	259.1	249.1	298.5	296.7	10.1	0.49	0.01	0.63
Final BW, kg	322.4	314.3	387.9	382.1	11.1	0.46	0.01	0.33
Final HH, cm	116.9	115.7	121.9	122.0	1.28	0.61	0.01	0.56
ADG, kg/d	1.29	1.33	1.82	1.74	0.07	0.70	0.01	0.33
DMI, kg/d	9.24	9.25	10.55	9.91	0.40	0.35	0.01	0.33
FCR, feed/gain	7.20	6.98	5.83	5.75	0.26	0.50	0.01	0.77
RFI, kg/d	-0.06	0.12	0.21	-0.17	0.23	0.61	0.95	0.15

[1]*P*-value for the effects of IGF-I selection line (L), gender (G) and the interaction term.

[2]FCR = feed conversion ratio; RFI = residual feed intake.

Table 3.5. Phenotypic partial correlations between performance, feed efficiency, and ultrasound composition traits and serum IGF-I concentrations in studies 1 (above diagonal) and 2 (below diagonal)

Trait[1]	ADG	DMI	FCR	RFI	LMAg	BFg	wIGF-I	iIGF-I	fIGF-I
ADG		0.64*	-0.59*	0.09	0.40*	0.37*	-0.07	0.20	0.14
DMI	0.61*		0.19	0.66*	0.24	0.47*	-0.10	0.18	-0.24
FCR	-0.50*	0.36*		0.54*	-0.22	-0.01	-0.01	-0.19	-0.49*
RFI	0.00	0.58*	0.56*		-0.16	0.05	-0.21	0.13	-0.40*
LMAg	0.41*	0.23	-0.21	0.05		0.34*	-0.11	0.02	0.45*
BFg	0.40*	0.38*	-0.05	0.14	0.21		0.17	0.17	0.01
wIGF-I	0.08	0.27*	0.12	0.22	0.14	0.18		0.00	0.12
iIGF-I	0.21	0.29*	0.05	0.16	0.07	0.15	0.00		0.44*
fIGF-I	0.19	0.10	-0.14	0.03	0.09	-0.02	-0.11	0.25*	

[1]FCR = feed conversion ratio (feed/gain); RFI = residual feed intake; LMAg = gain in longissimus muscle area; BFg = gain in 12th rib fat thickness; IGF-I = insulin-like growth factor-I; wIGF-I = weaning serum IGF-I concentration; iIGF-I = initial serum IGF-I concentration; fIGF-I = final serum IGF-I concentration.

*Correlations are different from zero ($P < 0.05$).

collected in evacuated serum vials and analyzed using an enzyme immunoassay procedure in our laboratory.

In studies 1 and 2, DMI was strongly correlated (> 0.60) with ADG and final BW. As expected, RFI was strongly correlated with DMI, but not with ADG or final BW in either study. In contrast, FCR was negatively correlated with ADG in both studies, and positively correlated with DMI in study 2, but not study 1. In both studies, RFI was strongly correlated (> 0.50) with FCR. Gain in BF during studies 1 and 2 were moderately correlated with both ADG (0.37 and 0.40, respectively) and DMI (0.47 and 0.38, respectively). In both studies, gain in LMA was moderately correlated ($P < 0.05$) with ADG and tended ($P < 0.15$) to be weakly correlated with DMI. Ultrasound carcass composition traits were not correlated with FCR or RFI in either study.

In study 1, serum IGF-I concentration was not correlated with ADG, DMI or gain in BF at either of the blood sampling times, although IGF-I concentration sampled at the end of the study was positively correlated with gain in LMA. In study 2, serum IGF-I concentration was not correlated with ADG at either of the sampling times, but IGF-I concentration sampled at weaning and at the start of the study were positively correlated with DMI. Serum IGF-I concentration was not correlated with gain in BF or LMA at any sampling times.

In study 1, weaning and initial IGF-I concentrations were not correlated with FCR or RFI, but final IGF-I concentration was negatively correlated with both FCR (-0.49) and RFI (-0.40). Regression analysis revealed that gender influenced the relationship between initial serum IGF-I concentration and RFI (Table 3.6). The

Table 3.6. Regression coefficient estimates (± SE) for regression of RFI (g/d) on serum IGF-I concentration and gender by serum IGF-I concentration interaction in studies 1 and 2

	b_0		b_1				*P*-value[1]	
IGF-I trait[2]	Heifers	Bulls	Heifers	Bulls	R^2	RMSE	IGF-I	G*IGF-I
Study 1								
Weaning	-105 ± 711	178 ± 631	-1.14 ± 3.76	-1.77 ± 2.37	0.092	0.896	0.53	0.89
Initial	1350 ± 1052	-1737 ± 1006	-9.49 ± 6.51†	5.38 ± 3.74†	0.203	0.840	0.62	0.03
Final	1172 ± 669	1092 ± 1314	-10.87 ± 4.46*	-6.30 ± 5.78	0.224	0.828	0.03	0.50
Study 2								
Weaning	389 ± 394	-827 ± 333	-3.41 ± 3.37	5.16 ± 2.04*	0.141	0.660	0.67	0.03
Initial	175 ± 619	-1095 ± 660	-1.69 ± 4.47	4.33 ± 2.69†	0.058	0.691	0.62	0.24
Final	94 ± 619	-364 ± 739	-1.14 ± 4.43	1.18 ± 2.74	0.011	0.708	0.99	0.65

[1]*P*-value for F-test of effects of IGF-I and gender (G) by IGF-I interaction.
[2]IGF-I = insulin-like growth factor-I.
*Regression coefficients are different from zero at $P < 0.05$.
†Regression coefficients are different from zero at $P \leq 0.15$.

regression coefficient tended ($P = 0.15$) to be greater than zero for bulls, and less than zero for heifers (5.38 vs. -9.49 g/d, respectively). In study 2, serum IGF-I concentration was not correlated with FCR or RFI at any of the sampling times. However, there was a significant ($P < 0.05$) gender by IGF-I concentration interaction at weaning. The regression coefficient between weaning IGF-I concentration and RFI was greater ($P < 0.05$) than zero for bulls, but was not different from zero for heifers (4.33 vs. -1.69 g/d, respectively).

The relationship between RFI and serum IGF-I concentration appeared to be affected by the time of blood sampling for IGF-I. For heifers in study 1, the regression coefficients relating RFI to serum IGF-I concentration became more negative as time of blood sampling during the study increased. The regression coefficient for IGF-I sampled at weaning was not significantly different from zero, whereas, the regression coefficients for IGF-I sampled at the start ($P = 0.15$) and end ($P < 0.05$) of the study were less than zero (-1.14, -9.49 and -10.87 g/d, respectively). For bulls in study 2, the regression coefficients for IGF-I became less positive as time of blood sampling increased. The coefficients for IGF-I were greater then zero when sampled at weaning ($P < 0.05$) and the start ($P = 0.11$) of the study, but not different from zero when sampled at the end of the study (5.16, 4.33 and 1.18 g/d, respectively). Similar consistent trends for the relationship between RFI and serum IGF-I concentrations were not observed for heifers in study 2 or bulls in study 1.

Bulls had 30 and 48% higher ($P < 0.05$) IGF-I concentrations at weaning and 70 to 100% greater ($P < 0.05$) IGF-I concentrations at the start and end of studies 1 and 2,

respectively, than heifers (Table 3.2). As expected, bulls were heavier ($P < 0.05$) at the start and end of the study, and had greater ($P < 0.05$) ADG than heifers in both studies. Likewise, bulls had improved ($P < 0.05$) FCR compared to heifers in study 1 (9.12 vs. 11.77 ± 0.47 DMI:gain) and study 2 (5.79 vs. 7.09 ± 0.26 DMI:gain). As expected, RFI was not affected by gender due to the fact that gender was included in the model used to compute RFI.

Bulls in study 1 had greater ($P < 0.05$) LMA at the start (62.1 vs. 48.1 ± 2.11 cm^2) and end (74.61 vs. 65.72 ± 2.53 cm^2) of the study, but gained ($P < 0.05$) less LMA during the study than heifers. However, bulls in study 1 gained ($P < 0.05$) less BF (0.18 vs. 0.53 ± 0.05 cm) during the study then heifers. As expected, bulls in study 2 gained ($P < 0.01$) more LMA (25.25 vs. 18.52 ± 1.81 cm^2) and gained ($P < 0.01$) less BF (0.26 vs. 0.37 ± 0.05 cm) during the study compared to heifers. The lower gain in LMA for bulls then heifers during study 1 was likely due to the fact that heifers were limit-fed, whereas, bulls were fed ad libitum a high-grain diet for 125 d at the EARS station prior to the start of the study. In study 2, previous plane of nutrition was similar for both bulls and heifers.

Discussion

In computing RFI, gender effects on the relationship between DMI and MBW and ADG were evaluated. Significant effects of gender and gender by MBW and ADG interaction terms were found in study 2, but not study 1. Therefore, the fixed effect of gender and the interaction terms were included in the model to computer RFI for both studies. The means ± SD for RFI were 0.00 ± 0.91 and 0.00 ± 0.90 kg/d for bulls and

heifers, respectively, in study 1, and 0.00 ± 0.77 and 0.00 ± 0.61 kg/d for bulls and heifers, respectively, in study 2. The standard deviation of RFI in study 1 was within the range (0.74 to 1.47 kg/d) previously reported for cattle fed roughage diets (Arthur et al., 2001b, c; Schenkel et al., 2004). Similarly, the standard deviation of RFI in study 2 was within the range (0.66 to 0.83 kg/d) reported for cattle fed a grain diet (Basarab et al., 2003; Nkrumah et al., 2004). Similar to our studies, previous studies have reported strong positive correlations between DMI and both ADG and BW in cattle fed both roughage- (Arthur et al., 2001c) and grain-based diets (Nkrumah et al., 2004). Furthermore, Arthur et al. (2001a) reported strong positive correlations of RFI with DMI and FCR. In contrast to our studies, several studies (Arthur et al., 2001c; Carstens et al., 2002; Nkrumah et al., 2004) reported positive correlations (0.14 to 0.25) between carcass fat composition traits and RFI in cattle fed roughage and grain-based diets. The lack of a correlation in our studies may be due to a small number of animals in each of the 2 studies and the relatively weak phenotypic correlations between feed efficiency and carcass fat composition traits typically reported. Collectively, these results indicate that the variation in RFI and the phenotypic correlations among performance and feed efficiency traits in our studies using calves divergently selected for serum IGF-I concentration were similar to previously reported studies using traditional contemporary groups.

IGF-I and Growth

Previous studies evaluating the relationship between serum IGF-I concentration and growth traits have reported conflicting results. Lund-Larson et al. (1977) collected

blood samples at 5, 7 and 10 months of age and reported that mean serum IGF-I concentration was positively related to rate of gain in bulls. Bishop et al. (1989) reported varying phenotypic correlations between serum IGF-I concentration sampled at 28-d intervals during a 140-d postweaning test and BW (ranged from -0.13 to 0.27) and ADG (ranged -0.23 to 0.21). Moore et al. (2005) reported no genetic correlation between a single postweaning serum IGF-I concentration and age-adjusted yearling weight in Angus bulls and heifers fed a roughage-based diet. Furthermore, Johnston et al. (2002) reported no genetic correlation between postweaning IGF-I concentration and ADG during a postweaning test. Following 5 yr of selection for low or high postweaning serum IGF-I concentration, Davis and Simmen (1997) reported negative genetic correlations of serum IGF-I concentration with final BW (-0.31) and ADG (-0.40) in Angus bulls and heifers fed a grain-based diet. However, following 11 yr of selection, Davis and Simmen (2006) found positive genetic correlations of serum IGF-I concentration with final BW (0.28) and ADG (0.29). There was a tendency ($P = 0.06$) for bulls and heifers from the low IGF-I selection line to have greater final BW in study 1, indicating a negative relationship between serum IGF-I concentration and final BW, but there was no effect of IGF-I selection line on final BW in study 2. In addition, there was no effect of IGF-I selection line on ADG or a correlation between serum IGF-I concentration and ADG in either study. These data suggest that other factors may be influencing the relationship of IGF-I concentration with growth and body size.

IGF-I and Carcass Composition

Insulin-like growth factor-I is reported to stimulate protein synthesis and satellite cell proliferation in skeletal muscle (Oksbjerg et al., 2004) suggesting a relationship with composition of growth. Anderson et al. (1988) collected sampled IGF-I concentration at 30-min intervals from 0800 to 2000 on d -1, 65, 135 and 201 of a 202d test. These authors reported that mean serum IGF-I concentration was negatively correlated with percentage of carcass fat and fat thickness. In contrast, Johnston et al. (2001; $r_g = 0.38$) and Moore et al. (2005; $r_g = 0.29$) reported positive genetic correlations between postweaning serum IGF-I concentration and end of test ultrasound BF. Following 8 yr of selection for low or high postweaning serum IGF-I concentration, Davis and Simmen (2000) reported negative genetic correlations between serum IGF-I concentration and carcass BF when either age-adjusted (-0.28) or BW-adjusted (-0.29) composition was used. However, following 10 yr of selection, Davis et al. (2003) reported no genetic correlation with end of study ultrasound BF. In study 1, there was no effect of IGF-I selection on final or gain in BF, or a correlation between serum IGF-I concentration and gain in BF; however, in study 2, bulls and heifers from the low IGF-I selection line had lower final and gain in BF, indicating a positive relationship between serum IGF-I concentration and BF.

Anderson et al. (1988) reported that mean serum IGF-I concentration was positively correlated with percentage of carcass protein. In contrast, Moore et al. (2005) reported a negative genetic correlation (-0.37) between postweaning serum IGF-I concentration and final LMA. Following 8 yr of selection for low or high postweaning

serum IGF-I concentration, Davis and Simmen (2000) reported weak positive genetic correlations between serum IGF-I concentration and LMA at an age-constant (0.17) or fat-constant (0.27) end point in bulls and heifers. Furthermore, Davis et al. (2003) reported a positive genetic correlation (0.20) between postweaning serum IGF-I concentration and final LMA following 10 yr of selection. In study 1, final IGF-I concentration was positively phenotypically correlated with gain in LMA; however, there was no effect of IGF-I selection line on final or gain in LMA in study 1 or 2.

IGF-I and Feed Efficiency

Previous studies have reported positive (Johnston et al., 2002, $r_g = 0.39$; Moore et al., 2005, $r_g = 0.57$) genetic correlations between postweaning IGF-I concentration and RFI in *Bos taurus* cattle fed roughage diets. Residual feed intake was measured shortly after weaning at approximately 9 to 11 months of age. These results are the justification for the use of serum IGF-I breeding values in selection for RFI by Australian breeding associations (Anonymous, 2007). However, Wolcott et al. (2006) reported negative genetic correlations between postweaning IGF-I concentration and RFI in implanted Brahman (-0.12) and non-adapted tropical composite steers (-0.80). Residual feed intake was measured on a high-grain diet following a growing phase to reach a mean initial BW of 400 kg. In our study, regression analysis indicated a gender by serum IGF-I concentration interaction for initial IGF-I concentration for study 1, and for weaning IGF-I concentration in study 2 such that relationships between IGF-I concentration and RFI were positive for bulls and negative for heifers. No previous studies have evaluated

the relationship between IGF-I concentration and RFI in bulls compared to heifers, but a possible explanation for the conflicting results may be due to composition of gain.

Prediction equations derived from carcass traits for bulls (Baker et al., 2006a) and heifers (Baker et al., 2006b) were used to estimate empty-body fat percentage from ultrasound measurements and gain in fat free empty-body weight computed. Bulls had a greater proportion of empty-body weight gain as fat free empty-body weight compared to heifers in study 1 (75.95 vs. 68.62 %, respectively) and study 2 (83.02 vs. 71.68 %, respectively). This difference between bulls and heifers corresponded to the positive relationships for bulls and negative relationships for heifers between IGF-I concentration and RFI. Similarly, Anonymous (2007) and Brown (2005) reported weak positive genetic and phenotypic correlations, respectively, in cattle fed a roughage-based diet (0.17 and 0.18, respectively) and weak negative genetic and phenotypic correlations, respectively, in cattle fed a grain-based diet (-0.22 and -0.12, respectively) where cattle would be expected to have a greater rate of lean tissue gain when younger and fed a roughage-based diet prior to a finishing phase. Arguably, rate of lean tissue gain may have influenced the positive relationships between IGF-I concentration and RFI observed by Moore et al. (2005) compared to the negative relationships observed by Wolcott et al. (2006). In the study by Moore et al. (2005), cattle were fed a roughage-based diet at 9 to 11 months of age, whereas, in the study by Wolcott et al. (2006), cattle were fed a grain-based diet following a growing phase to reach an initial BW of 400 kg indicating that these cattle were most likely older and closer to maturity, and most likely had a lower proportion of lean gain. These studies may indicate that diet type affected

the relationship between serum IGF-I concentration and RFI; however, in our studies, bulls had positive relationships compared to negative relationships for heifers when fed a roughage-based diet in study 1 or a grain-based diet in study 2.

Moore et al. (2005) reported that IGF-I sampled at weaning (201 d of age) and postweaning (310 d of age) were the same trait (r_g = 1.0). Similarly, Davis and Simmen (2006) reported strong genetic correlations between serum IGF-I concentrations sampled 14 (0.87) or 28 d apart (0.89). However, phenotypic correlations were weaker between serum IGF-I concentrations sampled 14 (0.76) and 28 d apart (0.65). In both of our studies, sampling time for IGF-I concentration appeared to effect the relationship between serum IGF-I concentration and RFI. For heifers in study 1, the regression coefficient became increasingly negative as IGF-I was sampled later during the study. In study 2, the regression coefficient for bulls became decreasingly positive as IGF-I was sampled later during the study. Brown (2005) also reported that the relationship between serum IGF-I concentration and RFI became increasingly negative as IGF-I was measured later in the growing (r_p = 0.18 and 0.04 for initial and final IGF-I concentration, respectively) and finishing period (r_p = -0.12 and -0.18 for initial and final IGF-I concentration, respectively) for Santa Gertrudis steers. Wolcott et al. (2006) reported that the relationship between IGF-I concentration and RFI became increasingly negative as IGF-I was sampled later in the finishing period for Brahman steers (r_g = -0.12, 0.03 and -0.54 for postweaning, initial and final IGF-I concentration, respectively), but became decreasingly negative for tropical composite steers (-0.80, -0.51 and -0.44 for postweaning, initial and final IGF-I concentration, respectively). Collectively, these

data suggest that as cattle become more physiologically mature the relationship between IGF-I concentration and RFI becomes increasingly negative both in terms of sampling IGF-I and measuring RFI.

This discussion of results demonstrates inconsistent relationships between IGF-I concentration and growth, carcass composition and feed efficiency traits. Insulin-like growth factor-I binding proteins (IGFBP) are proteins associated with circulating IGF-I and modulate the interaction of IGF-I with its receptor (Jones and Clemmons, 1995). Previous research has reported IGFBP-2 is negatively related to BW (Pagan et al., 2003) and positively related to ADG (Connor et al., 2000), but not related to ultrasound measurements of BF or LMA. In addition, Pagan et al. (2003) reported that IGFBP-3 was not related to BW or ultrasound measures of BF and LMA. Bulls and heifers selected for low or high serum IGF-I concentration had similar IGFBP-2 and IGFBP-3 concentrations even though calves selected for high IGF-I concentration had 65% greater serum IGF-I concentrations than those selected for low IGF-I concentration. This ratio of IGFBP to IGF-I concentration may have influenced the IGF-I selection line results in this study and future research should evaluate IGFBP concentrations as well as IGF-I concentrations to better assess the use of IGF-I as an indicator trait.

Implications

Research evaluating the relationship between IGF-I concentration and RFI has indicated inconsistent results. Our results and results from these studies indicate that the relationship between IGF-I concentration and RFI may be influenced by composition of

growth and sampling time for IGF-I. Thus, further research is necessary to evaluate this relationship and determine the usefulness of IGF-I as an indicator trait for RFI.

CHAPTER IV

RELATIONSHIP OF RESIDUAL FEED INTAKE WITH ENERGY EXPENDITURE IN GROWING BEEF CATTLE

Introduction

Feed costs are the largest variable expense for beef production, thus selection for improved feed efficiency could substantially improve profits. However, the typical measure of feed efficiency, feed conversion ratio (FCR), is negatively correlated with growth traits such that selection for improved FCR would result in larger mature cow size and increased feed requirements for maintenance (Archer et al., 1999). Thus, selection in the beef industry has primarily focused on output traits.

Residual feed intake (RFI) is a feed efficiency trait that quantifies inter-animal variation in dry matter intake that is unexplained by variation related to body weight and growth rate—efficient animals are those that consume less DMI than expected for a given BW and growth rate. Arthur et al. (2001a) concluded that RFI is a moderately heritable trait that is independent of mature size, and that considerable genetic variation exists to facilitate selection.

Herd et al. (2004) estimated that approximately one-third of the biological variation in RFI of growing calves could be explained by inter-animal differences in digestion, heat increment, composition of growth and activity, and posited that the remaining two-thirds was linked to inter-animal variation in energy expenditure. Only 5% of the variation in RFI can be explained be differences in carcass composition (i.e.

retained energy; Herd et al., 2004) indicating that calves with high RFI must have greater energy expenditure given their greater metabolizable energy intake compared to calves with low RFI.

Oxygen consumed by body tissues is transported by the heart and increased tissue oxygen demand results in vasodilation and increased blood flow suggesting that heart rate (**HR**) would be indicative of oxygen consumption and energy expenditure. Previous studies (Webster, 1967; Yamamoto et al., 1979) have demonstrated that energy expenditure is positively linearly related to HR. In addition, the accuracy of prediction of energy expenditure from HR was ± 10%. These researchers have also demonstrated that environmental conditions such as cold exposure and metabolizable energy of the diet that increase energy expenditure also increase heart rate. Therefore, the objective of this study was to evaluate differences in heart rate between RFI phenotypes.

Materials and Methods

Animals and Management

Study 1 and 2. Angus bulls and heifers from lines divergently selected for insulin-like growth factor-I (IGF-I) at the Eastern Agricultural Research Station (Ohio State University) were used in study 1 and 2. Calves used in this experiment were weaned on October 6, 2004 and October 5, 2005 and shipped to the O.D. Butler, Jr. Animal Science Complex at Texas A&M University on February 10, 2005 and January 11, 2006 for studies 1 and 2, respectively. In study 1, upon arrival at Texas A&M University, bulls (n = 17; initial BW = 367.1 ± 22.9 kg) and heifers (n = 22; initial BW = 286.4 ± 28.6 kg) were blocked by gender and BW, randomly assigned to pens (6 calves

per pen), and adapted to a roughage-based diet (ME = 1.95 Mcal/kg DM) for 24 d. In study 2, upon arrival, bulls (n = 27; initial BW = 297.5 ± 34.4 kg) and heifers (n = 29; initial BW = 256.0 ± 25.1 kg) were blocked by gender and BW, randomly assigned to pens (6 calves per pen), and adapted to a grain-based diet (ME = 2.85 Mcal/kg DM) for 32 d. Individual intakes were measured using Calan gate feeders and BW measured at 7-d intervals for 77 and 70 d in studies 1 and 2, respectively.

Study 3 and 4. Brangus heifers from Camp Cooley ranch were used in study 3 (N = 115; initial BW = 268.5 ± 23.8 kg) and 4 (N = 119; initial BW = 267.8 ± 25.8 kg). Heifers were weaned on August 17, 2005 and August 17, 2006 and shipped to the O.D. Butler, Jr. Animal Science Complex at Texas A&M University on September 6, 2005 and September 5, 2006 for studies 3 and 4, respectively. In both studies, upon arrival, heifers were blocked by BW and randomly assigned to pens (6 heifers per pen) and adapted to a roughage-based diet (ME = 2.00 and 1.93 Mcal/kg DM for studies 3 and 4, respectively) for 24 d. For both studies, individual intakes were measured using Calan gate feeders and BW measured at 7-d intervals for 70 d.

Diet Analysis and Calculations

Diet ingredient samples were collected weekly throughout each study and composited by weight for chemical analyses. Moisture analysis was conducted by drying in a forced-air oven for 48 h at 105^{O}C (AOAC, 1995) and was used to compute DMI from as-fed intake data. Chemical analysis was conducted by an independent laboratory (Cumberland Valley Analytical Services, Inc., Hagerstown, MD), and ME concentrations of the experimental diets computed using the Cornell Net Carbohydrate

and Protein System (Version 5.0, Cornell University, Ithaca, NY). Metabolizable energy intake (**MEI**) was computed by multiplying DMI by the formulated ME concentration of the diet. Ingredient and chemical composition of the experimental diets are presented in Table 4.1.

Growth rates of individual calves were modeled by linear regression of BW against day of study using the general linear model of SAS (SAS Inst., Cary, NC). Regression coefficients were used to compute initial and final BW, ADG and metabolic BW (MBW; mid-test $BW^{.75}$). Residual feed intake was defined as the difference between actual DMI and that predicted from the regression of DMI on MBW and ADG using model 4.1 for studies 1 and 2 and model 4.2 for studies 3 and 4:

(4.1) $DMI = ß_0 + ß_1MBW + ß_2ADG + ß_3gender + ß_4gender*MBW + ß_5gender*ADG + €,$

(4.2) $DMI = ß_0 + ß_1MBW + ß_2ADG + €$

where $ß_0$ = y-intercept, $ß_1$ = partial regression coefficient of MBW, $ß_2$ = partial regression coefficient of ADG, $ß_3$ = partial regression coefficient of gender, $ß_4$ = partial regression coefficient of gender by MBW interaction, $ß_5$ = partial regression coefficient of gender by ADG interaction, € = error term.

Heart Rate Measurements

Residual feed intake was calculated after d 77 and 56 of the test period for studies 1 and 2, respectively. Bulls and heifers were selected for heart rate measurements from those that were < 0.5 and > 0.5 SD from the mean RFI of 0.00 ± 0.89 and 0.00 ± 0.69 kg/d for study 1 (low RFI n = 10; high RFI n = 8) and 2 (low RFI n = 12;

Table 4.1. Ingredient and chemical composition of diets fed to calves in studies 1, 2, 3 and 4

Item	Study 1	Study 2	Study 3	Study 4
Ingredient, % as-fed				
Chopped alfalfa	35.00	12.80	35.00	35.00
Pelleted alfalfa	15.00	3.20	15.00	15.00
Dry rolled corn	20.95	74.83	20.95	20.95
Cottonseed hulls	21.50	2.13	21.50	21.50
Molasses	7.00	4.27	7.00	7.00
Urea	--	1.17	--	--
Salt	0.40	1.01	0.40	0.40
Vitamin ADE[1]	--	0.20	--	--
Vitamin E[2]	0.14	0.34	0.14	0.14
Trace mineral[3]	0.02	0.05	0.02	0.02
Chemical composition				
DM, %	88.26	88.85	89.36	88.05
CP, % DM	13.41	13.14	13.16	12.48
NDF, % DM	47.25	17.46	43.75	44.97
ME, Mcal/kg DM	1.95	2.85	2.00	1.93

[1]Vitamin ADE contained 2,200,000 IU vitamin A/kg, 440,000 IU vitamin D/kg and 8,800 IU vitamin E/kg of product.

[2]Vitamin E contained 44,000 IU/kg of product.

[3]Trace mineral contained minimum 19.0% Zn, 7.0% Mn, 4.5% CU, 4,000 ppm Fe, 2,300 ppm I, 1,000 ppm Se and 500 ppm Co.

high RFI n = 12), respectively. For studies 3 and 4, RFI was calculated after d 49 of the test period and heifers were selected for heart rate measurements from those that were < 1.0 and > 1.0 SD from the mean RFI of 0.00 ± 0.68 and 0.00 ± 0.69 kg/d for study 3 (low RFI n = 8; high RFI n = 8) and 4 (low RFI n = 8; high RFI n = 8), respectively.

Following the end of each test period, heart rate was determined at various feeding levels. In study 1, heart rate was determined for 2 consecutive 24 hr periods during ad libitum feeding (ad-libitum HR period) and for a 24 hr period on d 3 of fasting (fasting HR period). In study 2, heart rate was determined at restricted (100 g DM/$kg^{0.75}$; restricted HR period) and 1.1 x expected maintenance requirement (maintenance HR period) feeding levels for 2 consecutive 24 hr periods after a 48 hr adaptation to each feeding level. In study 3, heart rate was determined at a restricted (120 g DM/$kg^{0.75}$; restricted HR period) feeding level for 2 consecutive 24 hr periods after a 48 hr adaptation period. In study 4, heart rate was determined during ad libitum feeding (ad-libitum HR period) for 4 consecutive 24 hr periods and 1.1 x expected maintenance requirement feeding (maintenance HR period) for 2 consecutive 24 hr periods after a 48 hr adaptation period. Restricted DMI levels were chosen to be at the ad libitum DMI level of the calves with low RFI based on ad libitum DMI for prior 2 weeks. Expected maintenance DMI was computed as MBW multiplied by 110 kcal·$kg^{0.75\ -1}$·d^{-1} then divided by the Cornell Net Carbohydrate and Protein System derived ME content of the diet.

Heart rate was determined using a Polar equine transmitter and monitor (Model S610i; Polar Electro Inc., Kempele, Finland). The transmitter was attached to the animal

using a girth strap designed from 10 cm wide elastic with a velcro latch. The strap was placed just behind the shoulders and front legs with the negative electrode of the transmitter positioned on the right side of the animal 15 cm below the midline of the back and the positive electrode positioned on the left side of the animal parallel to the point of the elbow. The area around each electrode was clipped of hair and Electron II conductivity gel (Pharmaceutical Innovations Inc., Newark, NJ) was used to enhance the contact between skin and electrode. The monitor was placed in a pocket on the strap and collected data at 1 min intervals via wireless transmission from the transmitter. Each monitor was coded to receive data from a single transmitter, thus, multiple calves in the same vicinity could be measured simultaneously without disruption from other transmitters.

Statistical Analysis

Growth, feed intake and efficiency traits and heart rate measurements were analyzed separately by study. Data were analyzed using the mixed procedure of SAS (SAS Inst., Cary, NC) with RFI group (low vs. high) as a fixed effect. In addition, fixed effects of gender and IGF-I selection line and all 2-way interactions were included in the model for studies 1 and 2. The 3-way interaction was not evaluated due to single observations in some subclass groups for study 1 and was not significant and removed from the final model in study 2.

Results and Discussion

Summary statistics for performance and feed efficiency traits for all calves in each study are presented in table 4.2. Calves in study 1 had numerically greater initial

and final BW compared to the other studies, which is likely due to those calves being fed a grain-based diet for 120 d prior to the start of the study. Calves in study 1 consumed numerically more DMI compared to the other studies; however, this was likely due to the greater BW of these calves because DMI as percent of BW was similar among studies (2.82, 2.76, 2.76 and 2.88% for study 1, 2, 3 and 4, respectively). Calves in study 2 had numerically greater ADG and lower FCR than calves in the other studies due to being fed a grain-based diet compared to a roughage-based diet for calves in studies 1, 3 and 4, but, as expected, calves in studies 1, 3 and 4 had similar ADG and FCR. The SD of RFI was greater in study 1 compared to the other studies, even though calves in study 3 and 4 were fed a similar roughage diet. Calves in study 1 had numerically larger BW and initial 12^{th} rib fat thickness (0.53 vs. 0.37, 0.38 and 0.37 cm for study 1, 2, 3 and 4, respectively), thus, were likely closer to mature size. Similarly, Arthur et al. (2001c) reported a greater SD of RFI in Charolais bulls fed a roughage diet during a weanling (initial age = 274 d; SD = 0.77 kg/d) compared to a yearling (initial age = 430 d; SD = 1.1 kg/d) test.

Effect of RFI Group

Performance and feed efficiency. Angus bulls and heifers with low RFI consumed 22 and 17% less ($P < 0.05$) DMI and had 16 and 16% lower ($P < 0.05$) FCR than Angus bulls and heifers with high RFI in study 1 and 2, respectively, even though ADG and initial and final BW were similar between RFI phenotypes in both studies (Table 4.3). Previous studies (Carstens et al., 2002; Fox et al., 2004; Nkrumah et al., 2007) have reported similar differences in DMI (17 to 20% lower for calves with low

Table 4.2. Summary statistics (± SD) of performance and feed efficiency traits for calves in studies 1, 2, 3 and 4

Trait[1]	Study 1	Study 2	Study 3	Study 4
No. animals	39	56	115	119
Initial BW, kg	321.6 ± 48.2	276.0 ± 36.3	268.5 ± 23.8	267.8 ± 25.8
Final BW, kg	407.5 ± 62.2	351.1 ± 46.2	342.9 ± 28.9	337.7 ± 29.0
ADG, kg/d	1.12 ± 0.26	1.53 ± 0.32	1.06 ± 0.16	1.00 ± 0.13
DMI, kg/d	11.48 ± 1.48	9.70 ± 1.28	9.47 ± 1.04	9.71 ± 1.04
FCR, feed/gain	10.63 ± 1.88	6.48 ± 1.02	9.04 ± 1.31	9.80 ± 0.97
RFI, kg/d	0.00 ± 0.89	0.00 ± 0.69	0.00 ± 0.68	0.00 ± 0.68

[1]FCR = feed conversion ratio; RFI = residual feed intake.

Table 4.3. Effects of RFI group, IGF-I selection line and gender on performance and feed efficiency traits of Angus bulls and heifers selected for heart rate measurements in studies 1 and 2

	Low RFI				High RFI										
	Heifers		Bulls		Heifers		Bulls			*P*-value[1]					
Trait[2]	High Line	Low Line	High Line	Low Line	High Line	Low Line	High Line	Low Line	SE	R	G	L	R*G	R*L	G*L
Study 1															
No. animals	2	4	1	3	4	1	2	1							
Initial BW, kg	269.4	282.5	375.5	363.1	281.0	273.0	375.6	376.4	26.3	0.75	0.01	0.95	0.89	0.83	0.73
Final BW, kg	340.5	359.4	447.7	476.3	359.6	356.4	477.6	469.2	31.4	0.62	0.01	0.64	0.92	0.46	0.93
ADG, kg/d	0.92	1.00	0.94	1.47	1.02	1.08	1.32	1.21	0.20	0.66	0.02	0.31	0.97	0.26	0.46
DMI, kg/d	9.66	10.13	9.21	11.31	12.26	13.67	13.75	12.44	1.27	0.01	0.30	0.44	0.96	0.57	0.87
FCR, feed/gain	10.60	10.42	9.82	7.73	12.18	12.61	10.40	10.32	1.16	0.02	0.01	0.52	0.80	0.40	0.36
RFI, kg/d	-0.82	-1.14	-1.32	-1.10	0.93	2.22	1.73	0.87	0.48	0.01	0.85	0.90	0.94	0.40	0.30
Study 2															
No. animals	4	2	3	3	4	2	4	2							
Initial BW, kg	275.0	255.4	304.7	276.9	247.8	277.1	289.7	320.9	19.4	0.62	0.01	0.80	0.51	0.04	0.89
Final BW, kg	336.6	325.9	393.5	365.6	316.2	342.7	378.7	409.8	21.1	0.61	0.01	0.74	0.60	0.09	0.81
ADG, kg/d	1.26	1.44	1.81	1.81	1.39	1.34	1.82	1.82	0.11	0.83	0.01	0.69	0.75	0.44	0.65
DMI, kg/d	8.96	8.90	9.54	9.08	10.03	11.21	11.45	11.54	0.54	0.01	0.07	0.57	0.39	0.21	0.29
FCR, feed/gain	7.17	6.19	5.30	5.02	7.20	8.39	6.36	6.35	0.42	0.01	0.01	0.98	0.53	0.04	0.69
RFI, kg/d	-0.69	-0.88	-0.85	-0.92	0.67	1.18	1.24	0.92	0.24	0.01	0.73	0.95	0.21	0.50	0.28

[1]*P*-value for RFI group (R), gender (G), IGF-I selection line (L) and interaction terms.
[2]FCR = feed conversion ratio; RFI = residual feed intake.

Table 4.4. Performance and feed efficiency traits of Brangus heifers with low and high RFI selected for heart rate measurements in studies 3 and 4

Trait[1]	Low RFI	High RFI	SE	*P*-value
Study 3				
No. animals	8	8		
Initial BW, kg	271.4	274.3	12.4	0.82
Final BW, kg	352.6	348.3	14.2	0.76
ADG, kg/d	1.16	1.06	0.09	0.29
DMI, kg/d	8.78	10.69	0.38	0.01
FCR, feed/gain	7.66	10.43	0.79	0.01
RFI, kg/d	-1.02	1.11	0.15	0.01
Study 4				
No. animals	8	8		
Initial BW, kg	277.6	268.8	11.9	0.47
Final BW, kg	349.0	344.7	13.5	0.76
ADG, kg/d	1.02	1.09	0.09	0.48
DMI, kg/d	8.87	11.53	0.38	0.01
FCR, feed/gain	8.80	10.82	0.53	0.01
RFI, kg/d	-1.07	1.39	0.21	0.01

[1]FCR = feed conversion ratio; RFI = residual feed intake.

RFI) and FCR (19 to 21% lower for calves with low RFI) between RFI phenotypes. In study 2, there was a RFI group by IGF-I selection line interaction for initial BW such that Angus bulls and heifers with low RFI from the high IGF-I selection line had numerically 9% greater initial BW than bulls and heifers with low RFI from the low IGF-I selection line (289.7 vs. 265.8 kg, respectively), whereas, bulls and heifers with high RFI from the high IGF-I selection line had 10% lower initial BW than bulls and heifers with high RFI from the low IGF-I selection line (268.8 vs. 299.0 kg, respectively). Furthermore, there was a RFI group by IGF-I selection line interaction for FCR such that bulls and heifers from the low IGF-I selection line with low RFI had 23% lower ($P < 0.05$) FCR than bulls and heifers from the low IGF-I selection line with high RFI (5.66 vs. 7.37, respectively), but FCR was similar between bulls and heifers with low and high RFI from the high IGF-I selection line (6.26 and 6.78, respectively).

Brangus heifers with low RFI consumed 18 and 23% less ($P < 0.05$) DMI and had 27 and 19% lower ($P < 0.05$) FCR than Brangus heifers with high RFI in study 3 and 4, respectively, even though ADG and initial and final BW were similar (Table 4.4). These differences in FCR between RFI phenotypes are slightly numerically greater than the differences observed in studies 1 and 2 due to the criteria for selection of calves for heart rate measurement: Angus bulls and heifers were selected from those < 0.5 or > 0.5 SD from the mean RFI in studies 1 and 2, whereas, Brangus heifers in studies 3 and 4 were selected from those < 1.0 or > 1.0 SD from the mean RFI.

Heart rate. In study 1, Angus bulls and heifers with low RFI consumed 17% less ($P < 0.05$) DMI (10.33 vs. 12.44 kg/d, respectively) and MEI (224.9 vs. 269.2 kcal·kg$^{0.75}$

$^{-1}\cdot d^{-1}$, respectively) during the ad-libitum heart rate measurement period than bulls and heifers with high RFI, which is similar to the difference (22%) during the test period (Table 4.5). In addition, bulls and heifers with low RFI had lower ($P < 0.10$) ad-libitum HR, but similar fasting HR compared to bulls and heifers with high RFI. Bulls and heifers with low RFI also had lesser ($P < 0.10$) change in HR between ad-libitum and fasting HR periods (29.9 vs. 35.4 beats/min, respectively). In study 4, Brangus heifers with low RFI consumed 25% less ($P < 0.05$) DMI and MEI than Brangus heifers with high RFI during the ad-libitum HR period, but as intended, DMI and MEI were similar between RFI phenotypes during the maintenance HR period (Table 4.6). Similar to study 1, Brangus heifers with low RFI had lower ($P < 0.10$) HR during the ad libitum HR period, but similar HR during the maintenance HR period compared to Brangus heifers with high RFI. In addition, heifers with low RFI had a lesser ($P < 0.10$) change in HR between ad-libitum and maintenance HR periods.

The results of studies 1 and 4 suggest similar energy expenditure between RFI phenotypes when DMI is held similar, but a greater increase in energy expenditure for calves with high RFI when calves are allowed free access to feed due to a greater increase in DMI. Gabarrou et al. (1997) reported similar results in poultry where energy expenditure was similar between RFI phenotypes (418 and 488 $kJ\cdot kg^{0.75\ -1}\cdot d^{-1}$ for birds with low and high RFI, respectively) when feed was deprived, but a greater energy expenditure for birds with high RFI (652 vs. 507 $kJ\cdot kg^{0.75\ -1}\cdot d^{-1}$, respectively) when allowed free access to feed (DMI = 80 vs. 112 g/d for birds with low and high RFI, respectively) resulting in greater energy expenditure due to feeding (164 vs.

Table 4.5. Effects of RFI group, IGF-I selection line and gender on heart rate measurements of Angus bulls and heifers in studies 1 and 2

	Low RFI				High RFI										
	Heifers		Bulls		Heifers		Bulls			*P*-value[1]					
Trait[2]	High Line	Low Line	High Line	Low Line	High Line	Low Line	High Line	Low Line	SE	R	G	L	R*G	R*L	G*L
Study 1															
Ad libitum DMI, kg/d	9.75	10.46	10.55	10.59	12.82	12.76	12.33	11.83	1.55	0.04	0.86	0.96	0.53	0.71	0.76
Ad libitum MEI, kcal/kg$^{.75}$	239.12	245.54	210.14	204.33	299.51	307.70	239.82	229.94	26.23	0.01	0.01	0.98	0.30	0.98	0.64
Ad libitum HR, beats/min	85.46	84.20	80.35	72.88	86.89	90.40	87.63	80.98	4.67	0.06	0.04	0.29	0.48	0.57	0.18
Fasting HR, beats/min	50.91	46.87	53.55	51.51	49.96	52.61	51.93	50.15	3.50	0.91	0.22	0.51	0.40	0.34	0.86
HR change, beats/min	34.54	37.33	26.76	21.21	36.93	37.80	35.70	30.83	4.88	0.08	0.01	0.57	0.20	0.88	0.23
Study 2															
Restricted DMI, kg/d	8.14	7.34	9.35	8.67	7.35	8.21	9.41	9.71	0.47	0.36	0.01	0.80	0.31	0.04	0.73
Restricted MEI, kcal/kg$^{.75}$	272.57	250.56	269.13	270.44	260.49	272.14	286.20	273.81	12.86	0.43	0.16	0.55	0.47	0.58	0.98
Restricted HR, beats/min	80.01	90.41	90.84	89.11	74.74	78.10	84.01	83.08	3.60	0.01	0.02	0.25	0.76	0.52	0.08
Maint. DMI, kg/d	3.71	3.52	4.09	3.90	3.41	3.61	4.06	4.33	0.15	0.59	0.01	0.82	0.12	0.04	0.86
Maint. MEI, kcal/kg$^{.75}$	123.42	120.31	114.06	116.09	119.83	120.35	119.37	121.16	1.97	0.20	0.02	0.79	0.01	0.52	0.21
Maint. HR, beats/min	68.04	68.03	69.11	65.64	65.03	59.56	65.91	59.94	4.61	0.10	0.98	0.22	0.87	0.51	0.73
HR change, beats/min	11.98	22.38	21.73	23.47	9.71	18.54	18.11	23.15	4.41	0.40	0.05	0.03	0.93	0.87	0.27

[1]*P*-value for RFI group (R), gender (G), IGF-I selection line (L) and interaction terms.
[2]MEI = metabolizable energy intake; HR = heart rate.

Table 4.6. Heart rate measurements of Brangus heifers with low and high RFI in studies 3 and 4

Trait[1]	Low RFI	High RFI	SE	*P*-value
Study 3				
Restricted DMI, kg/d	8.68	9.29	0.42	0.17
Restricted MEI, kcal/kg$^{.75}$	210.74	230.24	9.04	0.05
Restricted HR, beats/min	88.43	91.10	3.77	0.49
Study 4				
Ad libitum DMI, kg/d	9.15	12.14	0.78	0.01
Ad libitum MEI, kcal/kg$^{.75}$	213.63	284.81	14.48	0.01
Ad libitum HR, beats/min	87.40	94.14	3.27	0.06
Maintenance DMI, kg/d	4.66	4.63	0.17	0.87
Maintenance MEI, kcal/kg$^{.75}$	110.06	111.21	1.80	0.53
Maintenance HR, beats/min	63.55	63.50	3.76	0.99
HR change, beats/min	23.86	30.64	3.26	0.06

[1]MEI = metabolizable energy intake; HR = heart rate.

89 kJ·kg$^{0.75\ -1}$·d^{-1}, respectively). Furthermore, Basarab et al. (2003) reported greater energy expenditure for calves with high RFI compared to those with low RFI when allowed free access to feed (751 vs. 681 kJ·kg$^{0.75\ -1}$·d^{-1}, respectively).

As intended, DMI and MEI were similar between RFI phenotypes during the restricted and maintenance HR periods in study 2. However, in study 2, there was a RFI group by IGF-I selection line interaction for restricted and maintenance DMI such that bulls and heifers with low RFI from the low IGF-I selection line had numerically 8 and 5% lower DMI during the restricted and maintenance HR periods, respectively, compared to bulls and heifers with low RFI from the high IGF-I selection line, whereas, bulls and heifers with high RFI from the low IGF-I selection line had numerically 7 and 6% greater DMI during the restricted and maintenance HR periods, respectively, compared to bulls and heifers with high RFI from the high IGF-I selection line. This was likely due to a similar interaction ($P < 0.05$) for MBW during the restricted and maintenance HR periods, because no interaction was observed for computed MEI, which adjusted DMI to metabolic body size. Furthermore, there was a RFI group by gender interaction for MEI during the maintenance HR period such that bulls with low RFI had 6% lower ($P < 0.05$) MEI than heifers with low RFI (115.1 vs. 122.0 kcal·kg$^{0.75\ -1}$·d^{-1}, respectively), whereas, bulls and heifers with high RFI had similar MEI (120.4 and 119.9 kcal·kg$^{0.75\ -1}$·d^{-1}, respectively). In study 3, as in study 2, DMI and MEI were intended to be similar. However, Brangus heifers with low RFI had numerically 7% lower DMI, but numerically greater MBW during the restricted HR period (82.5 vs. 80.7 kg$^{0.75}$, respectively) resulting in lower ($P < 0.05$) MEI compared to Brangus heifers with

high RFI. In retrospect, it appears that the chosen restricted DMI level (120 g DM/$kg^{.75}$) was slightly greater than the ad-libitum DMI of the heifers with low RFI, thus, heifers with low RFI could not consume similar DMI to calves with high RFI.

Unexpectedly, Angus bulls and heifers with low RFI had greater ($P < 0.05$) HR during the restricted HR period, and tended ($P = 0.10$) to have greater HR during the maintenance HR period than bulls and heifers with high RFI in study 2 indicating greater energy expenditure for calves with low RFI. However, in study 3, Brangus heifers with low RFI had similar HR during the restricted HR period to those with high RFI. The results of study 3 agree with those of study 1 and 4 such that, when DMI is held similar between RFI phenotypes, energy expenditure is similar. In contrast, Nkrumah et al. (2006) reported greater energy expenditure for steers with high RFI than steers with low RFI (163.9 vs. 129.3 $kcal \cdot kg^{0.75\ -1} \cdot d^{-1}$, respectively) when DMI was fixed at 2.5 x maintenance requirements for both phenotypes. However, the results of study 2 are inconsistent with either the results of study 3 or Nkrumah et al. (2006). No previous studies have evaluated the relationships between heart rate and RFI. The contrasting results between study 2 and 3 may have been influenced by diet (grain vs. roughage-based diet, respectively). Relationships of other physiological measurements and RFI are influenced by diet: Anonymous (2007) reported positive genetic correlations between insulin-like growth factor-I concentration and RFI in cattle fed roughage based diets, but negative genetic correlations in cattle fed grain-based diets.

Heart rate is an imperfect indicator of energy expenditure. Previous studies (Webster, 1967; Yamamoto et al., 1979) have reported strong positive linear

relationships between heart rate and energy expenditure, but the slope of this relationship varies among animals requiring the calibration of HR to energy expenditure for each animal. Energy expenditure could be estimated within ± 10% once calibration equations were determined (Yamamoto et al., 1979). Brosh (2007) concluded that determination of the oxygen pulse (oxygen consumed per heart beat) was a satisfactory method of calibrating HR to energy expenditure. In our studies, calibration of oxygen consumption to heart rate (oxygen pulse) was not performed, thus, results should be interpreted cautiously. However, our data suggests that calves with low RFI have lower energy expenditure than calves with high RFI, which is consistent with previous studies.

Effects of Gender and IGF-I Selection Line

As expected, bulls were heavier ($P < 0.05$) at the start and end of the study and had greater ($P < 0.05$) ADG than heifers in study 1 and 2. In study 1, bulls and heifers consumed similar amounts of feed, which resulted in an improved FCR for bulls compared to heifers. However, in study 2, bulls consumed more ($P < 0.10$) DMI and had lower ($P < 0.05$) FCR than heifers. The average RFI, which is statistically zero, was similar between bulls and heifers in study 1 and 2 as a result of including gender in the model to compute RFI. Hennessy and Arthur (2004) reported similar RFI between steers and heifers even when computation of RFI did not account for the effect of gender, but FCR was also similar between genders in their study.

In study 1, heifers consumed more ($P < 0.05$) MEI than bulls (272.7 vs. 221.4 $kcal \cdot kg^{0.75\ -1} \cdot d^{-1}$, respectively) during the ad libitum HR period, which is likely due to similar DMI but lower ($P < 0.05$) MBW (81.8 vs. 99.8 $kg^{0.75}$ for heifers and bulls,

respectively) of heifers compared to bulls. In addition, heifers had greater HR during the ad-libitum HR period than bulls (86.5 vs. 80.7 beats/min, respectively) due to their greater MEI. In study 2, bulls had greater ($P < 0.05$) DMI during the restricted and maintenance HR periods than heifers. Bulls had greater ($P < 0.05$) HR during the restricted HR period than heifers, but HR during the maintenance HR period was similar.

For both study 1 and 2, IGF-I selection line had no influence on growth, intake or feed efficiency traits. In addition, IGF-I selection line did not influence HR during any of the measurement periods for study 1 or 2. However, in study 2, the change in HR between restricted and maintenance HR periods was greater ($P < 0.05$) for calves from the low IGF-I selection line than those from the high IGF-I selection line (21.8 vs. 15.3 beats/min, respectively).

Implications

Research has determined that calves with low RFI phenotypes consume less DMI, but have similar BW, ADG and relatively similar carcass composition (i.e. retained energy) suggesting lower energy expenditure. Our results and others demonstrate that indeed calves with low RFI have lower energy expenditure indicating that selection of calves with low RFI phenotypes will improve the energetic efficiency of beef production.

CHAPTER V

RELATIONSHIPS BETWEEN HEPATIC MITOCHONDRIAL FUNCTION AND RESIDUAL FEED INTAKE IN GROWING BEEF CATTLE

Introduction

Feed costs are the largest variable expense for beef production, however, the typical measure of feed efficiency, feed conversion ratio (FCR), is negatively correlated with growth traits such that selection for improved FCR would result in larger mature cow size and increased feed requirements for maintenance (Archer et al., 1999). Thus, selection in the beef industry has primarily focused on output traits.

Residual feed intake (RFI) is a feed efficiency trait that quantifies inter-animal variation in dry matter intake that is unexplained by variation related to body weight and growth rate—efficient animals are those that consume less DMI than expected for a given BW and growth rate. Arthur et al. (2001a) concluded that RFI is a moderately heritable trait that is independent of mature size and that considerable genetic variation exists to facilitate selection. Herd et al. (2004) estimated that approximately one-third of the biological variation in RFI of growing calves could be explained by inter-animal differences in digestion, heat increment, composition of growth and activity, and posited that the remaining two-thirds was linked to inter-animal variation in energy expenditure.

Mitochondria consume 80 to 90% of cellular oxygen consumption (Harper et al., 2002), thus, differences in mitochondrial function could have a substantial impact on energy expenditure. Previous studies have reported differences in function of

mitochondria from skeletal muscle (Bottje et al., 2002; Iqbal et al., 2004), liver (Bottje et al., 2002; Iqbal et al., 2005) and intestine (Ojano-Dirian et al., 2005) between low and high efficient broilers. Furthermore, Kolath et al. (2006a) recently reported that calves with low RFI had greater coupling of oxidative phosphorylation in skeletal muscle mitochondria than calves with high RFI. Given that the liver of the ruminant animal accounts for 12 to 24% of the daily heat production (McBride and Kelly, 1990), the objective of this study was to determine if calves with divergent RFI phenotypes differ in hepatic mitochondrial function.

Materials and Methods

Animals and Management

Study 1. Angus bulls (n = 27; initial BW = 297.5 ± 34.7 kg) and heifers (n = 29; initial BW = 256.0 ± 25.1 kg) from divergent insulin-like growth factor-I (IGF-I) selection lines created at the Eastern Agricultural Research Station (Ohio State University) were used in this study. Calves arrived in College Station, Texas on January 11, 2006 at approximately 11 months of age, after weaning on October 5, 2005. Calves were blocked by BW and randomly assigned to pens (6 calves per pen), and adapted to a high grain diet (ME = 2.85 Mcal/kg DM; Table 5.1) for 32 d. Individual intakes were measured using Calan-gate feeders and BW measured weekly for 70 d.

Study 2. Santa Gertrudis steers (N = 119; initial BW = 308.4 ± 28.1 kg) from King Ranch were used in this study. Steers arrived in McGregor, Texas on October 30, 2006 at approximately 8 months of age after weaning on September 21, 2006. Calves were randomly assigned to 1 of 2 pens each equipped with 8 GrowSafe feed bunks and

adapted to a roughage-based diet (ME = 2.21 Mcal/kg DM) for 28 d. Individual intakes were measured using the GrowSafe Feed Intake System and BW measured at 14-d intervals for 70 d.

Diet ingredient samples were collected weekly throughout each study and composited by weight for chemical analyses. Moisture analysis was conducted by drying in a forced-air oven for 48 h at 105^{O}C (AOAC, 1995). Chemical analysis was conducted by an independent laboratory (Cumberland Valley Analytical Services, Inc., Hagerstown, MD), and ME concentrations of the experimental diets computed using the Cornell Net Carbohydrate and Protein System (Version 5.0, Cornell University, Ithaca, NY). Ingredient and chemical composition of the experimental diets are presented in Table 5.1.

Growth rates of individual calves were modeled by linear regression of BW against day of study using the general linear model of SAS (SAS Inst., Cary, NC). Regression coefficients were used to compute initial and final BW, ADG and metabolic BW (MBW; mid-test BW$^{.75}$). Moisture analysis of diet ingredient samples was used to determine average daily DMI from as-fed feed intake data. Residual feed intake was defined as the difference between actual DMI and that predicted from the regression of DMI on MBW and ADG using the following model:

(5.1) $DMI = ß_0 + ß_1MBW + ß_2ADG + €$

where $ß_0$ = y-intercept, $ß_1$ = partial regression coefficient of MBW, $ß_2$ = partial regression coefficient of ADG, € = error term.

Table 5.1. Ingredient and chemical composition of diets fed to calves in studies 1 and 2

Item	Study 1	Study 2
Ingredient composition, % as-fed		
Chopped alfalfa	12.80	--
Chopped haygrazer	--	40.05
Dry rolled corn	74.83	18.47
Pelleted alfalfa	3.20	--
Cottonseed hulls	2.13	8.05
Soybean hulls	--	19.05
Cottonseed meal	--	8.70
Molasses	4.27	5.00
Urea	1.17	--
Salt	1.01	0.40
Vitamin ADE[1]	0.20	0.13
Vitamin E[2]	0.34	0.11
Trace mineral[3]	0.05	0.013
Rumensin 80®[4]	--	0.019
Tylan 40®[5]	--	0.013
Chemical composition		
DM, % AF	88.85	90.87
CP, % DM	13.14	11.65
NDF, % DM	17.46	48.78
ME, Mcal/kg DM	2.85	2.21

[1]Vitamin ADE contained 2,200,000 IU vitamin A/kg, 440,000 IU vitamin D/kg and 8,800 IU vitamin E/kg of product.

[2]Vitamin E contained 44,000 IU/kg of product.

[3]Trace mineral contained minimum 19.0% Zn, 7.0% Mn, 4.5% CU, 4,000 ppm Fe, 2,300 ppm I, 1,000 ppm Se and 500 ppm Co.

[4]Rumensin 80 contained 176 g of monensin per kg of product.

[5]Tylan 40 contained 88 g of tylosin per kg of product.

Mitochondrial Function Measurements

In study 1, RFI was calculated after d 56 of test within gender and calves with low and high RFI were selected for mitochondrial function measurements from those that were < 0.5 and > 0.5 SD from the mean RFI of 0.00 ± 0.77 and 0.00 ± 0.61 kg/d for bulls and heifers, respectively. Liver biopsies and mitochondrial function measurements of heifers were performed 2 wk following d 70, whereas, liver biopsies of bulls were performed 8 wk following d 70. In study 2, RFI was calculated after d 56 of test and steers with low and high RFI were selected for mitochondrial function measurements from those that were < 1.0 and > 1.0 SD from the mean RFI of 0.00 ± 0.86 kg/d, respectively. Steers were moved to College Station, TX and liver biopsies performed 2 wk following d 70.

All surgical procedures were approved by the Animal Use and Care Committee of Texas A&M University. In study 1 and 2, liver samples were taken via percutaneous liver biopsy procedure. An imaginary line was drawn from the tuber coxae to the point of the shoulder, hair clipped and the area in the right 10^{th} intercostal space thoroughly cleaned with 7.5% povidone iodine solution (Triad Disposables, Inc., Brookfield, WI), then washed with a 70% isopropyl alcohol solution. Prior to use all surgical instruments were sanitized using a 0.5 % chlorhexidine diacetate solution (Nolvasan; Fort Dodge Laboratories, Fort Dodge, IA). A small stab incision was made after administration of 1 mL of lidocaine hydrochloride (Vedco Inc., St. Joseph, MO) and 2 to 3 g of liver collected with a Courtney bovine liver biopsy needle (Sontec Instruments Inc., Englewood, CO). Immediately after collection, liver tissue samples were placed on ice in

chilled isolation medium (250 mM sucrose, 10 mM Tris●HCl, 1 mM EGTA, and 0.5 % BSA, pH 7.4) and transported 10 min to the laboratory. Liver tissue samples were drained of isolation medium, transferred to chilled watch glass and weighed. Tissue homogenization and mitochondrial isolation were performed according to Ramsey et al. (2004) with the exception that a centrifuge speed of 10,000 x *g* was used in the final 3 steps.

In study 1, isolated mitochondria samples were shipped overnight on ice in an insulated container to Washington State University for measurement of oxygen consumption and proton-leak kinetics. In study 2, oxygen consumption and proton-leak kinetics of isolated mitochondria were measured at Texas A&M University. Mitochondrial protein concentration was determined using a Bradford protein assay. Respiration rates and proton-leak kinetics of isolated mitochondria were determined according to the procedures of Bevilacqua et al. (2004). In addition to the respiration measurements outlined by Bevilacqua et al. (2004), respiration rates were measured in the presence of 500 mM carbonyl cyanide p-[trifluoromethoxy]-phenyl-hydrazone (**FCCP**; uncoupler) immediately after measurement of state 4 respiration rates. From oxygen consumption measurements, the acceptor control ratio (**ACR**; ratio of state 3: state 2 respiration) and respiratory control ratio (**RCR**; ratio of state 3: state 4 respiration) were computed. Due to the time constraints of the mitochondrial oxygen consumption technique, only 4 or 6 calves (equal number of calves with low and high RFI) were measured on each day. Samples with non-respiring mitochondria were discarded and those calves repeated on subsequent days.

Statistical Analysis

Performance, mitochondrial oxygen consumption and proton-leak data were analyzed separately by gender. Performance data were analyzed using the mixed procedure of SAS (SAS Inst., Cary, NC) with RFI group as a fixed effect. Means of mitochondrial oxygen consumption measurements for calves with low and high RFI were determined using the mixed procedure of SAS with day as a random effect assuming a var-(co)variance structure of variance components. In addition, IGF-I selection line and the interaction term were included as fixed effects in analysis of performance traits and mitochondrial oxygen consumption measurements for bulls and heifers in study 1. Examination of significant interactions resulted in removal of the interaction term and the use of a reduced model to assess the effect of RFI group on performance traits and mitochondrial oxygen consumption measurements.

Mitochondrial proton leak kinetics for calves with low and high RFI were compared by non-linear regression techniques using the NLIN procedure of SAS (Crescenzo et al., 2006). Data for each gender were fit to the following model:

(5.2) $y = (a_1 + (a_2 * \text{RFI group})) \cdot (b_1 + (b_2 * \text{RFI group}))^x$

where y = oxygen consumption, a_1 = the overall y-intercept, a_2 = the effect of RFI group on the y-intercept, b_1 = the overall base for the exponent x, b_2 = the effect of RFI group on the base and x = adjusted membrane potential.

The repeated measurements of membrane potential were adjusted for the random effect of calf within gender and RFI group using the mixed procedure of SAS. This procedure aligned the proton leak curve of calves within RFI group and gender without affecting

the variation of the individual data points of individual calves, which allowed analysis of the relationship between oxygen consumption and membrane potential. Residual feed intake group was defined as 0 for calves with low RFI and 1 for calves with high RFI. Thus, if parameter a_2 or b_2 was significantly different from zero (alpha = 0.05), then RFI groups differed in the y-intercept or slope of the curve, respectively.

Results and Discussion

Summary statistics of performance traits are presented in Table 5.2 for bulls, heifers and steers. As expected, bulls and heifers in study 1 had numerically greater ADG compared to steers in study 2, which is most likely due to greater metabolizable energy content of the diet fed in study 1 compared to study 2. However, bulls and heifers consumed numerically similar DMI compared to steers, which resulted in numerically lower FCR for bulls and heifers compared to steers. There was less variation in RFI among bulls and heifers compared to steers based on SD of RFI, which could be due to bulls and heifers being fed a grain-based diet compared to steers being fed a roughage-based diet.

Performance traits for calves with low and high RFI selected for mitochondrial measurements are presented in Table 5.3 for bulls, heifers and steers. Calves with low RFI consumed 18, 13 and 24% less ($P < 0.05$) DMI and had 15, 12, and 27% lower ($P < 0.05$) FCR than calves with high RFI for bulls, heifers and steers, respectively, even though, ADG and BW were similar. Previous studies have reported similar differences between calves with low and high RFI (Fox et al., 2004; Nkrumah et al., 2004; Brown, 2005).

Table 5.2. Summary statistics (± SD) of performance and feed efficiency traits for all calves in studies 1 and 2

	Study 1		Study 2
Trait[1]	Bulls	Heifers	Steers
No. head	27	29	119
Initial BW, kg	297.5 ± 34.7	256.0 ± 25.1	308.4 ± 28.1
Final BW, kg	384.7 ± 39.6	319.9 ± 25.4	366.6 ± 32.7
ADG, kg/d	1.78 ± 0.26	1.30 ± 0.15	0.83 ± 0.16
DMI, kg/d	10.20 ± 1.25	9.24 ± 1.14	9.48 ± 1.00
RFI, kg/d	0.00 ± 0.77	0.00 ± 0.61	0.00 ± 0.86
FCR, feed/gain	5.79 ± 0.65	7.13 ± 0.87	8.65 ± 0.94

[1]RFI = residual feed intake; FCR = feed conversion ratio.

Table 5.3. Performance and feed efficiency traits of calves with low and high RFI selected for mitochondrial function measurements

Trait[1]	Low RFI	High RFI	SE	*P*-value
Bulls				
No. animals	8	8		
Initial BW, kg	298.8	309.5	20.1	0.60
Final BW, kg	386.6	399.9	21.5	0.55
ADG, kg/d	1.79	1.84	0.11	0.65
DMI, kg/d	9.45	11.50	0.39	0.01
RFI, kg/d	-0.79	0.95	0.25	0.01
FCR, feed/gain	5.30	6.27	0.30	0.01
Heifers				
No. animals	7	7		
Initial BW, kg	259.7	254.8	13.2	0.72
Final BW, kg	324.6	320.2	12.9	0.74
ADG, kg/d	1.32	1.33	0.07	0.88
DMI, kg/d	8.75	10.03	0.47	0.02
RFI, kg/d	-0.69	0.71	0.19	0.01
FCR, feed/gain	6.66	7.57	0.43	0.06
Steers				
No. animals	6	8		
Initial BW, kg	316.5	304.0	11.6	0.30
Final BW, kg	381.5	358.9	13.5	0.12
ADG, kg/d	0.93	0.78	0.09	0.13
DMI, kg/d	8.36	10.99	0.43	0.01
RFI, kg/d	-1.43	1.68	0.29	0.01
FCR, feed/gain	7.43	10.21	0.38	0.01

[1]RFI = residual feed intake; FCR = feed conversion ratio.

Table 5.4. Function of isolated liver mitochondria in calves with low and high RFI

Trait[1]	Low RFI	High RFI	SE	*P*-value
Bulls				
State 2 respiration[2]	47.92	53.37	3.32	0.13
State 3 respiration	78.40	90.93	5.35	0.04
State 4 respiration	48.75	53.71	3.75	0.22
FCCP respiration	153.27	183.47	15.48	0.08
ACR	1.65	1.70	0.06	0.40
RCR	1.61	1.71	0.06	0.13
Heifers				
State 2 respiration	52.94	54.56	4.63	0.74
State 3 respiration	116.37	97.59	8.42	0.06
State 4 respiration	55.24	52.36	5.18	0.59
FCCP respiration	230.89	195.64	19.37	0.11
ACR	2.18	1.80	0.13	0.02
RCR	2.12	1.88	0.12	0.09
Steers				
State 2 respiration	28.82	28.17	1.85	0.73
State 3 respiration	102.04	90.06	7.67	0.15
State 4 respiration	21.42	20.77	1.45	0.66
FCCP respiration	41.49	40.30	3.05	0.70
ACR	3.78	3.36	0.19	0.05
RCR	5.20	4.70	0.40	0.23

[1]FCCP = carbonyl cyanide p-[trifluoromethoxy]-phenyl-hydrazone; ACR = acceptor control ratio (ratio of state 3:state 2 respiration); RCR = respiratory control ratio (ratio of state 3:state 4 respiration).

[2]Respiration rates are presented as nanomoles $O_2 \cdot$ mg mitochondrial protein$^{-1} \cdot$ min^{-1}

Calves with low and high RFI had similar state 2 respiration rates for bulls, heifers and steers (Table 5.4). However, previous studies have reported that muscle mitochondria from calves with low RFI have greater state 2 respiration rates (Kolath et al., 2006a) and that liver mitochondria from high efficiency broilers have lower state 2 respiration rates (Bottje et al., 2002) than their low efficiency counterparts. Bulls with low RFI had lower ($P < 0.05$) state 3 respiration rates, whereas, heifers with low RFI had greater ($P < 0.10$) state 3 respiration rates and steers with low RFI tended ($P = 0.15$) to have greater state 3 respiration rates than their high RFI counterparts. Bottje et al. (2002) reported greater state 3 respiration rates in liver mitochondria of broilers with high efficiency compared to low efficiency. Furthermore, Kolath et al. (2006a) reported greater state 3 respiration rates in muscle mitochondria of calves with low RFI compared to calves with high RFI. State 4 respiration rates were similar between RFI phenotypes for bulls, heifers and steers. Similarly, Kolath et al. (2006a) reported similar state 4 respiration rates in skeletal muscle mitochondria of calves with low and high RFI. In contrast, Bottje et al. (2002) reported lower state 4 respiration rates in liver mitochondria of high efficiency broilers compared to low efficiency broilers.

Bulls with low RFI tended ($P = 0.08$) to have lower FCCP respiration rates than bulls with high RFI, whereas, heifers with low RFI tended ($P = 0.11$) to have greater FCCP respiration rates than heifers with high RFI. Steers with low and high RFI had similar FCCP respiration rates. These results suggest that the mitochondria of bulls with high RFI and heifers with low RFI are more responsive to changes in the proton motive force such that respiration rates adapt to cellular energy changes more readily. However,

given the conflicting results of this study and no previous reports of FCCP respiration rates in animals differing in feed efficiency, a definite conclusion can not be drawn.

Heifers and steers with low RFI had greater ($P < 0.05$) ACR than their high RFI counterparts, whereas, bulls with low and high RFI had similar ACR. The RCR was similar between calves with low and high RFI for bulls, heifers and steers. These results are consistent with previous studies that have demonstrated greater ACR, but similar RCR in liver mitochondria of broilers (Bottje et al., 2002). The acceptor control ratio is a measure of oxygen consumption in the presence of ADP. Thus, lower ACR is indicative of less control of oxidative phosphorylation by ADP. Previous research has suggested that oxidation of substrates and an increase in phosphorylation potential (ratio of [ATP]:[ADP] + [P_i]) in the liver are important mechanisms signaling satiety (Hong et al., 2000; Oba and Allen, 2003a, b). Therefore, the greater control of oxidative phosphorylation by ADP in the liver of calves with low RFI may result in a quicker satiety response to oxidation of substrates contributing to the less than expected feed intake of this phenotype.

The reason for the discrepancy in the mitochondria respiration rates of bulls compared to heifers and steers is unknown, but may be due to additional measurements taken on bulls prior to liver biopsies where feed intake was restricted. During the 5 wk period of additional measurements, bulls with low and high RFI were restricted to similar feeding levels such that bulls with high RFI had greater feed intake restriction relative to ad libitum intake. Bulls were allowed 1 wk adaptation to ad libitum intake before liver biopsies. However, the greater feed restriction of bulls with high RFI most

likely caused greater lipolysis and ketone production in the liver of these bulls. Feed restriction could have affected liver expression of growth hormone receptor, which may not recover after 7 d of refeeding (Radcliff et al., 2006). These changes in liver metabolism may have resulted in the different mitochondrial function observed in bulls compared to heifers and steers.

Liver mitochondrial protein concentrations were similar between calves with low and high RFI for bulls, heifers and steers (Table 5.5). Previous studies have not reported mitochondrial protein concentrations of tissues, but the lack of a difference between calves with low and high RFI suggests that the results obtained regarding *in vitro* respiration rates would be similar per gram of fresh liver.

Non-linear regression techniques indicated that there was a significant (Probability $b_1 = 1.0$; $P < 0.05$) relationship between oxygen consumption and membrane potential for bulls, heifers and steers (Figure 5.1-5.3). Furthermore, the non-linear regression model explained 91.5, 85.1 and 90.8% of the variation in mitochondrial oxygen consumption. However, there was no significant difference ($P > 0.05$) in this relationship between calves with low and high RFI for bulls, heifers or steers, which is represented by the similarity of the estimates for parameters a_2 and b_2 with zero. Previous research has indicated that proton leak accounts for 26 and 52% of oxygen consumption in liver and muscle, respectively, and has been demonstrated to account for ~ 20% of the standard metabolic rate in rats (Rolfe and Brown, 1997). However, previous studies evaluating mitochondrial function in animals differing in feed efficiency have not determined proton leak kinetics. Kolath et al. (2006a) reported

Table 5.5. Liver mitochondrial protein concentrations (mg/g of fresh tissue) of calves with low and high RFI

RFI group	Bulls	Heifers	Steers
Low RFI	3.34	3.04	2.43
High RFI	2.79	2.69	2.08
SE	0.39	0.99	0.34
P-value	0.18	0.73	0.33

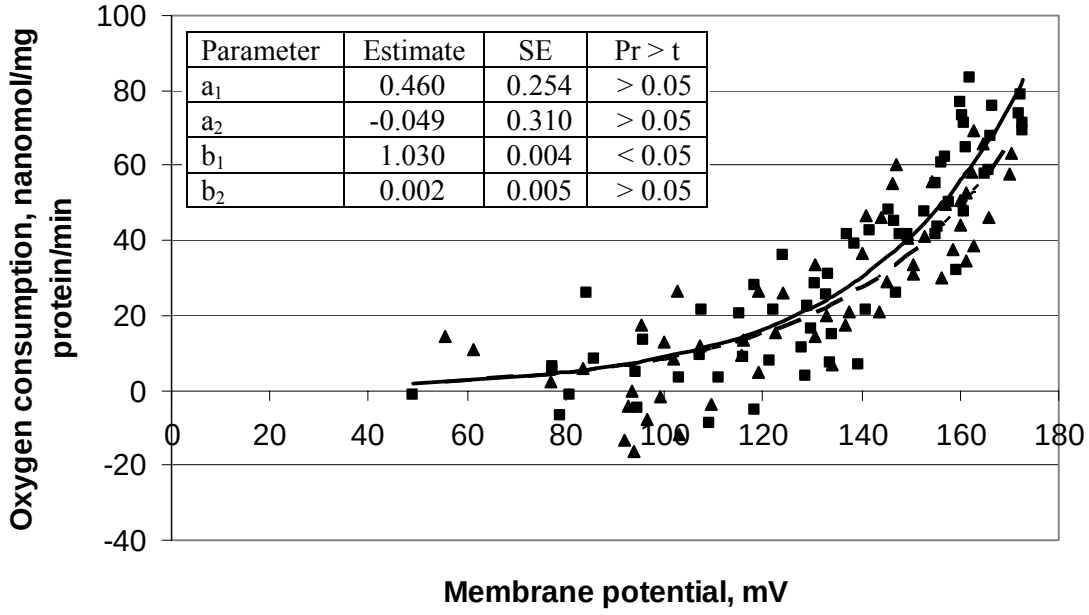

Figure 5.1. Mitochondrial proton-leak kinetics of bulls with low (▲) and high (■) residual feed intake (RFI). Predicted values from non-linear regression for bulls with low (--) and high (—) RFI are represented by the regression lines. Inserted table shows parameter estimates for non-linear regression equation. a_1 = parameter estimating the y-intercept of the regression line; b_1 = parameter estimating the slope of the exponential equation; a_2 = parameter estimating the effect of RFI group on the y-intercept; b_2 = parameter estimating the effect of RFI group on the slope of the exponential equation.

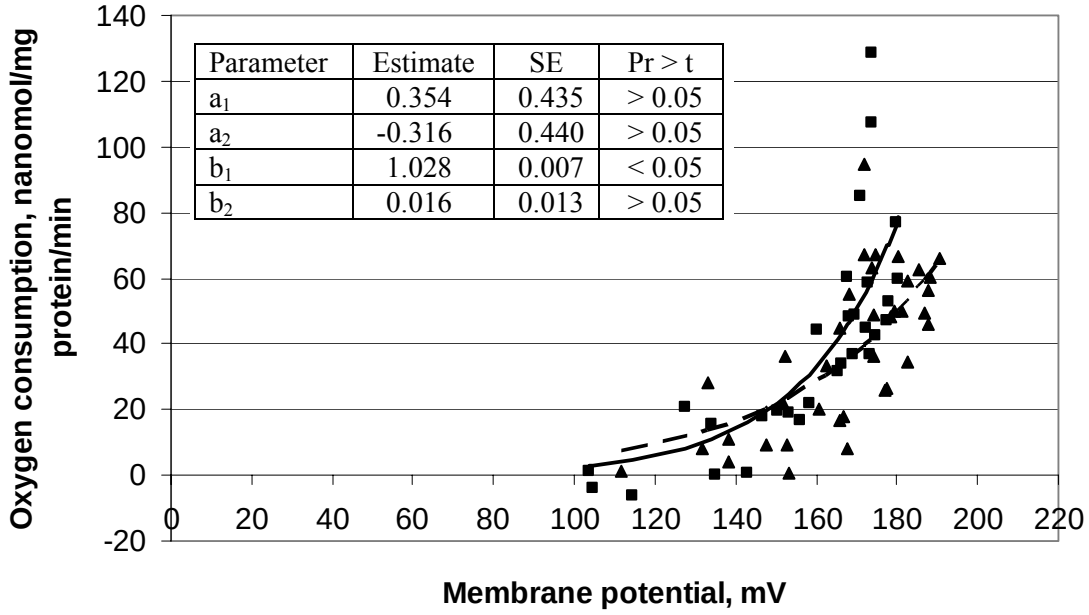

Figure 5.2. Mitochondrial proton-leak kinetics of heifers with low (▲) and high (■) residual feed intake (RFI). Predicted values from non-linear regression for heifers with low (--) and high (—) RFI are represented by the regression lines. Inserted table shows parameter estimates for non-linear regression equation. a_1 = parameter estimating the y-intercept of the regression line; b_1 = parameter estimating the slope of the exponential equation; a_2 = parameter estimating the effect of RFI group on the y-intercept; b_2 = parameter estimating the effect of RFI group on the slope of the exponential equation.

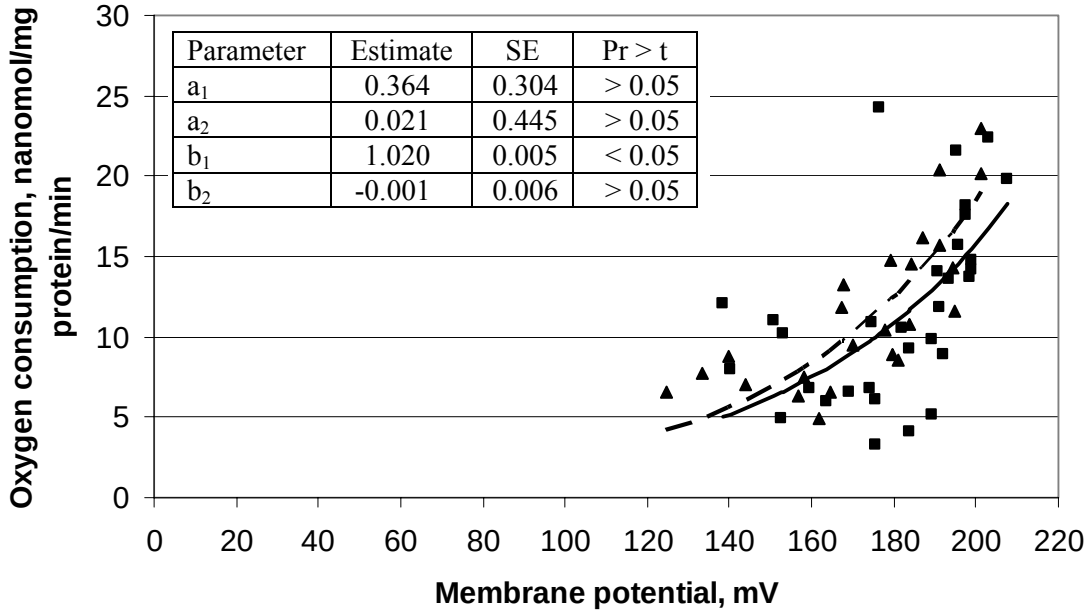

Figure 5.3. Mitochondrial proton-leak kinetics of steers with low (▲) and high (■) residual feed intake (RFI). Predicted values from non-linear regression for steers with low (--) and high (—) RFI are represented by the regression lines. Inserted table shows parameter estimates for non-linear regression equation. a_1 = parameter estimating the y-intercept of the regression line; b_1 = parameter estimating the slope of the exponential equation; a_2 = parameter estimating the effect of RFI group on the y-intercept; b_2 = parameter estimating the effect of RFI group on the slope of the exponential equation.

larger RCR values (an indicator of oxidative phosphorylation coupling) in muscle mitochondria of calves with low RFI compared to calves with high RFI. Furthermore, Bottje et al. (2002) reported greater RCR values in muscle mitochondria of broilers with high feed efficiency compared to those with low feed efficiency. However, Bottje et al. (2002) reported similar RCR values in liver mitochondria of broilers, which is similar to our study. Therefore, variation in proton leak rates of liver mitochondria may have a minimal contribution to the differences in energy expenditure between calves with low and high RFI.

Implications

Calves with low RFI that typically consume ~20% less feed than their high RFI counterparts have liver mitochondria which exhibit greater metabolic control by ADP suggesting effects on satiety signals from the liver. However, differences in efficiency of feed use between calves with low and high RFI does not appear to be due to proton leak rates of liver mitochondria. Further research is needed to evaluate mitochondrial function in various tissues and relationships with RFI.

CHAPTER VI

CHARACTERIZATION OF RESIDUAL FEED INTAKE IN BRANGUS HEIFERS AND RELATIONSHIPS WITH REPRODUCTIVE TRAITS

Introduction

Feed costs are the largest variable expense for beef production, thus selection for improved feed efficiency could substantially improve profits. However, the typical measure of feed efficiency, feed conversion ratio (FCR), is negatively correlated with growth traits such that selection for improved FCR would result in larger mature cow size and increased feed requirements for maintenance (Archer et al., 1999). Thus, selection in the beef industry has primarily focused on output traits. Residual feed intake (RFI) is a feed efficiency trait that quantifies inter-animal variation in dry matter intake that is unexplained by variation related to body weight and growth rate—efficient animals are those that consume less DMI than expected for a given BW and growth rate. Arthur et al. (2001a) concluded that RFI is a moderately heritable trait that is independent of mature size and that considerable genetic variation exists to facilitate selection.

In addition to feed costs, reproductive efficiency has a large impact on herd profitability: lower pregnancy rates and long postpartum intervals result in increased heifer replacement rates, thus increasing feed and other costs (Werth et al., 1991). Previous research has reported a positive relationship between fat composition, as indicated by body condition score, and reproductive performance (DeRouen et al., 1994;

Spitzer et al., 1995). Hall et al. (1995) reported that heifers fed to gain weight at a high rate (1.0 kg/d) had greater fat composition and attained puberty at a younger age than heifers fed to gain weight at a moderate rate (0.6 kg/d) indicating that heifers were able to attain puberty at a younger age due to increased fat composition. Basarab et al. (2003) and Nkrumah et al. (2004) reported a positive correlation between carcass fat composition and RFI suggesting that RFI phenotypes may differ in reproductive performance. Arthur et al. (2005) reported similar calving rates in mature females after 1.5 generations of divergent selection for RFI. However, no studies have evaluated the relationship between RFI and reproductive performance in beef heifers. Therefore, the objective of this study was to evaluate reproductive performance of Brangus heifers with differing RFI phenotypes.

Materials and Methods

Animals and Management

RFI testing period. A total of 348 purebred Brangus heifers (initial age = 232.5 ± 11.7 d; initial BW = 273.8 ± 25.9 kg) from Camp Cooley Ranch were used in this study. Performance tests were conducted in 3 consecutive yr (N = 114, 115 and 119 for yr 1, 2 and 3, respectively) to identify heifers with low, medium and high RFI phenotypes. Diet composition and management during the RFI testing period and computation of RFI using meta-analysis techniques are presented in chapter II of this dissertation.

For determination of pubertal status, blood samples were collected weekly via jugular venipuncture using evacuated serum tubes (Becton, Dickson and Company, Franklin Lakes, NJ), and serum harvested after centrifugation (800 x *g* at 4^{O}C for 15

min). Serum samples were analyzed for progesterone using radioimmunoassay procedures (Diagnostic Systems Laboratories, Inc., Webster, TX). Heifers with progesterone levels of > 1.0 ng/mL for 2 consecutive weeks or > 2.0 ng/mL for 1 week were considered to be pubertal. The date of first elevated progesterone was used to compute age at puberty. In addition, ovarian ultrasound was performed on d 63 of the test in each year to verify progesterone results.

Post-RFI testing period. At the end of the RFI testing period, heifers were returned to Camp Cooley Ranch and reproductive data collected for their first parity. After returning to the ranch, heifers were managed as necessary by the ranch for financial success resulting in some heifers being sold prior to the first breeding season and between the breeding and calving season. Therefore, 113, 112 and 70 heifers had palpation records for yr 1, 2 and 3, respectively. Furthermore, 102 and 82 heifers had calving records for yr 1 and 2, respectively. Heifers from yr 3 had not yet completed their first calving season and thus, calving data includes only heifers from yr 1 and 2.

Heifers were synchronized using Estrumate® (Schering-Plough Animal Health Ltd., Wellington, New Zealand) and exposed to artificial insemination on an average date of April 19, 2005, April 21, 2006 and April 19, 2007 at an average age of 440.7, 440.5 and 441.2 d for yr 1, 2 and 3, respectively. Bulls were introduced in May of each year and removed by mid-July. Pregnancy rates were determined by palpation per rectum beginning in late August approximately 45 d after removal of bulls. In addition, BW of heifers was collected at the time of palpation. Calves were weighed at birth and

gender of the calf determined. Calves were again weighed at weaning and adjusted 205-d weaning weight calculated.

Reproductive Traits

For each heifer, pregnancy status was determined as non-pregnant, pregnant to artificial insemination or pregnant to natural service. Calving date, gender of calf and weaning date were recorded for each heifer. A binomial code (1 = yes; 0 = no) was used to indicate cycling, pregnancy, calving and weaning status of each heifer and gender of each calf such that the following reproductive traits could be computed. First service pregnancy rate is ratio of the number of heifers bred to artificial insemination to the number of heifers exposed to artificial insemination. Pregnancy rate is the ratio of the number of heifers bred to artificial insemination or natural service to the number of heifers mated. Calving rate is the ratio of the number of calves born alive or still to the number of heifers mated remaining in the herd at calving. Weaning rate is the ratio the number of calves weaned to the number of calves born. Percent net calf crop is ratio of the number of calves weaned to the number of heifers mated remaining in the herd at calving.

Statistical Analysis

All heifer and calf performance traits were adjusted to remove the random effect of test using the mixed procedure of SAS. Heifers were classified into low, medium and high RFI groups that were < 0.5, ± 0.5 and > 0.5 SD, respectively, from the mean RFI of 0.00 ± 0.71 kg/d. Heifer and calf performance traits were evaluated using the MIXED procedure of SAS with a model that included the fixed effects of RFI group and breeding

contemporary group for dam performance traits and calf birth weight or weaning contemporary group for calf weaning weight. Comparisons of least square means between RFI groups were performed using Tukey's post hoc test. Chi-square tests were performed for reproductive traits using the FREQ procedure of SAS to compare proportions of heifers in each RFI group.

Results and Discussion

Management of heifers at the ranch resulted in similar ($P = 0.91$) proportions of heifers with low, medium and high RFI being sold prior to the breeding season (16.07, 13.04 and 16.33%, respectively). However, there was an association ($P < 0.05$) between RFI group and the proportion of heifers sold prior to the calving season such that heifers with high RFI had the largest proportion sold (16.22, 13.48 and 30.30% for heifers with low, medium and high RFI, respectively).

Reproductive traits of heifers are presented in table 6.1. Of the 348 heifers tested, 104 (29.89%) were cycling by the end of the 70-d RFI testing period, which is an average age of 302 d. McCartor et al. (1979) reported Brangus heifers fed various dietary treatments attained puberty at an average BW of 321 kg, which is similar to the final BW of heifers in this study (342 kg). However, the average age at puberty (495 d) of heifers was considerably greater in the study by McCartor et al. (1979) compared to the average age of Brangus heifers at the end of our study. Furthermore, Moseley et al. (1977) reported that 63% of Brahman x Hereford F-1 heifers attained puberty by 246 d post-weaning. Thus, the low proportion of heifers cycling by the end of the 70-d RFI testing period was typical of Brahman x British crossbred heifers.

Table 6.1. Reproductive traits of heifers with low (< 0.5 SD), medium (± 0.5 SD) and high (> 0.5 SD) RFI

Trait[1]	Low RFI	Med RFI	High RFI	SE	*P*-value
No. heifers with progesterone records	112	138	98		
Cycling, %	32.14	28.26	29.59	--	0.80
Age at puberty, d	279.2	272.8	270.6	5.8	0.29
Maximum P4, ng/mL	8.95	8.41	8.25	1.04	0.77
No. heifers with palpation records	94	119	82		
1st service pregnancy rate, %	57.14	52.73	49.33	--	0.60
Overall pregnancy rate, %	89.36	85.71	79.27	--	0.17
No. heifers with calving records[2]	62	76	46		
Age at calving, d	731.6	733.8	739.4	6.0	0.42
Calving day[3]	35.4	40.5	41.5	5.8	0.46
Calving rate, %	80.65	78.95	78.26	--	0.95
Weaning rate, %	83.67	81.67	69.44	--	0.23
Net calf crop, %	67.21	64.47	54.35	--	0.37
% male calves	52.00	48.33	52.78	--	0.89

[1]P4 = progesterone.
[2]Calving data only includes heifers from year 1 and 2.
[3]January 1 is day 1 each calving season.

The proportion of heifers cycling by the end of the 70-d RFI testing period was similar among RFI phenotypes. Of those heifers that were cycling, age at puberty was also similar among RFI phenotypes; however, heifers with low RFI were numerically 9 d older than heifers with high RFI. There have been no other studies evaluating the relationship between age at puberty and RFI. Our data suggests that selection for improved RFI may result in heifers being slightly older at puberty, but that the number of heifers attaining puberty by a given date would be similar. In addition, maximum progesterone levels were similar among RFI phenotypes suggesting similar quality of the corpus luteum developed.

There was no association between first service or overall pregnancy rate and RFI phenotype group; however, heifers with low RFI had numerically 8 and 10 percentage unit greater first service and overall pregnancy rates than heifers with high RFI, respectively. Calving rate, weaning rate and net calf crop were similar among RFI phenotypes, but as with pregnancy rates, heifers with low RFI had numerically 14 and 13 percentage unit greater weaning rate and net calf crop than heifers with high RFI, respectively. Collectively, these data suggest that selection for improved RFI may further reduce input costs by reducing the number of non-pregnant females and the number of replacement heifers needed. Arthur et al. (2005) reported similar pregnancy (90.5 and 90.2%), calving (89.2 and 88.3%) and weaning (81.5 and 80.2%) rates of females after 1.5 generations of divergent selection for low or high RFI. Previous studies have reported no relationship between reproductive traits and measures of feed efficiency in other species: egg production was similar between laying hens with low

Table 6.2. Performance traits of heifers and progeny for heifers with low (< 0.5 SD), medium (± 0.5 SD) and high (> 0.5 SD) RFI

Trait[1]	Low RFI	Med RFI	High RFI	SE	*P*-value
Heifer performance					
BW at palpation, kg	474.7	477.6	480.2	6.5	0.71
Calf performance					
Birth wt., kg	33.9	33.6	33.3	1.1	0.85
205-d adjusted weaning wt., kg	262.0	263.4	260.4	7.9	0.93
Average daily gain, kg/d	1.02	1.02	1.00	0.03	0.84

and high RFI (Luiting et al., 1991) and number born alive were not correlated with FCR in swine (Hermesch et al., 2000). In addition, the percentage of male calves was similar among RFI groups in this study.

Age of heifers at calving and calving day was similar among RFI phenotypes. Arthur et al. (2005) reported a trend ($P < 0.10$) for females from the low RFI selection line to calve later in the calving season than females from the high RFI selection line (215 vs. 210 d, respectively). In our study, heifers with low RFI numerically calved 6 d earlier in the calving season than heifers with high RFI.

Weight of heifers at palpation was similar among RFI groups (Table 6.2). Arthur et al. (2005) reported that BW of females from divergent RFI selection lines was similar throughout the reproductive cycle. However, these authors reported that rib fat thickness was greater in females from the high RFI selection line at the start of mating season each year, but similar at weaning compared to females from the low RFI selection line. Body condition score (i.e. fat cover) is positively related with pregnancy rate (Spitzer et al., 1995) suggesting that females with high RFI would have greater pregnancy rates. However, this result was not observed in the study by Arthur et al. (2005). In our study, neither additional BW nor ultrasound measurements of fat thickness were collected.

Heifers with low RFI had calves of similar birth weight, 205-d adjusted weaning weight and ADG compared to heifers with medium or high RFI. Similar to our results, Arthur et al. (2005) reported no difference in calf birth weight, 220-d adjusted weaning weight or ADG between females divergently selected for low or high RFI. In addition, Luiting et al. (1991) reported that egg weight was similar between laying hens with low

and high RFI. Based on similar weaning weights and ADG of calves, our data indicate that milk production of heifers was likely similar among RFI phenotypes. Arthur et al. (2005) reported similar milk yield between females divergently selected for low or high RFI.

Implications

Adoption of feed intake technology and selection for improved RFI is increasing dramatically in the beef industry. However, few studies have evaluated the impact of selection for improved RFI on female reproductive efficiency. Results of this study indicate that selection for improved RFI will not negatively impact female reproduction. However, further research is necessary to evaluate long-term reproductive function of females differing in RFI.

CHAPTER VII

SUMMARY

The results of this dissertation indicate that residual feed intake was strongly positively correlated with feed intake and feed conversion ratio, but independent of growth and body size. In addition, residual feed intake was less impacted by differences in carcass composition than other feed efficiency traits and could easily be adjusted to account for these differences. Thus, selection for improved residual feed intake has the potential to improve gross feed efficiency with minimal affects on growth and carcass composition. Calves differing in feed efficiency also differed in energy expenditure determined by heart rate; however, measures of energy efficiency in liver mitochondria were similar between RFI phenotypes. Identification of physiological indicators such as insulin-like growth factor-I (IGF-I) would enhance selection for improved residual feed intake. Results from this dissertation indicate that the relationship between residual feed intake and IGF-I is complex and can be influenced by diet, stage of maturity of the animals tested, breed and age of sampling for IGF-I. Further research is necessary to determine the influence of these factors on this relationship and the usefulness of IGF-I as an indicator for residual feed intake. Along with feed costs, reproductive efficiency has a large impact on the profitability of a beef operation, but little is known about the relationship between residual feed intake and reproductive traits. Preliminary data herein indicates that selection for improved residual feed intake could result in heifers attaining puberty at an older age, but having an improved net calf crop percentage. Further

research is necessary to evaluate the relationship between residual feed intake and life-time reproductive performance of females.

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