INFLUENCE OF DIET, PRODUCTION TRAITS, BLOOD HORMONES AND METABOLITES, AND MITOCHONDRIAL COMPLEX PROTEIN CONCENTRATIONS ON RESIDUAL FEED INTAKE IN BEEF CATTLE

A Dissertation

presented to

the Faculty of the Graduate School

at the University of Missouri-Columbia

In Partial Fulfillment

of the Requirements for the Degree

Doctor of Philosophy

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by

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JULY 2009

The undersigned, appointed by the dean of the Graduate School, have examined the dissertation entitled:

INFLUENCE OF DIET, PRODUCTION TRAITS, BLOOD HORMONES AND METABOLITES, AND MITOCHONDRIAL COMPLEX PROTEIN CONCENTRATIONS ON RESIDUAL FEED INTAKE IN BEEF CATTLE

presented by Michael Patrick Davis,

a candidate for the degree of Doctor of Philosophy,

and hereby certify that, in their opinion, it is worthy of acceptance.

Professor Monty Kerley

Professor James Williams

Professor Duane Keisler

Professor Mark Ellersieck

Dedication

This dissertation is dedicated to my parents for the help that they have given me throughout the completion of the degree.

ACKNOWLEDGEMENTS

I would like to express a sincere thanks to Dr. Monty Kerley for his guidance in the research projects reported in this dissertation. I appreciate and thank the members of my committee; Dr. James Williams, Dr. Duane Keisler, and Dr. Mark Ellersieck.

Care and management of livestock are important in the research projects reported in this dissertation. I would like to thank the UMC beef farm crew for their care and management of the livestock that were used in the research projects reported in this dissertation. I would also like to thank Jim Porter for his help in analysis conducted during this project.

Research projects presented in this dissertation required help from multiple individuals. I appreciate the time and effort that was given to the projects by Joe Golden and Matt Brooks. Furthermore, thank you to all the graduate students for their assistance and friendship during my doctor of philosophy program.

I am grateful to my family for their help and encouragement in continuing my education. I sincerely appreciated the love and support by my father, Mike Davis, mother, Elaine Davis, sister, Rebecca Davis, and the rest of the family during the completion of my doctor of philosophy degree.

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ABSTRACT

Residual feed intake (RFI) is the difference between measured feed intake and predicted feed intake of an animal. Intake prediction is computed from a regression of intake on gain and metabolic body weight. Residual feed intake is used as a measure of metabolic efficiency. As RFI increases, feed intake (FI) and feed conversion ratio (FCR) increase with no change in postweaning growth and body weight in steers. Identification and selection for lower RFI cattle would improve herd feed efficiency without influencing growth. Steer residual feed intake measured in the growing phase, is related to residual feed intake during the finishing phase. Animals with low residual feed intake in the growing phase had lower residual feed intake and improved feed efficiency in the finishing phase. Serum concentrations of glucose and mitochondrial function are related to metabolic efficiency and may differ between residual feed intake phenotypes. Serum concentrations of glucose at weaning were greater ($P < 0.05$) in low (efficient) compared to high (inefficient) RFI steers. Mitochondrial complex protein concentrations I:II and I:III ratios were greater ($P < 0.05$) in low extreme versus high extreme RFI steers. Diets varied in rumen undegradable protein content were used to determine impact of intestinal amino acid supply on growth performance. Increasing rumen bypass amino acids in no

roughage diets during the growing phase tended ($P < 0.15$) to influence ADG and FCR in the growing phase such that as rumen bypass amino acid level increased growth and feed efficiency improved in the growing phase. Steers fed post ruminal absorbable amino acid levels below that required for growth in growing phase tended ($P < 0.15$) to have improved feed efficiency in the finishing phase. Also, during the growing phase as bypass amino acids increased subcutaneous and intramuscular fat deposition decreased in steers during the finishing phase. Feeding a level of bypass amino acids below optimum for growth to steers during the growing phase decreased ($P < 0.05$) *longissimus dorsi* muscle area in steers during the finishing phase.

CHAPTER 1

Literature Review

INTRODUCTION

The United States Department of Agriculture reported (2002) that feed accounted for approximately 60% of the total production cost for cattle (Elstien, 2002). Animal selection for decreased feed intake (FI) without adversely effecting performance would improve efficiency and profitability of the beef production system.

Historically selection for feed to gain ratio (F:G) has been used by beef producers to improve feed efficiency . This method of selection will produce more output with less input required. Feed to gain ratio is linked to frame size because large framed steers will be have a lower feed to gain than small framed steers when fed to a specific weight endpoint (Thonney et al., 1981). Large framed animals will have a greater average daily gain (ADG) and relative growth rate (RGR) than small framed animals because these parameters are correlated with metabolic mid-weight (Nkrumah et al., 2004). Therefore it would be inferred that as F:G improves, frame size and mature weight would increase. Cattle raised on pasture showed an increase in live weight production and net income with a decrease in frame size (Long et al., 1975). Cows with larger mature weight were associated with lower cow calf pair efficiency (Albertini et al., 2008). Therefore to

improve production efficiency, a selection parameter is needed that will decrease FI independent of growth.

Beef cattle have genetic variation in efficiency that is independent of size and growth rate (Arthur et al., 1997). This is measured as residual feed intake (RFI) and was proposed by Koch et al. (1963). Residual feed intake is the difference between the animal's actual FI and expected FI calculated by regressing actual FI against ADG and metabolic mid-weight during a 70 d test period (Archer et al., 1997). Postweaning tests for RFI determined it was a moderately heritable trait with substantial genetic variation within the population (Arthur et al., 1997). Residual feed intake was genetically and phenotypically correlated with FI and F:G ratio but not ADG in Angus bulls and heifers during a 70 d test period postweaning (Arthur et al., 2001). Progeny of parents selected for reduced RFI consumed less feed during the test period without influencing growth (Herd et al., 1997). Research was also reported that females with lower RFI at weaning required less FI as cows with same level of performance (Arthur et al., 1999). Therefore RFI could be used to improve feed efficiency without influencing growth and mature size of beef cattle.

Presently an RFI measurement requires the determination of animal FI over a 70 d period, which is expensive and time consuming (Herd et al., 2003). Developing an easier, less expensive method would increase the use of RFI as a selection criterion to improve feed efficiency (Herd et al., 2003). Previous research reported RFI was genetically correlated to serum concentrations of insulin-like growth factor-I (IGF-I) in Angus cattle at weaning (Moore et al., 2003) and selection for lower weaning serum IGF-

I concentrations improved feed efficiency in beef cattle (Moore et al., 2005). Also previous research reported that FI influenced insulin and glucose concentrations in beef heifers (Yelich et al., 1996). Yambayamba et al. (1996) reported that serum concentrations of glucose, insulin, and IGF-I in beef heifers were elevated due to increased FI. Richardson et al. (2004) reported that RFI is correlated with blood concentrations of insulin, glucose, urea, leptin and creatinine.

Differential expression and activity of mitochondrial proteins have been linked to differences in feed efficiency of beef cattle. *Longissmus dorsi* muscle mitochondrial protein content of NAD4, CORE I, COX II, and ANT I was increased in steers with improved efficiency (Sandelin et al., 2004). Also activity of muscle mitochondria complex I and II differed between high and low F:G steers (Sandelin et al., 2004).

The dissertation will review the effects of RFI on postweaning weight measurements, growth, and carcass composition. These physiological changes can influence blood hormone and metabolite levels, so the relationship of selected blood metabolites and hormones with RFI will be investigated. Finally the review investigates the relationship between feed efficiency and mitochondrial function and complex protein concentrations in poultry and cattle.

EFFECT OF RESIDUAL FEED INTAKE ON PRODUCTION TRAITS

Residual feed intake is genetically and phenotypically correlated to FI in Angus bulls and heifers (Arthur et al., 2001). Low RFI steers consumed 19.1% less dry matter

than high RFI steers (Gomez et al., 2007). Also low RFI bulls and heifers exhibited a 17% decline in FI compared to high RFI bulls and heifers (Ribeiro et al., 2007). Richardson et al. (1998) reported that steer progeny from low RFI parents consumed less feed than steer progeny from high RFI parents. Golden et al. (2008) reported that low RFI steers ate fewer times and consumed less feed than high RFI steers. Low RFI Angus heifers and bulls tended to show a higher dry matter digestibility compared to high RFI Angus bulls and heifers (Richardson et al., 1996). Cattle with lower RFI may be capable of greater dry matter digestibility, spend less time at the bunk and have lower FI.

Residual feed intake of Angus bulls and heifers was phenotypically and genotypically correlated in a negative fashion with F:G but shared no relationship with postweaning growth measurements (Arthur et al., 2001). However Herd et al. (2002a) reported that selection against RFI produced steers that grew faster on pasture. Steers and bulls shared no relationship between RFI and ADG, relative growth rate, or metabolic midpoint weight (Nkrumah et al., 2004). Also, ADG and body weight during the test period was not correlated to RFI in crossbred steers (Homm et al., 2007). Gomez et al. (2007) found that ADG and metabolic weight was not correlated with RFI in Santa Gertrudis steers. Arthur et al. (1999) reported that mature cow liveweight was not phenotypically correlated with postweaning RFI measurement. Herd and Bishop (2000) used data from British Hereford cattle to show that mature cow size was genetically independent of RFI measured during the postweaning performance test so selection against RFI would not increase mature cow size. Therefore selecting for RFI will

improve F:G and efficiency of beef cattle without increasing their mature size or influencing ADG.

Residual feed intake of growing dairy heifers had a high positive genetic correlation with roughage and metabolizeable energy intake of lactating dairy heifers (Nieuwhof et al., 1992). Arthur et al. (1999) reported a positive correlation between postweaning RFI and RFI measured on four year old cows. Beef cows expressing low RFI postweaning tended to produce more pounds of calf at weaning per pound of intake compared to cows expressing high RFI postweaning (Herd et al., 1998). Therefore selection for decreased RFI postweaning will produce more efficient cows that consume less feed per pound of calf produced.

EFFECT OF RESIDUAL FEED INTAKE ON CARCASS MEASUREMENTS

Carcass quality grade is primarily influenced by the amount of subcutaneous and intramuscular fat. Basarab et al. (2003) reported that low RFI steers tended to have less dissectible carcass and intermuscular fat and significantly less fat in the butt and loin than medium and high RFI steers. Furthermore low RFI steers showed a slower accretion rate of empty body fat compared to the medium and high RFI steers (Basarab et al., 2003). Steers of low RFI parents had less subcutaneous fat over the rib and tended to have less fat over the rump compared to steers of high RFI parents, but no differences existed between groups for intramuscular fat or marbling score (McDonagh et al., 2001). Data

sets from Angus heifers and bulls showed positive phenotypic and genotypic correlations between RFI and rib fat depth (Arthur et al., 2001). Richardson et al. (2001) reported that carcass fat (intermuscular + subcutaneous) was greater in progeny of high RFI parents compared to progeny of low RFI parents. Low RFI crossbred steers at the end of the feeding period did not differ in fat thickness over the 12th rib compared to high RFI steers (Kolath et al., 2006). Progeny of low RFI parents was more efficient than high RFI parents with no effect on fat depth at the 12th rib (Herd et al., 1997). Selection for low RFI will improve feed efficiency and may decrease carcass subcutaneous fat, but this decline in fat does not influence intramuscular fat, marbling score, or carcass quality grade.

Meat tenderness is another parameter that influences eating quality. Decreased calpastatin activity is associated with greater tenderness in beef cattle (Wulf et al., 1996). Myofibril fragmentation index measures the breakdown of structural units that occur as an initial step of protein degradation and meat tenderization (McDonagh et al., 2001). McDonagh et al. (2001) reported that after one generation of divergent selection for RFI, steer progeny of low RFI parents had significantly more calpastatin, lower m-calpain/calpastatin and lower myofibril fragmentation indexs than steer progeny of high RFI parents. M-calpain is an inhibitor of calpastatin and decreases calpastatin activity which tends to improve meat tenderness. Therefore selection for lower RFI animals in this one study increased calpastatin levels at a faster rate than m-calpain, which would lowered myofibril fragmentation index.

Selection for RFI did not influence ribeye muscle area in Angus crossbred steers (McDonagh et al., 2001). Also Kolath et al. (2006) reported low RFI crossbred steers did not differ from high RFI crossbred steers in loin eye muscle area. Residual feed intake showed no correlation with loin eye muscle area using records from Angus bulls and heifers (Arthur et al., 2001). Low RFI animals had a lower yield grade and a higher percentage of lean meat yield, compared to high RFI animals (Nkrumah et al., 2004). Progeny from low RFI bulls and heifers did not differ in loin eye muscle area compared to progeny from high RFI bulls and heifers (Herd et al., 1997). Richardson et al. (2001) reported that progeny of low RFI parents had greater change in loin eye muscle area compared to progeny of high RFI parents during the RFI test period.

EFFECT OF RESIDUAL FEED INTAKE ON CONCENTRATIONS OF BLOOD METABOLITES AND HORMONES

Since RFI influences FI, it could influence glucose, insulin, and insulin-like growth factor I (IGF-I). High RFI steers had greater concentrations of glucose and insulin levels were not different between high and low RFI steers (Kolath et al., 2006). At the beginning of the RFI test period plasma glucose concentrations were positively correlated and at the end of the RFI test period plasma insulin concentrations were positively correlated with RFI in Angus steers (Richardson et al., 2004). Angus beef cattle had a positive genetic correlation between weaning serum concentrations of IGF-I and RFI (Moore et al., 2003). Also Herd et al. (2002b) reported that selection of cattle

for lower IGF-I concentrations at weaning in cattle should lower RFI and improve feed efficiency. However Lancaster et al. (2007) reported no phenotypic correlation between RFI and serum concentrations of IGF-I in crossbred steers at the beginning or end of the RFI test feeding period. Further research needs to determine if the relationship between RFI and serum concentrations of glucose, insulin and IGF-I is consistent enough to be predictive of RFI.

As RFI decreases, fat deposition decreases and percent lean meat yield increases. Therefore changes in serum concentrations of urea, leptin, and creatinine will be investigated. Urea concentrations sampled at weaning were positively related with RFI measurement in steers (Richardson et al., 2004). Inefficient steers had greater concentrations of serum urea nitrogen compared to efficient steers during the finishing phase (Harvey et al., 1993). Data from steer progeny divergently selected for RFI showed a positive correlation between RFI and serum leptin concentrations at the end of the RFI test period (Richardson et al., 2004). Leptin concentrations were positively correlated with backfat content in finishing beef steers (Geary et al., 2003). Data from steers divergently selected for RFI showed a negative association between RFI and plasma creatinine concentrations quantified at the beginning of the RFI test period (Richardson et al., 2004). Mean plasma creatinine values were higher for bulls compared to steers at 168 d of feeding, and this was associated with increased muscle protein accretion and decreased muscle protein degradation (Morgan et al., 1993). As RFI decreases, the efficiency of muscle accretion will improve while fat deposition will

decrease as characterized by decreased concentrations of urea, leptin and increased concentrations of creatinine.

EFFECT OF EFFICIENCY ON MITOCHONDRIAL FUNCTION

The mitochondrial inner membrane has five multi-subunit complexes that take in electrons, conduct oxidative phosphorylation, and produce ATP. Complex I (NADH:Coenzyme Q oxidoreductase) is 900 kD, with 43 subunits and passes electrons from reduced nicotinamide adenine (NADH) dinucleotide to Coenzyme Q oxidoreductase (Voet and Voet, 2004). Broilers with high F:G had increased NAD3 (Complex I) expression in liver mitochondria compared to broilers with low F:G (Iqbal et al., 2005). However high F:G broilers showed lower expression of ND4 and ND6C (Complex I) compared to low F:G broilers in duodenal mitochondria (Ojano-Dirain et al., 2005). Bottje et al. (2004) reported decreased activity of complex I in high F:G broilers compared to low F:G broilers in breast muscle and liver mitochondria. Ojano-Dirain et al. (2005) reported high F:G had lower Complex I activity in duodenum mitochondria compared to Low F:G broilers. High F:G steers had lower expression of NAD4 (complex I) in LM muscle compared to low F:G steers (Sandelin et al., 2004). Also complex I activity was greater in high F:G steers compared to low F:G steers (Sandelin et al., 2004). In broilers and steers the improved efficiency may result from difference in complex I subunit expression.

Complex II (Succinate: Coenzyme Q oxidoreductase) contains succinate dehydrogenase and passes electrons from succinate to coenzyme Q (Voet and Voet, 2004). Succinate is provided from the citric acid cycle. Low F:G broilers had increased subunit 70 (complex II) in liver mitochondria compared to high F:G broilers (Iqbal et al., 2005). However in lymphocytes (Lassiter et al. 2006) complex II subunit 30S and in duodenum (Ojano-Dirain et al., 2005) complex II subunit 70S expression were lower in low compared to high F:G broilers. Complex II activity in breast, liver and duodenal mitochondria decreased in high compared to low F:G broilers (Bottje et al., 2004; Ojano-Dirain et al., 2005). Expression of complex II subunits was similar between low and high F:G steers but high F:G steers had higher complex II activity compared to low F:G steers (Sandelin et al., 2004). Improvement of feed efficiency caused differential expression of complex II subunits in broilers, but not steers and complex II activity changed for broilers and steers.

Complex III (Coenzyme Q: cytochrome C oxidoreductase) could also be called Cytochrome bc_1 complex passes electrons from a reduced Coenzyme Q to cytochrome C (Voet and Voet, 2004). Breast muscle mitochondria complex III subunits Cytochrome C_1 and core I were increased in high F:G compared to low F:G broilers (Iqbal et al., 2004). Iqbal et al. (2005) reported that liver mitochondria of high F:G broiler showed increased expression of subunit VII (complex III) compared to low F:G broilers. Furthermore duodenal mitochondria complex III protein subunits core I, core II and Cytochrome C_1 in high F:G broilers had higher expression compared to low F:G broilers (Ojano-Dirain et al., 2005). However, lymphocyte mitochondria from high F:G broilers exhibited lower

amounts of Cytochrome C_1 (Complex III) compared to low F:G broilers (Lassiter et al., 2006). Complex III activity was decreased in high F:G broilers compared to low F:G broilers in breast muscle, liver and duodenum (Bottje et al., 2004; Ojano-Dirain et al., 2005). High F:G steers had lower expression of Core I (Complex III) compared to low F:G steers (Sandelin et al., 2004). The subunits of complex III were differentially expressed with an improvement in feed efficiency in steers and broilers. Activity of complex III increased with an improvement in feed efficiency in broilers.

Complex IV (Cytochrome c Oxidase) catalyzes the one electron oxidation of four consecutive reduced cytochrome c molecules and the concomitant reduction of one O_2 molecule to yield H_2O (Voet and Voet, 2004). High F:G broilers showed increased expression of complex IV subunits COX II and COX IVb in liver mitochondria compared to low F:G broilers (Iqbal et al., 2005). Lassiter et al. (2006) showed that high F:G broilers exhibited higher amounts of COXII compared to low F:G broilers. However Ojano-Dirain et al. (2005) found COXII expression in broiler duodenum mitochondria was lower in high F:G broilers compared to low F:G broilers. Low F:G steers showed an increased COXII expression in muscle mitochondria compared to high F:G steers (Sandelin et al., 2004). Complex IV activity was decreased in breast muscle and liver mitochondria of high F:G broilers compared to low F:G broilers (Bottje et al., 2004). Complex IV subunits were differentially expressed with an improved feed efficiency of broilers and steers. Broilers exhibited an increased complex VI activity with improved efficiency.

Complex V (proton-translocation ATP synthase) is physically distinct from complex I-IV and acquires energy through coupling or transduction from these complexes to phosphorylate ADP to ATP (Voet and Voet, 2004). Lymphocyte mitochondria of low F:G broilers exhibited increased expression of α-ATP synthase (complex V) compared to high F:G broilers (Lassiter et al., 2006). Low F:G broilers had increased expression of α-ATP synthase (complex V) in liver mitochondria compared to high F:G broilers (Iqbal et al., 2005). High F:G steers showed lower expression of channel protein ANT I in muscle mitochondria compared to low F:G steers (Sandelin et al., 2004). Also high F:G broilers had decreased complex V activity in duodenum mitochondria compared to low F:G broilers (Ojano-Dirain et al., 2005). Complex V subunits were differentially expressed with improved feed efficiency in broilers and ATP/ADP channel protein expression is increased with improved feed efficiency in steers. Broilers had increased complex V activity with improved efficiency.

Complexes I to IV provide energy to complex V for ATP synthesis. During this process there may be leaking of electrons which would result in production of reactive oxygen species such as super oxide (O_2^-) and hydrogen peroxide (H_2O_2; Boveris and Chance, 1973). Use of uncoupler (antimycin) in pigeon heart mitochondria increased H_2O_2 production in state four respiration with malate, glutamate, and succinate as substrates (Boveris and Chance, 1973). High F:G broilers had increased liver mitochondrial peroxide production compared to low F:G broilers (Iqbal et al., 2005). Bottje et al. (2004) reported that mitochondria from low F:G broilers had a more tightly coupled respiratory chain which resulted in less electron leak and reactive oxygen species

production. High F:G broilers exhibited increased electron leak due to a defect in the mitochondrial respiratory chain at complexes I and III in breast and leg muscle and complexes I, II, and III in the duodenum (Bottje et al., 2004). Peroxide production was increased but electron leak was similar for low RFI steers compared to high RFI steers (Kolath et al., 2006). High F:G broilers and low RFI steers have an increased reactive oxygen species production compared to low F:G broilers and high RFI steers but broiler electron leak increased with improve efficiency while steer electron leak is similar between low and high RFI animals.

During the process of ATP synthesis there is uptake of O_2 and the formation of water. The respiration rate or flux rate is linked to the efficiency of the electron transport chain and synthesis of ATP. Bottje et al. (2002) reported that breast and leg muscle mitochondria of low F:G broilers had increased respiratory control ratio compared to high F:G broilers when using energy substrate glutamate and malate but not succinate. Furthermore muscle mitochondria of low RFI steers exhibited greater state two and three respiration rate and respiratory control ratio compared to high RFI steers (Kolath et al., 2006). Kolath further suggested that a greater respiratory control ratio is indicative of greater coupling between respiration and oxidative phosphorylation and improved efficiency of electron transfer. This evidence showed that efficient animal have an improved efficiency of electron transfer in the electron transport chain compared to inefficient animals.

Bottje et al. (2004) reported that high F:G broiler muscle mitochondria has increased protein oxidation compared to low F:G broiler mitochondria. Also liver

mitochondria of high F:G broilers showed increased protein carbonyl expression compared to low F:G broilers (Iqbal et al., 2005). Protein carbonyls in mucosal mitochondria were greater in high compared to low F:G broilers (Ojano-Dirain et al., 2007). Lymphocyte mitochondria of high F:G broilers had increased level of protein carbonyls compared to low F:G broilers (Lassiter et al., 2006). Broiler data could be interpreted that decreased efficiency is linked to increased production of protein carbonyls.

CONCLUSION

As RFI decreased, dry matter digestibility increased and FI and time at the bunk decreased. Furthermore RFI shows no relationship with growth rate but a negative correlation with feed efficiency. Since RFI has no relationship with growth rate, selection against RFI would not influence cow mature size. The lower RFI phenotype at weaning would produce cows that produce more calf at weaning per pound of intake.

Change in FI will change plasma concentrations of glucose, insulin, and IGF-I. There has been conflicting studies on the relationship of RFI and IGF-I and further experimentation is needed to determine if there is a relationship between RFI and IGF-I and if it can be used as a RFI predictor. There is a positive relationship between postweaning glucose and insulin and RFI, and further studies are needed to determine if these blood metabolites could be used as a predictor of RFI.

As steer RFI decreased there is improved efficiency of muscle accretion, decreased subcutaneous and intermuscular fat deposition without altering intramuscular fat content. In one study, the selection against RFI increased calpastatin activity in relation to m-calpain and decreased myofibril fragmentation index but did not influence tenderness of the meat. The improvement in efficiency of muscle accretion leads to increased creatinine and decreased urea and leptin concentrations.

The effects of feed efficiency on mitochondria function have been studied in poultry and beef steers. Research has shown differential expression of mitochondrial subunits for complexes one to five in broilers. Activity of mitochondrial complexes one to five was also different between low and high F:G broilers. The differences in feed efficiency of steers were accompanied by differences in expression of subunits from mitochondrial complexes one, three, four, and ADP/ATP channel as well as differences in complex one and two activity. Research with poultry measured increased protein oxidation, peroxide production, electron leak and decrease in respiration and receptor control ratio in high F:G compared to low F:G broilers. Research showed in beef steers that respiration rate, receptor control ratio, and peroxide production increased with no change in electron leak for low compared to high RFI steers. Since feed efficiency is altered by selection against RFI further research is needed to determine if the effect in mitochondrial complex protein concentration, activity and function could be used as markers for RFI prediction.

Based on this literature review this dissertation will research the effect of RFI on serum concentrations of glucose, insulin and IGF-I in beef steers. Also this dissertation

will research the effects of RFI on concentrations of mitochondrial complex I, II, and III protein concentrations in steer lymphocytes. Finally there will be a project looking at the effect of RFI on steer performance as the ratio of absorbable amino acid to energy is increased.

CHAPTER 2

Relationship between residual feed intake, diet, production traits and serum concentrations of glucose, insulin and insulin-like growth factor I (IGF-I) in beef steers

ABSTRACT

This experiment was conducted to investigate the relationship between diet, production traits, residual feed intake (RFI) and serum glucose, insulin, and IGF-I. Also this experiment will investigate if single time-point measures of blood glucose, insulin or insulin-like growth factor one (IGF-I) in calves at weaning or after being placed on feed were descriptive of their RFI. Eighty-two spring-born steers were weaned in late September and arrived at the University of Missouri Beef Research and Teaching Farm in late October. After a 14 d acclimation period to the high corn diet and GrowSafe feed intake (FI) system, two day consecutive weights (W0) were collected and steers were allocated to four different dietary treatments. One dietary treatment was a traditional growing-steer diet (Control, n = 20) and the other three diets contained no roughage with increasing bypass amino acid levels (Low, n = 22; Medium, n = 19; High, n = 21). Steers had ad libitum access to their respective dietary treatment and water daily during the 84 d feeding period. At the end of the feeding period two day consecutive weights (W84) were taken and these were used along with W0 to calculate metabolic midweight

(MMWT) and average daily gain (ADG) during the feeding trial. Feed intake data from the GrowSafe FI system along with growth data were used to calculate feed conversion ratio (FCR) over the 84 d feeding period. Blood samples were collected immediately before weaning and on d 84 of the feeding period. Residual feed intake was calculated as the difference between actual and predicted FI. Predicted FI was calculated by two regression models. Actual FI was regressed against ADG and MMWT in the first regression model. Residual feed intake calculated from regression model one was different ($P < 0.05$) between dietary treatments. Actual FI was regressed against ADG, MMWT, and dietary treatment in the second regression model. The effects of RFI on production traits and serum metabolites collected at weaning and postweaning were tested using RFI numbers generated from regression model two. Partial phenotypic correlations were calculated between RFI, FI, FCR, ADG, W0, W84, and insulin (WINS), glucose (WGLC), and IGF-I (WIGF-I) concentrations preweaning and at d 84 insulin (84INS), glucose (84GLC), and IGF-I (84IGF-I). In addition to phenotypic correlations, RFI was analyzed as a continuous variable and if found significant a nonparametric approach was used to segregate RFI measures into three distinct groups (Low was RFI < 0.5 SD below the mean RFI, n = 25; Medium was RFI ± 0.5 SD above or below the mean, n = 30; and High was RFI > 0.5 SD above the mean, n = 27). Since treatment may have influenced production traits and serum metabolite concentrations, it was included in the model with RFI and RFI group as a covariate. Steer FCR, but not FI significantly ($P < 0.05$) decreased with removing roughage and increasing bypass amino acid level in the diet. Steers ADG was influenced ($P < 0.05$) with no change ($P > 0.09$)

in W84 as roughage was removed and bypass amino acid level was increased. Control diet steers had lower ($P < 0.05$) ADG than medium and high diet steers. Low diet steers tended ($P < 0.15$) to have lower ADG than high diet steers with medium diet steer being intermediate and not different. Diets differing in roughage and bypass amino acid level did not differ ($P < 0.05$) in serum glucose, insulin, and IGF-I quantified at the end of the feeding period. As anticipated, RFI was highly correlated ($P < 0.05$; R = 0.69) with FI and FCR ($P < 0.05$; R = 0.53) during the 84 d when steers were on feed. Residual feed intake influenced ($P < 0.05$) FI ($R^2 = 0.48$) and FCR ($R^2 = 0.41$). Low RFI steers had lower ($P < 0.05$) FI and FCR compared to high RFI steers with medium RFI steers having an intermediate FCR and FI that was different ($P < 0.05$) from the other two groups. Steer ADG, W0, and W84 were not correlated ($P > 0.15$) with RFI. Residual feed intake was correlated ($P < 0.05$; R = -0.25) with preweaning serum concentrations of glucose, but not correlated ($P > 0.15$) with other serum metabolites and hormones. Residual feed intake influenced ($P < 0.05$; $R^2 = 0.11$) WGLC. Low and medium RFI steers had higher ($P < 0.05$) serum WGLC than high RFI steers. The increasing bypass amino acid levels improved feed efficiency. Steers with a lower RFI had decreased FI and improved feed efficiency without adversely affecting postweaning gain. Weaning serum concentrations of glucose were phenotypically related to RFI.

INTRODUCTION

United States Department of Agriculture reported that feed accounts for about 60% of the total production cost for cattle (Elstien, 2002). Decreased feed intake (FI) and increased growth through improved feed efficiency would allow production cost to be reduced and profitability of their herd to be improved. Dietary manipulation that improves growth and decreases FI also has the potential to improve profitability. Decreasing forage level in growing steer diets during the growing phase improved gain to feed (G:F) without altering FI (Gorocica-Buenfil and Loerch, 2005). Previous research conducted in our laboratory demonstrated that adding bypass protein to no roughage diets improved feed efficiency (Mueller et al., 2004). Limited research has been conducted studying no-roughage diets optimized for bypass amino acids in growing beef steers. Our hypothesis was that optimizing bypass amino acids and removing roughage from the diet would improve feed efficiency and growth in growing cattle. Therefore performance of beef steers fed diets containing roughage diets and no roughage with different levels of bypass amino acid will be investigated in this paper.

Concentration of glucose, insulin, and IGF-I was positively influenced by FI in beef heifers (Yelich et al., 1995; 1996; Yambayamba et al., 1996). Feed restriction of steers during the growing phase negatively influenced serum concentrations of glucose and IGF-I (Ellenberger et al., 1989). The removal of roughage and the increase in bypass amino acid levels may alter FI. Therefore the relationship between serum concentrations of glucose, insulin, IGF-I, and dietary bypass amino acid level in beef steers will be examined in this paper.

The past method used to improve feed efficiency is selection for improved FCR. However, FCR will be linked to frame size because large framed steers have a lower FCR than small framed steers at the same weight (Thonney et al., 1981). Therefore selection for improved FCR may increase cattle growth and frame size which could be detrimental to beef production. Residual feed intake (RFI) proposed by Koch et al. (1963) is an alternative measure of feed efficiency to FCR that accounts for energy requirements independent of growth. Genetic variation in RFI is large, the trait is moderately heritable, and research findings lend support to the hypothesis that selection for low RFI can improve feed efficiency of beef cattle (Arthur et al., 1997; Richardson et al., 1998). Currently measuring individual FI is required to compute RFI. Development of a more rapid method to predict RFI could lead to expanded selection of more efficient livestock.

Significant differences in serum concentrations of IGF-I exist between progeny of sires suggesting evidence for genetic variation in expression of that trait (Herd et al., 2002b). Selection against IGF-I should lead to increased growth rate, improved feed efficiency, and lower subcutaneous fat thickness (Herd et al., 2002b). Moore et al. (2003) reported that IGF-I had a positive genetic correlation with fat parameters and RFI. Selection for lower serum concentrations of IGF-I has resulted in cattle with lower RFI that are leaner and have greater growth potential (Moore et al., 2005). Recently, Lancaster et al. (2008) reported that genetic selection for postweaning IGF-I concentrations had minimal effect on RFI in beef cattle. Furthermore they reported serum IGF-I concentrations at weaning and prior to the RFI test period had no phenotypic correlation with RFI. Also serum concentrations of IGF-I were not different between

high and low net feed conversion Angus cattle (Richardson et al., 1996). Kolath et al. (2006) reported that serum concentrations of glucose quantified prior to slaughter were lower in low versus high RFI steers with no change in serum insulin concentrations. Steers divergently selected for RFI had serum concentrations of glucose prior to RFI test period that were positively correlated with RFI and serum insulin concentrations quantified at the end of the RFI test period that were positively correlated with RFI (Richardson et al., 2004). Based on previous research of the relationship between serum metabolites insulin, glucose, IGF-I, and RFI we hypothesize that these metabolites may be useful indicators of RFI in beef cattle. Therefore the relationship between RFI, diet, production traits and serum concentrations of glucose, insulin, and IGF-I will be examined in this paper. We further sought to determine if serum concentrations of glucose, insulin, and IGF-I could be used as an accurate indicator of RFI.

MATERIALS AND METHODS

Experimental Design

The use of animals in this experiment was approved by the University of Missouri Animal Care and Use Committee. Eighty-two spring-born Angus (straight-bred or crossbred steers) steers were used in this experiment. Steers were weaned in late September and arrived at the University of Missouri Beef Research and Teaching Farm on October 31, 2006. Upon receiving the animals, electronic ID tags (Allflex US INC., Dallas-Fort Worth Airport, TX) were attached to the exterior of the left ear to aid in

tracking individual FI with the GrowSafe FI system (GrowSafe Systems Ltd., Airdrie, AB, Canada). Steers were placed on a receiving diet for 14 d prior to the feeding period to allow for acclimation to the high concentrate diet and FI system. Water and receiving diet were provided ad libitum during this period. After the receiving period two day consecutive weights were taken on November 7 and 8, 2006 to determine initial body weight (W0) and steers were randomly assigned to eight concrete pens (24' x 54'). Each pen contained approximately 11 steers and two feeding bunks that allowed single animal access to a feed tube. Two pens were assigned to one of four dietary treatments. Dietary treatments consisted of a traditional growing steer diet (Control, n = 20) and three diets with no roughage and increasing bypass amino acid level (Low, n = 22; Medium, n = 19; High, n = 21; Table 2.1and 2.2). The phase 1 diet was fed through the first 42 d and the phase 2 diet was fed from 42 d through 84 d. Two phases of each dietary treatment were fed to maintain dietary treatments over the entire feeding period. All feed ingredients except corn and hay were mixed and pelleted and fed as a supplement. The pelleted supplement, corn and hay were mixed as a total mixed ration using a truck-mounted ribbon mixer. Steers were fed once daily at approximately 0800, and the animals had ration and water available at all times.

Production Trait Collection and Calculation

Feed intake over the 84 d feeding period for each animal was measured with the GrowSafe (GrowSafe Systems Ltd., Airdrie, AB, Canada) automated FI system. Two day body weights were collected at d 0 (W0; 285 ± 20 kg) and d 84 of the feeding trial

(W84; 412 ± 36), to calculate average daily gain (ADG = kg gain/84 d), and metabolic mid-weight (MMWT; ((W0 + W84)/2) ^0.75)). Feed conversion ratio (FCR; kg FI/kg ADG) was computed as the ratio of daily FI to ADG. Individual FI, MMWT, ADG and treatment were used to calculate predicted FI. Two models were used to calculate predicted FI. Regression model one calculated predicted FI by regressing ADG and MMWT against daily FI using the regression (REG) procedure of SAS (Proc REG; SAS Institute, 2003). The model fitted was:

$$Y_i = \beta_0 + \beta_1 ADG + \beta_2 MMWT$$

where Y_i = expected daily FI of animal i; β_0 = the regression intercept; β_1 = partial regression coefficient of FI on ADG; and β_2 = partial regression coefficient of FI on MMWT. To calculate RFI, predicted FI was subtracted from actual FI (Basarab et al., 2003). Analysis of variance found RFI was significantly different ($P < 0.05$) across dietary treatments (Table 2.3). To account for differences due to diet regression model two was used to calculate predicted FI. Regression model two calculated predicted FI by regressing daily FI during the 84 d feeding period against ADG, MMWT, treatment and treatment by independent variable interactions. The interactions of treatment by ADG and treatment by MMWT were found not significant ($P > 0.15$) and removed from regression model two. The model fitted was:

$$Y_i = \beta_0 + \beta_1 treatment + \beta_2 ADG + \beta_3 MMWT$$

where Y_i = expected daily FI of steer *i*; β_0 = the regression intercept; β_1 = partial regression coefficient of FI on ADG; β_2 = partial regression coefficient of FI on MMWT; β_3 = partial regression coefficient of FI on treatment (Control, Low, Medium, and High). The RFI value for each animal was calculated as the difference between daily FI over the 84d period and predicted FI (Barsarab et al., 2003). Since RFI was influenced by dietary treatment, regression model two accounting for treatment was used to predict FI, calculate RFI, and the RFI value was then used to investigate the phenotypic relationship between RFI, production traits and serum metabolites quantified at weaning and postweaning in beef steers.

Blood Metabolite and Hormone Collection and Analysis

Blood samples were collected in BD vaccutainer tubes at weaning (WGLC, WINS, and WIGF-I) and prior to feeding on d 84 (84GLC, 84 INS, and 84 IGF-I) via jugular venipuncture. Samples were placed on ice, held at 4ºC, and centrifuged within 24 to 48 hr after collection at 2,000 X g for 20 minutes. Serum was harvested and stored at -20º C until analysis. Serum glucose concentrations were quantified using the enzymatic colorimetric procedure, thermo glucose oxidase method (Thermo Electron, Louisville, CO 80027) according to the manufacture's instructions. Serum insulin concentrations were quantified using Cygnus Technologies ultra-sensitive immunoenzymetric assay (Cygnus Technologies, Inc, Southport, NC 28461) according to the manufacture's instructions. Serum concentrations of IGF-I were quantified in triplicate after acidified extraction via a double-antibody RIA validated by Lalman et al. (2000).

Statistical Analysis

Treatment effects on measures of feed efficiency, production traits and serum concentrations of glucose, insulin, and IGF-I at weaning and d 84 on feed were determined using general linear model (GLM) procedures of SAS (Proc GLM; SAS Institute, 2003). Steer was the experimental unit for all traits. The diet (Control, Low, Medium, and High) was the treatment and treatment means were determined using the least squares means statement of SAS. Least squares means of significant treatment effect were analyzed and found different at P-value of 0.05.

Partial phenotypic correlations among performance traits, measures of feed efficiency, and serum metabolites glucose, insulin and IGF-I quantified at weaning and d 84 of trial were computed using correlation (CORR) procedures of SAS (Proc CORR; SAS Institute, 2003) with partial option used to adjust for treatment effects. The effects of continuous variable RFI on production traits and serum glucose, insulin, and IGF-I quantified at weaning and d 84 of trial were analyzed using Proc GLM procedures of SAS (Proc GLM; SAS Institute, 2003). Steer was the experimental unit for all traits. Since treatment may have influenced feed efficiency measures, production traits, and serum metabolites it was included in the model as a covariate when examining the effects of RFI on these measurements. The model included the independent variable of RFI, covariate treatment and the dependent variables FI, ADG, W0, W84, WGLC, WINS, WIGF-I, 84GLC, 84INS, and 84IGF-I. Independent variable RFI was found significant ($P < 0.06$) for dependent variables FCR, FI, and WGLC. To examine the relationship

between RFI extremes and these dependent variables, RFI was partitioned into three groups termed Low (RFI < 0.5 SD below the mean RFI; n =25), Medium (RFI ± 0.5 SD above or below the mean; n = 30) and High (RFI > 0.5 SD above the mean; n = 27) (Nkrumah et al., 2004). Then GLM procedures of SAS (Proc GLM; SAS Institute, 2003) are used to examine differences between RFI groups. Since treatment may have influenced these traits it was included as a covariate when examining the effects of RFI group on these traits. The model included the independent variable of RFI group (low, medium, and high), covariate treatment, and the dependent variable FCR, FI, and WGLC. Least squares means for RFI groups were analyzed and found different at P-value of 0.05.

RESULTS AND DISCUSSION

Dietary Effects on Production Traits and Serum Metabolites

During the 84 d feeding period FCR and not FI was influenced ($P < 0.05$) by dietary treatments. Steers on the high and medium diets had a similar ($P > 0.15$) FCR that was lower ($P < 0.05$) than steers on the low and control diets (Table 2.3). Steers on the low diet had lower ($P < 0.05$) FCR than steers on the control diet (Table 2.3). In agreement with the present study the reduction of corn silage improved G:F without altering FI during the growing phase in beef steers (Gorocica-Buenfil et al., 2005). Mueller et al. (2004) reported steers fed a no-roughage diet not optimized for amino acid flow had poorer feed conversion ratio than steers feed a diet formulated for optimized amino acid flow. Therefore increasing postruminal amino acid supply improved FCR.

Gain during the 84 d feeding period was influenced ($P < 0.05$) by dietary treatment, but W84 was not influenced ($P > 0.09$) by dietary treatments (Table 2.3). Steers fed the medium and high diets exhibited similar ($P > 0.15$) ADG and had greater ($P < 0.05$) ADG than steers fed the control diet. Steers fed the low diet had intermediate ADG that tended to differ ($P < 0.15$) from steers on the high diet. Increasing postruminal amino acid supply tended to increase ADG. Supplementation with excess amino acids improved methionine and leucine use for protein deposition by growing cattle (Awawdeh et al., 2006). Dietary increase in bypass amino acids improved amino acid utilization for protein deposition in growing cattle. The tendency for improvement in ADG due to increasing bypass amino acid level in the present study may be due to improved amino acid utilization for protein deposition.

Serum insulin, glucose and IGF-I at the end of the feeding period were not influenced ($P > 0.15$) by dietary treatments (Table 2.4). Feed intake positively influenced serum insulin, glucose, and IGF-I in growing beef heifers (Yelich et al., 1995; 1996). Feed restriction in heifers caused lower serum concentrations of glucose, insulin, and IGF-I but when they were placed on the control feeding protocol concentrations of glucose, insulin, and IGF-I became similar to heifers allocated to the control protocol during the entire study (Yambayamba et al., 1996). During the growing phase feed restriction decreased serum concentrations of glucose and IGF-I in steers compared to those fed ad libitum (Ellenberger et al., 1989). Dietary treatment did not influence FI in this experiment, therefore no change in serum insulin, glucose, and IGF-I were observed in steers on different dietary treatments.

Relationship between Residual Feed Intake, Diet, and Production Traits

Analysis of variance of RFI calculated from predicted FI using regression model one was influenced ($P < 0.05$) by dietary treatment (Table 2.3). The control diet had the greatest ($P < 0.05$) RFI compared to the other three dietary treatments which were not different ($P > 0.05$) from each other. Dietary treatment was found significant ($P < 0.05$) when included in regression model two to predict FI. The inclusion of treatment when modeling FI increased the model R^2 from 0.43 to 0.53. Since dietary treatment influenced RFI, regression model two, accounting for treatment, was used to predict FI and calculate RFI values. Residual feed intake values calculated from predicted feed intake values using regression coefficients for treatment in the regression model were not influenced ($P > 0.15$) by dietary treatment. These RFI values were used to investigate the phenotypic relationship between RFI, production traits, and serum glucose, insulin, and IGF-I. When the effect of independent variables RFI and RFI group was examined against dependent variables the covariate of treatment was used to adjust for treatment effects on those dependent variables.

The comparison of RFI and FI yielded a significant ($P < 0.05$; R = 0.69) partial correlation (Table 2.5) and RFI influenced ($R^2 = 0.48$; $P < 0.05$) FI. Analysis of RFI group on FI showed that the low RFI steers had the lowest ($P < 0.05$) FI (8.15 ± 0.14 kg), high RFI steers had the greatest ($P < 0.05$) FI (9.74 ± 0.14 kg) and medium RFI steers had an intermediate FI (8.79 ± 0.13 kg) which was different ($P < 0.05$) than the other two groups (Table 2.6). Comparison of RFI and FCR yielded a significant ($P < 0.05$; R =

0.53) partial correlation and RFI influenced ($R^2 = 0.41$; $P < 0.05$) FCR. Comparison of RFI group and FCR showed that low RFI steers had a lower ($P < 0.05$) FCR (5.61 ± 0.17 kg/kg) than high RFI (6.52 ± 0.17 kg/kg) steers (Table 2.6). The medium RFI steers had an intermediate FCR (6.06 ± 0.16 kg/kg) that was different ($P < 0.05$) from the other RFI groups (Table 2.6). Previous research by Richardson et al. (2001) reported that steers of high RFI parents had greater FI values than steers of low RFI parents. Also low RFI bulls, steers, and heifers had 17% to 19% lower feed intake than high RFI bulls, steers, and heifers (Ribeiro et al., 2007; Gomez et al., 2007). As steer RFI increases there is an increase in the FCR (Nkrumah et al., 2004; Gomez et al., 2007) In agreement with previous research the present study showed that as RFI decreased there was a decrease in steer FCR and FI.

Correlations between W0, W84, ADG and RFI were all nonsignificant ($P > 0.15$; Table 2.5). Also RFI did not influence W0 ($R^2 = 0.00$; $P > 0.99$), W84 ($R^2 = 0.07$; $P > 0.99$), and ADG ($R^2 = 0.09$; $P > 0.99$). The weight and growth measurements during the feeding period for each RFI group are depicted in Table 2.6. Since statistical analysis showed RFI did not influence ($P > 0.15$) postweaning growth and weight measurements, no statistical analysis was reported between these measurements and RFI group. In agreement with our findings others found no relationship between RFI and postweaning weight and growth measurements (Arthur et al., 2001; Lancaster et al., 2007; Gomez et al., 2007; Homm et al., 2007).

Relationship between Residual Feed Intake, Serum Metabolites, and Hormones

Moore et al. (2003) reported that RFI had a low positive genetic correlation with weaning serum concentration of IGF-I in Angus cattle. Furthermore, there was a phenotypic relationship between RFI and serum concentration of glucose prior to RFI test period and serum concentration of insulin at the end of the RFI test period (Richardson et al., 2004). Therefore, all three blood parameters relationships with RFI were investigated. Preweaning and postweaning concentrations of IGF-I were genetically correlated and postweaning concentration of glucose and insulin were phenotypically correlated with RFI (Moore et al., 2005; Richardson et al., 2004) therefore, further analysis was done on preweanning and postweaning concentrations of these parameters. Preweaning and d 84 analysis for RFI yielded significant (R = -0.25; $P < 0.05$) partial correlation coefficients for serum concentrations of WGLC and nonsignificant ($P > 0.15$) partial correlation coefficients for WINS, WIGF-I, 84GLC, 84INS, and 84IGF-I (Table 2.5). Serum concentrations of glucose, insulin, and IGF-I quantified at weaning and d 84 of the feeding period for RFI groups are depicted in Table 2.7. Residual feed intake influenced ($P < 0.05$) serum WGLC ($R^2 = 0.11$) and did not influence ($P > 0.15$) serum WINS ($R^2 = 0.01$), WIGF-I ($R^2 = 0.07$), 84GLC ($R^2 = 0.01$), 84INS ($R^2 = 0.02$), and 84IGF-I ($R^2 = 0.02$). High RFI steers (89.08 ± 2.00 mg/dL) had lower ($P < 0.05$) serum WGLC than low RFI steers (95.54 ± 2.13 mg/dL) and medium RFI steers (94.95 ± 1.97 mg/dL) which did not differ ($P > 0.15$). Since RFI did not show a significant ($P > 0.15$) effect on the other serum measures, RFI group effect analysis for those serum measures were not reported. Serum concentrations of IGF-I at weaning and at the end of a 70 d feeding period had no phenotypic correlation with RFI in Brangus heifers (Lancaster et

al., 2007). Richardson et al. (1996) found postweaning serum IGF-I concentrations were not different between high and low net feed conversion Angus bulls and heifers. These results agreed with the present study that serum concentrations of IGF-I taken at weaning or postweaning are phenotypically unrelated to RFI. Richardson et al. (2004) reported similar results for weaning serum concentrations of insulin but differing results for weaning serum concentrations of glucose to the present study. Also this laboratory reported similar results for the relationship between serum glucose concentrations and RFI at the end of the test period as the present study. However, their results differed from the present study in relationship between RFI and serum insulin concentrations at the end of the RFI test period. In the Richardson study, steers were progeny of a divergent selection for RFI which differed from the present study where steers had no previous RFI selection pressure placed on them. Kolath et al. (2006) reported that serum concentrations of glucose differed between high and low RFI steers but serum insulin concentrations remained unchanged. These results were based on samples taken 10 d prior to slaughter, which were longer into the feeding phase than the samples of the present research. Based on these data, there may be a phenotypic relationship between RFI and serum concentrations of glucose at weaning.

CONCLUSION

Increasing bypass amino acids in diet improved feed efficiency without altering FI. Growing steers fed diets of different roughage and bypass amino levels did not differ

in concentration of serum metabolites glucose, insulin, and IGF-I. Further research is needed to determine how feeding diets to growing steers that differ in roughage content and amino acid levels during the growing phase influence steer finishing performance and carcass characteristics.

Residual feed intake is a measure of feed efficiency that shows a phenotypic relationship with FI and FCR but no relationship with other production traits measured. Selection for RFI potentially improves feed efficiency through decreased FI and FCR. Phenotypically we found no relationship between RFI and postweaning growth and weight measurement however, further research is needed to determine if selection pressure placed on RFI influences postweaning growth and weight measurements. Serum concentrations of glucose at weaning had a negative phenotypic correlation to RFI.

Table 2.1. Diet composition fed to steers during the first 42 d of the feeding period.

	Treatment[a]			
Ingredient (% as-fed)	Control	Low	Medium	High
Whole Shell Corn	78.62	89.30	85.87	82.57
Blood meal	2.70	1.50	5.10	8.70
Dried Distillers Grains	5.00	5.00	5.00	5.00
Hay	10.00	-------	-------	-------
Tallow	2.00	1.72	2.00	2.00
Urea	0.30	0.70	0.30	-------
Limestone	1.00	1.10	1.10	1.10
KCl	0.20	0.50	0.50	0.50
Salt	0.10	0.10	0.05	0.05
Vitamin Mix[b]	0.05	0.05	0.05	0.05
Mineral Premix[c]	0.03	0.03	0.03	0.03
Calculated Values				
NEm,Mcal/kg	2.11	2.20	2.20	2.18
NEg, Mcal/kg	1.43	1.52	1.51	1.49
CP,%	14.10	14.40	16.20	18.40

[a]Dietary treatments consist of a traditional growing steer diet (Control) and three growing steer diets of increasing bypass amino acid levels (Low, Medium, and High).
[b]Contained (as-fed basis) 4,000,000 IU of vitamin A, 800,000 IU of vitamin D, and 1,250 IU of vitamin E/kg.
[c]Contained (as-fed basis) 10% Fe, 10% Mn, 10% Zn, 2% Cu, 1,500 ppm Se, 1,000 ppm I, and 500 mg/kg Co.

Table 2.2. Diet composition fed to steers from d 42 to d 84 of the feeding period.

	Treatment[a]			
Ingredient (% as-fed)	Control	Low	Medium	High
Whole Shell Corn	78.62	94.90	89.82	87.32
Blood meal	2.70	--------	0.30	3.20
Dried Distillers Grains	5.00	--------	5.00	5.00
Hay	10.00	--------	-------	-------
Tallow	2.00	1.72	2.00	2.00
Urea	0.30	1.40	1.00	0.65
Limestone	1.00	1.20	1.15	1.15
KCl	0.20	0.55	0.50	0.50
Salt	0.10	0.15	0.15	0.10
Vitamin Mix[b]	0.05	0.05	0.05	0.05
Mineral Premix[c]	0.03	0.03	0.03	0.03
Calculated Values				
NEm,Mcal/kg	2.11	2.20	2.21	2.20
NEg, Mcal/kg	1.43	1.52	1.53	1.52
CP,%	14.10	13.90	14.20	15.70

[a]Dietary treatments consist of a traditional growing steer diet (Control) and three diet of increasing bypass amino acid levels (Low, Medium, and High).
[b]Contained (as-fed basis) 4,000,000 IU of vitamin A, 800,000 IU of vitamin D, and 1,250 IU of vitamin E/kg.
[c]Contained (as-fed basis) 10% Fe, 10% Mn, 10% Zn, 2% Cu, 1,500 ppm Se, 1,000 ppm I, and 500 mg/kg Co.

Table 2.3. Least squares means (standard error) for measures of feed efficiency and production traits between steer fed diets of different level of roughage and dietary bypass amino acids.

	Treatment[a]			
Items[b]	Control	Low	Medium	High
No. of steers	20	22	19	21
W0 (kg)	284.64 (4.65)	279.38 (4.43)	288.64 (4.77)	285.67 (4.54)
W84 (kg)	400.59 (7.90)	402.15 (7.54)	421.63 (8.11)	421.52 (7.71)
ADG (kg/d)	1.38 (0.07)[c]	1.46 (0.06)[cd]	1.58 (0.07)[d]	1.62 (0.07)[d]
FI (kg/d)	9.19 (0.22)	8.77 (0.21)	8.86 (0.22)	8.83 (0.21)
FCR (kg FI/kg ADG)	6.82 (0.21)[c]	6.21 (0.20)[d]	5.65 (0.21)[e]	5.60 (0.20)[e]
RFI (kg/d)[f]	0.52 (0.15)[c]	-0.01 (0.14)[d]	-0.22 (0.15)[d]	-0.29 (0.14)[d]

[a]Dietary treatments consist of a traditional growing steer diet (Control) and three growing steer diets of increasing bypass amino acid levels (Low, Medium, and High).
[b]Trait abbreviations: FI = average daily feed intake during the 84 d feeding period, FCR = feed conversion ratio during the 84 d feeding period, RFI = residual feed intake during the 84 d feeding period, ADG = average daily gain during the 84 d feeding period, W0 = weight at beginning of feed trial, and W84 = weight at d 84 on feed
[c,d,e]Least square means within a row with different subscripts differ ($P < 0.05$).
[f]Treatment regression coefficient was not included in the model for calculation of expected FI used in the RFI calculation.

Table 2.4. Least squares means (standard error) for serum hormones and metabolites of steers fed different levels of roughage and dietary bypass amino acids.

	Treatment[a]			
Items[b]	Control	Low	Medium	High
No. of steers	20	22	19	21
84GLC (mg/dL)	89.75 (2.03)	90.66 (1.89)	91.88 (2.03)	92.29 (1.97)
84INS (ng/mL)	3.52 (0.69)	2.45 (0.66)	2.35 (0.71)	2.36 (0.68)
84IGF-I (ng/mL)	371.16 (20.63)	393.33 (19.17)	408.99 (20.63)	399.67 (19.62)

[a]Dietary treatments consist of a traditional growing steer diet (Control) and three growing steer diet of increasing bypass amino acid levels (Low, Medium, and High).
[b]Trait abbreviations: 84INS = serum concentrations of insulin at d 84 of the feeding trial, 84GLC = serum concentrations of glucose at d 84 of feeding trial, 84IGF-I = serum concentrations of insulin like growth factor I at d 84 of the feeding period.

Table 2.5. Partial phenotypic correlations[a] between feed efficiency measures, production traits, and serum metabolites measured at weaning and d 84 of the feeding trial.

Traits[b]	RFI
FCR	**0.53**
FI	**0.69**
ADG	-0.01
W0	-0.01
W84	-0.01
WGLC	**-0.25**
WINS	-0.09
WIGF-I	-0.14
84GLC	-0.04
84INS	0.02
84IGF-I	-0.03

[a]Partial phenotypic correlations that are bold are significant ($P < 0.05$) from 0.
[b]Trait abbreviations: FI = average daily feed intake during 84 d of the feeding period, RFI = residual feed intake during the 84 d feeding period, FCR = feed conversion ratio during the 84 d feeding period, ADG = average daily gain during the 84 d feeding period, W0 = weight at beginning of feed trial, W84 = weight at d 84 on feed, WINS = weaning serum concentrations of insulin, WGLC = weaning serum concentrations of glucose, WIGF-I = weaning serum concentrations of insulin-like growth factor I, 84INS = serum concentrations of insulin at d 84 of the feeding trial, 84GLC = serum concentrations of glucose at d 84 of feeding trial, 84IGF-I = serum concentrations of insulin like growth factor I at d 84 of the feeding period.

Table 2.6. Least-squares means (standard errors) for residual feed intake and production traits of low-, medium-, or high residual feed intake (RFI) steers.

	RFI[a]		
Items[b]	Low	Medium	High
No. of steers	25	30	27
RFI (kg/d)	-0.77 (0.06)[c]	0.01 (0.05)[d]	0.70 (0.06)[e]
W0 (kg)	289.36 (3.97)	275.21 (3.63)	290.07 (3.81)
W84 (kg)	415.03 (6.92)	400.27 (6.33)	419.92 (6.65)
ADG (kg/d)	1.50 (0.06)	1.49 (0.05)	1.55 (0.06)
FCR (kg of FI/kg of gain)	5.61 (0.17)[c]	6.06 (0.16)[d]	6.52 (0.17)[e]
FI (kg/84d)	8.15 (0.14)[c]	8.79 (0.13)[d]	9.74 (0.14)[e]

[a]Low = RFI less than 0.5 SD below the mean; Medium = RFI was ± 0.5 SD above or below the mean; High = RFI greater than 0.5 SD above the mean.
[b]RFI = residual feed intake during the 84 d feeding period, FCR = feed conversion ratio during the 84 d feeding period, FI = average daily feed intake during the 84 d feeding period, W0 = weight at the beginning of the trial, W84 = weight at the end of the trial, ADG = average daily gain during the trial.
[c,d,e]Least square means within a row with different subscripts differ ($P < 0.05$).

Table 2.7. Least squares means (standard error) for weaning and d 84 serum concentrations of glucose, insulin and IGF-I of low- medium- or high residual feed intake steers.

	RFI[a]		
Item[b]	Low	Medium	High
No. of steers	25	30	27
WGLC (mg/dL)	95.54 (2.13)[c]	94.95 (1.97)[c]	89.08 (2.00)[d]
WINS (ng/mL)	4.95 (1.24)	4.90 (1.14)	5.11 (1.19)
WIGF (ng/mL)	265.48 (16.73)	233.26 (15.51)	222.09 (15.74)
84GLC (mg/dL)	89.40 (1.68)	94.93 (1.56)	88.73 (1.61)
84INS (ng/mL)	2.64 (0.62)	3.00 (0.57)	2.32 (0.60)
84IGF (ng/mL)	400.53 (18.02)	397.48 (16.50)	381.99 (17.66)

[a]Low = RFI less than 0.5 SD below the mean; Medium = RFI was ± 0.5 SD above or below the mean; High = RFI greater than 0.5 SD above the mean.
[b]WGLC = serum glucose concentrations quantified at weaning, WINS = serum insulin concentrations quantified at weaning, WIGF-I = serum insulin-like growth factor one concentrations quantified at weaning, 84GLC = serum glucose concentrations quantified at d 84 on feed, 84INS = serum insulin concentrations quantified at d 84 on feed, 84IGF-I = serum insulin like growth factor one concentrations quantified at d 84 on feed.
[c,d]Least square means within a row with different subscripts differ ($P < 0.05$).

CHAPTER 3

Mitochondrial protein complex ratios differ between residual feed intake phenotypes in cattle

ABSTRACT

Rate of oxygen uptake by muscle mitochondria and concentrations of respiratory chain proteins differed between high and low residual feed intake (RFI) animals. The hypothesis of this research was that complex I, II, and III mitochondrial protein concentrations harvested from lymphocytes would be correlated to RFI phenotype of beef steers. Individual feed intake (FI) was recorded for 88 Hereford crossbreed steers over 63 d using the GrowSafe FI system. Residual feed intake was computed as the residual of measured minus predicted FI. Predicted FI was calculated using coefficients for averaging daily gain (ADG) and metabolic midweight (MMWT) generated from linear regression of measured FI on MMWT and ADG. Lymphocytes were isolated from extreme low RFI (Low RFI = -1.32 ± 0.14 kg/d; n = 10) and extreme high RFI (High RFI = 1.34 ± 0.15 kg/d; n = 8) steers. Immunocapture of mitochondria complex I, II and III proteins from the lymphocyte was done using the MitoProfile complex I, II, and III Immunocapture kit (Mitosciences, Eugene, OR 97403). Lymphocytes were harvested from the blood. Protein concentrations of complex I, II, III, and total protein were quantified using bicinchoninic acid colorimetric procedures. High RFI steers consumed

more ($P < 0.05$) feed and had a lower ($P < 0.05$) gain to feed (G:F) compared to low RFI steers. The initial body weight, final body weight and ADG during the RFI test period was not correlated ($P > 0.15$) to RFI and was similar ($P > 0.15$) between low and high RFI steers. Only complex I protein concentrations tended to be correlated ($P = 0.15$) with RFI (correlation coefficient = -0.35). Ratios of complex I to II and complex I to III were correlated ($P < 0.05$) with RFI (coefficients = -0.55 and -0.67, respectively), and tended to be correlated ($P < 0.15$) with FI (coefficients = -0.44 and -0.41 respectively) and G:F (coefficients = 0.41 and 0.45, respectively). Residual feed intake is correlated to mitochondrial complex ratios I to II and I to III.

INTRODUCTION

United States Department of Agriculture reported that feed accounts for approximately 60% of the total production cost for cattle (Elstien, 2002). Since the greatest input cost in a beef production system is feed cost, decreasing feed intake (FI) without altering production and growth of beef cattle would improve feed efficiency and profitability of the system. Residual feed intake (RFI) is a measure of feed efficiency proposed by Koch et al. (1963) that accounts for energy requirements independent of growth. Genetic variation within the population is large, the trait is moderately heritable, and selection for low RFI can improve feed efficiency of beef cattle (Arthur et al., 1997; Richardson et al., 1998). Residual feed intake is measured as the residual of measured and predicted FI values.

Cellular energy is produced predominately by the mitochondria. Mitochondrial protein complexes subunits were differentially expressed in the liver (Iqbal et al., 2005), breast (Iqbal et al., 2004) and duodenum (Ojano-Dirain et al., 2005) between efficient and inefficient birds. Rats with lower mitochondrial protein content exhibited improved feed efficiency and improved rate of growth (Lutz and Stahly, 2003). Sandelin et al. (2004) reported expression of NAD4 (complex I), core I (complex III), Cox II (complex IV), and ANT1 (ADP/ATP) in muscle were higher in efficient than inefficient steers. Lymphocytes from inefficient broilers exhibited lower amounts of core I, Cytochrome C_1, and α-ATP synthase and higher amounts of 30 S and COX II in mitochondria compared to efficient broilers (Lassiter et al., 2006). Research findings to date support the hypothesis that feed efficiency is influenced by mitochondrial protein content and complex protein concentrations of the respiratory chain in broilers, rats, and steers. This research had the objective to determine if mitochondrial complex protein content and ratios was related to RFI (efficiency independent of growth effects) in cattle.

MATERIALS AND METHODS

Animal Management

The use of animals in this experiment was approved by the University of Missouri Animal Care and Use Committee. Ten extreme low RFI (Low RFI) and eight extreme high RFI (High RFI) spring-born straight-bred or crossbred steers sired by Hereford bulls

were selected from a pool of 88 steers to examine the relationship between mitochondrial complex protein concentration and RFI.

Upon receiving the animals, electronic ID tags (Allflex USA, Inc., Dallas Ft. Worth Airport, TX) were attached to the exterior of the left ear to aid in tracking individual FI with the GrowSafe FI system (GrowSafe Systems Ltd., Airdrie, AB Canada). Steers were placed on a receiving diet for 14 d prior to the feeding period to allow for acclimation to high concentrate diet and FI system. Water and receiving diet were provided at ad libitum during this period. Two-day consecutive weights were taken on d 13 and 14 to determine initial body weight and steers were randomly assigned to one of 15 pens. Each pen contained approximately six steers and one feed bunk restricted single animal feeding at any given time. Steers had ad libitum access to experimental diet (Table 3.1) and water. All feed ingredients except corn, blood meal, dried distillers grains and feather meal were mixed, pelleted and blended into the diet as a supplement. The pelleted supplement, corn, blood meal, dried distiller grains and feather meal were mixed as a total mixed ration and added to bunks once daily at approximately 0800.

Production Trait Collection and Calculation

Individual FI over the 63 d feeding period for each animal was measured with the GrowSafe (GrowSafe Systems Ltd., Airdrie, AB Canada) automated FI system (Wang et al., 2006). Consecutive two day weights were taken at initiation (IBWT) and 63 d (FBWT) of feeding and were used to calculate metabolic midweight (MMWT) and average daily gain (ADG) for the feeding period. Gain:feed (G:F) was computed as the

ratio of ADG to FI. Individual FI, MMWT, and ADG were used to calculate predicted FI. Predicted FI was calculated by regressing FI against MMWT and ADG using the general linear model (GLM) procedures of SAS (Proc GLM; SAS Institute, 2003). The model fitted was:

$$Y_i = \beta_0 + \beta_1 ADG + \beta_2 MMWT$$

where Y_i = expected daily FI of animal i; β_0 = the regression intercept; β_1 = partial regression coefficient of actual FI on ADG; and β_2 = partial regression coefficient of actual FI on MMWT. To calculate RFI, predicted FI was subtracted from measured FI (Basarab et al., 2003). Ten extreme low RFI (Low RFI = -1.32 kg/d) steers and eight extreme high RFI (High RFI = 1.34 kg/d) steers were selected for evaluation of mitochondria complex I, II, and III protein concentrations harvested from lymphocytes.

Lymphocyte Isolation and Preparation of Homogenate

Lymphocytes were isolated from blood according to procedures of Kolath (2006) with modifications. Blood was collected via jugular venipuncture into ACD vaccutainer tubes (Becton, Dickinson and Company; Franklin Lake, NJ) and stored at room temperature until lymphocyte isolation. Five to six milliters (mL) of blood was removed from three ACD vaccutainer tubes and placed in four Accuspin tubes (Sigma-Aldrich Co., St. Louis, MO). Tubes were centrifuged at 1,000 *x g* for 40 min at 18° to 25° C. Lymphocyte layers were removed to a 15 mL centrifuge tube (Corning Inc., Corning, NY) and volume brought to 15 mL with phosphate buffered saline (0.137 M NaCl, 0.0027 M KCl, 0.0022 M KH_2PO_4, 0.0097 M Na_2HPO_4, pH 7.4). The tube was

centrifuged at 300 *x g* for 15 min to pellet, supernatant removed and cells washed with 10 mL of phosphate-buffered saline. The tube was centrifuged at 300 *x g* for 10 min and the supernatant was removed. Cells were suspended in 1 mL of lymphocyte incubation buffer (150 mM KCl, 25 mM Tris, 2 mM EDTA, 10 mM KH_2PO_4, pH 7.4 with 0.1% BSA and 200 ug/mL) and placed at room temperature for 5 min. To disrupt cellular and mitochondrial memebranes, lymphocyte homogenate was frozen and thawed with liquid nitrogen five times (Lassiter et al., 2006). Lymphocyte homogenate was centrifuged at 12,000 *x g* for 15 min and supernatant removed. Lymphocyte homogenate was suspended in 1 mL medium II (230 m*M* mannitol, 70 m*M* sucrose, 20 m*M* Tris-HCL, 5 m*M* KH_2PO_4, pH 7.4). Lymphocyte homogenate was held at -80°C until further analysis. Protein concentrations of each sample were determined using bicinchoninic acid colorimetric procedures (Pierce Biotechnology, Inc., Rockford, IL).

Immunocapture and Measurement of Mitochondrial Protein Complexes

Immunocapture of mitochondrial protein complexes was done using a mitoprofile immunocapture kit (Mitosciences, Eugene, OR 97403). One hundred eighty microliters (μL) of lymphocyte homogenate was incubated with 20 μL of lauryl maltoside stock (200 m*M* n-dodecyl-β-D-maltopyranoside; Mitosciences MS 910) and 2 μL of protease inhibitor cocktail (Sigma P8340) on ice for 30 min. Then lymphocyte homogenate was centrifuged at 16,000 *x g* for 20 min and the pellet containing cellular debris was discarded. Ten μL of antibody containing beads (Mitosciences, Eugene, OR 97403) was added to the supernatant to bind mitochondrial complex protein. The bead supernatant

combination was incubated for 3 hr on a nutator at room temperature and placed at 4°C overnight. Beads were collected by centrifugation at 1,000 *x g* for 1 min and supernatant was removed. Beads were incubated two times for 5 min in bead wash buffer (0.1 M n-dodecyl-β-D-maltopyranoside, 0.137 M NaCl, 0.0027 M KCl, 0.0022 M KH_2PO_4, 0.0097 M Na_2HPO_4, pH 7.4) at room temperature and then incubated on the nutator in 50 μL of 1% sodium dodecyl sulfate (Sigma L4509) solution at room temperature for 20 min to remove protein from the beads to the supernatant. Protein concentrations of the supernatant of each sample were determined using bicinchoninic acid colorimetric procedures (Pierce Biotechnology, Inc., Rockford, IL).

Statistical analysis

Individual correlation coefficients were calculated using correlation (CORR) procedures of SAS (Proc CORR; SAS Institute, 2003) for RFI, FCR, IBWT, FBWT, FI, ADG, mitochondria complexes I, II, and III protein concentrations and the ratios of complex protein concentrations I to II, I to III and II to III. The ratios of complex protein concentrations I to II and I to III were regressed on RFI and G:F using Proc GLM (SAS Institute, 2003). The model included the (independent variables) ratios of complex protein concentrations I to II and I to III and the (dependent variables) of RFI or G:F. The differences in IBWT, FBWT, FCR, ADG, FI, protein concentrations of mitochondrial complexes I, II, III and ratios I to II, I to III, and II to III between extreme low and extreme high RFI steers were determined using PROC GLM of SAS (SAS Institute, 2003). Steer was the experimental unit for all traits. The model included the

independent variable of RFI group (low and high RFI steers) and dependent variables IBWT, FBWT, G:F, ADG, FI, protein concentrations of mitochondrial complexes I, II, III and ratios I to II, I to III, and II to III. The RFI group (low and high RFI steers) means were determined using least squares means statement of SAS. Least square means of significant ($P < 0.05$) RFI group effects were analyzed and found different at P-value of 0.05.

RESULTS AND DISCUSSION

Production Traits

No difference ($P > 0.15$) existed in IBWT, FBWT and ADG during the RFI test period between low RFI and high RFI steers (Table 3.2). Steer RFI was not correlated ($P > 0.15$) with IBWT, FBWT, and ADG (Table 3.3). However RFI was correlated ($P < 0.05$) to FI and G:F during the RFI test period. High RFI steers had a greater ($P < 0.05$) FI and lower G:F compared to low RFI steers. Kolath et al. (2006) reported that body weight and ADG did not differ but FI was greater and G:F was lower for high RFI compared to low RFI steers. Residual feed intake exhibited a strong positive correlation to DM intake but no correlation with ADG in Santa Gertrudis steers (Gomez et al., 2007). Average daily DM intake was positively correlated, G:F was negatively correlated and ADG was not correlated with RFI in Angus, Simmental, and Simmental X Angus crossbred steers (Homm et al., 2007). The present study agreed with previous research

that as RFI decreases steers consumed less feed and have an improved feed efficiency with no change in growth rate compared to high RFI steers.

Mitochondrial Complex Protein Concentrations and Ratios

Lymphocyte mitochondria complex I protein concentrations tended ($P = 0.15$) to be negatively correlated to RFI, but was not correlated ($P > 0.15$) with G:F and FI (Table 3.3). Mitochondria protein complex II and III concentrations were not correlated ($P > 0.15$) with RFI, G:F, or FI . Lymphocyte mitochondria complex I, II, and III concentrations were not different ($P > 0.22$) between low and high RFI steers (Table 3.4). Breast muscle mitochondria of low G:F broilers exhibited greater expression of CORE I (complex III) and Cytochrome C1 (complex III) (Iqbal et al., 2004). Lower amounts of mitochondria protein subunit core I (complex III) and Cytochrome C 1 (Complex III), and higher amounts of mitochondria protein 30 S (complex II) in low G:F versus high G:F broilers was reported by Lassiter et al. (2006). Expression of NAD4 (complex I) and core I (complex III) in *longissimus dorsi* muscle (LM) mitochondria was greater in high G:F compared to low G:F Angus steers and groups had similar complex II mitochondrial protein subunit expression (Sandelin et al., 2004). Furthermore there was an increase in LM muscle mitochondria complex I concentration tended to exist in low RFI compared to high RFI crossbreed steers (Davis et al., 2008) which agreed with present research results.

Mitochondria complex protein concentration ratios I to II and I to III were negatively correlated ($P < 0.05$) with RFI, and tended ($P < 0.15$) to be positively

correlated with G:F (Table 3.3). Also lymphocyte mitochondria complex protein ratios I to II and I to III tended to be negatively correlated ($P < 0.15$) with FI (Table 3.3). Lymphocyte mitochondria complex protein concentration ratios I to II and I to III were greater ($P < 0.05$) in low RFI compared to high RFI steers (Table 3.4). Lymphocyte mitochondria complex protein ratio II to III was not correlated ($P > 0.15$) to RFI, G:F, and FI (Table 3.3). Furthermore lymphocyte mitochondria complex protein ratio II to III did not differ ($P > 0.15$) between low and high RFI steers (Table 3.3). Ratios of complex proteins were more influenced by RFI. Complex I protein concentrations in relation to complex II and III protein concentrations increased with an improvement in efficiency while complexes II and III protein concentrations did not change with an improved efficiency. We hypothesize that a greater ratio of complex I proteins to complex II and III proteins would allow more rapid shuttling of NADH into the mitochondria and subsequent return to phosphorylation ratio homeostasis, resulting in more efficient animals. We further hypothesize that this in turn would result in satiety being reached at lower caloric intake in efficient compared to inefficient steers.

Since individual correlations of mitochondria complex protein concentration ratios I to II and I to III were significant with RFI, these were examined in a model to determine the amount of RFI and G:F variability that could be explained by these ratios. The model, which included mitochondria complex protein concentration ratios I to II as independent variables and RFI as the dependent variable, was significant ($P < 0.05$) with a $R^2 = 0.30$, whereas when G:F replaced RFI as the dependent variable the model was not significant ($P > 0.05$) with and $R^2 = 0.16$. When the model included only the

mitochondria complex protein concentration ratio I to III as the independent variable and RFI as the dependent variable significance ($P < 0.05$) was achieved with an $R^2 = 0.45$, whereas when G:F replaced RFI as the dependent variable the model was not significant ($P > 0.05$) with and $R^2 = 0.20$. These results show that ratios of mitochondria complex protein concentration I to II and I to III were responsible for significant variation in RFI among steers. We also concluded from our research that mitochondria isolated from lymphocytes could be used to study respiratory chain differences among RFI groups.

CONCLUSION

Steers with a low RFI consumed less feed and had improved feed efficiency without any change in growth rate. Examination of lymphocyte mitochondria proteins found a tendency for a negative relationship between mitochondria complex I protein concentrations and RFI. Mitochondria complex I protein concentrations were negatively related to RFI when mitochondria complex I protein concentration was normalized with complex II and III.

Table 3.1 Diet Composition

Ingredient (% as fed)	
Whole Shell Corn	88.40
Blood meal	1.00
Dried Distillers Grains	8.00
Feather Meal	1.60
Dyna K[a]	0.27
Limestone	0.60
Salt	0.08
Trace Mineral Premix[b]	0.02
Vitamin Premix[c]	0.02
Rumensin 80	0.01
Chemical Composition[d] (% of DM)	
NEm, Mcal\kg	2.16
NEg, Mcal\kg	1.49
CP %	13.60

[a]Contained (as-fed basis) 50% K, 46.4% Cl.
[b]Contained (as-fed basis) 4,000,000 IU of vitamin A, 800,000 IU of vitamin D, and 1,250 IU of vitamin E/kg.
[c]Contained (as-fed basis) 10% Fe, 10% Mn, 10% Zn, 2% Cu, 1,500 ppm Se, 1,000 ppm I, and 500 mg/kg Co.
[d]Calculated using tabular values(NRC, 2000) and feed label guarantees.

Table 3.2. Least squares means (standard errors) of performance measurements of high or low residual feed intake (RFI) steers.

	Residual feed intake		
Item[a]	Low	High	P-value
No. of steers	10	8	
Initial BW, kg	381.13 (13.41)	390.63 (14.99)	0.64
Final BW, kg	489.66 (17.35)	497.27 (19.39)	0.77
ADG, kg/d	1.71 (0.09)	1.68 (0.10)	0.78
G:F, kg ADG/kg FI	0.21 (0.01)	0.15 (0.01)	<0.01
FI, kg/d	8.38 (0.42)	11.17 (0.47)	<0.01
RFI, kg/d	-1.32 (0.14)	1.34 (0.15)	<0.01

[a]BW = body weight; ADG = average daily gain; G:F = gain to feed; ADFI = average daily feed intake

Table 3.3. Phenotypic correlations[a] between residual feed intake, production traits, and mitochondrial protein concentration and ratios of low and high residual feed intake steers.

Trait[b]	RFI	G:F	FI
G:F	**-0.82**		
FI	**0.74**	**-0.69**	
IBWT	0.07	-0.37	**0.67**
FBWT	0.03	-0.21	**0.68**
ADG	-0.09	0.28	**0.48**
CI	-0.35	0.20	-0.31
CII	0.06	-0.11	0.01
CIII	0.15	-0.12	-0.02
CI:CII	**-0.55**	0.41	-0.44
CI:CIII	**-0.67**	0.45	-0.41
CII:CIII	-0.11	0.02	0.06

[a]Phenotypic correlations that are bold are significant ($P < 0.05$) from 0.
[b]Trait abbreviations: FI = daily feed intake, RFI = residual feed intake, ADG = average daily gain, IBWT = weight at beginning of feed trial, FBWT = weight at d 63 on feed, G:F = gain to feed during the 63 d feeding period, CI = mitochondria protein complex I concentrations, CII = mitochondria protein complex II protein concentrations, CIII = mitochondria protein complex III concentrations, CI:CII = ratio of mitochondria protein complex I to II concentrations, CI:CIII = ratio of mitochondria protein complex I to III concentrations, CII:CIII = ratio of mitochondria protein complex II to III concentrations.

Table 3.4. Least squares means (standard errors) of lymphocyte mitochondria complex protein concentrations and ratios from steers of high or low residual feed intake (RFI).

	Residual feed intake		
Item	Low	High	P-value
No. of steers	10	8	
Mitochondrial Protein Complex I, μg/mg	11.72 (0.94)	9.93 (1.05)	0.22
Mitochondrial Protein Complex II, μg/mg	10.70 (1.06)	11.34 (1.18)	0.69
Mitochondrial Protein Complex III, μg/mg	9.87 (0.96)	10.66 (1.07)	0.59
Mitochondrial Protein Complex I:II	1.12 (0.06)	0.90 (0.07)	0.03
Mitochondrial Protein Complex I:III	1.23 (0.07)	0.94 (0.07)	0.01
Mitochondrial Protein Complex II:III	1.10 (0.07)	1.09 (0.08)	0.88

CHAPTER 4

Effect of postruminal amino acid supply during the growing phase on residual feed intake, growth performance and ultrasound carcass measurements

ABSTRACT

This study was conducted to investigate the effects of increasing ruminal bypass amino acid level in the diet during the growing phase on performance, residual feed intake (RFI) and ultrasound carcass measurements. This study further investigated if an interaction between bypass amino acid level in the diet and residual feed intake during the growing phase existed on growth performance, residual feed intake and carcass measurements in the finishing phase. Eighty-seven spring-born steers were weaned in early November and arrived at the University of Missouri Beef Research and Teaching farm in early December. The growing phase dietary treatments were no roughage diets with increasing bypass amino acid level (Low, n = 29; Medium, n = 29; High, n = 29) and fed for 63 d. Then steers were placed on a single finishing diet during the second 63 d test period (finishing period). At 116 d on feed, 53 d into finishing period, ultrasound measurements of 12th rib fat thickness (BF), intramuscular fat percentage (IMF) and 12th rib longissmus dorsi muscle area (LMA) was obtained. Residual feed intake during the growing (RFI63) and finishing phase ($RFI126_1$ and $RFI126_2$) was calculated as the difference between actual and predicted FI. Predicted FI during the growing (PFI63)

phase was calculated by regression of growing phase FI against ADG63 and MMWT63. Predicted FI during the finishing ($PF126_1$, and $PFI126_2$) phase was calculated using two regression models. Regression model one regressed finishing FI against ADG126 and MMWT126. Regression model two regressed finishing FI against ADG126, MMWT126, and LMA. Partial correlation coefficients were calculated between RFI measurements and performance traits collected during the growing and finishing phase and ultrasound carcass measurements. In addition to partial correlation coefficients, RFI during the growing phase was analyzed as a continuous variable against performance traits, finishing phase RFI measurements and ultrasound carcass characteristics. Upon statistical significance a nonparametric approach was used to segregate steers into three distinct RFI groups based on growing phase RFI value (low was RFI < 0.5 SD below the mean RFI, n = 27; medium was RFI ± 0.5 SD above or below the mean, n = 34; and high was RFI > 0.5 SD above the mean, n = 26). The interaction between RFI63 and level of bypass amino acid during the growing phase was found not significant ($P > 0.15$) leading to main effects examination. Steer FCR63 and ADG63 tended ($P < 0.15$) to be influenced by dietary treatment while FI63, RFI63, and W63 were not influenced ($P > 0.15$) by dietary treatment. Steers on the High diet had improved ($P < 0.05$) FCR63 and ADG63 compared to steers on the Low diet while steers on the Medium diet had intermediate FCR63 and ADG63 that was similar ($P > 0.15$) to the other dietary treatments. Growing phase dietary amino acid treatment influenced ($P < 0.05$) FCR126 but not ($P > 0.05$) ADG126, FI126, W126, $RFI126_1$ and $RFI126_2$. Steers fed Low diet during the growing phase had lower ($P < 0.05$) FCR126 than steers fed Medium diet and

tended to have lower ($P < 0.15$) FCR than steers fed High diet. Dietary treatment influenced ($P < 0.05$) BF and IMF and tended to influence ($P < 0.06$) LMA. Steers fed Low diet had increased ($P < 0.05$) BF and IMF and decreased ($P < 0.05$) LMA in the finishing phase compared to steers fed the High diet. Steers fed Low diet had greater ($P < 0.05$) BF and tended to have greater ($P < 0.07$) IMF in finishing phase and lower ($P < 0.05$) LMA compared to steers fed the Medium diet. Medium diet steers had greater ($P < 0.05$) BF, IMF and similar ($P > 0.15$) LMA compared to High diet steers. Growing phase residual feed intake was correlated ($P < 0.05$) with FI63, FCR63, FCR126, $RFI126_1$ and $RFI126_2$. Steer RFI63 influenced ($P < 0.05$) steer FCR63, FI63, FCR126, $RFI126_1$ and $RFI126_2$. Low RFI steers had decreased ($P < 0.05$) FCR63, FI63, FCR126, $RFI126_1$ and $RFI126_2$ than high RFI steers. Low RFI steers had lower ($P < 0.05$) FI63 and tended ($P < 0.07$) to have lower FCR63 compared to medium RFI steers, but were not different ($P > 0.15$) for FCR126, $RFI126_1$ and $RFI126_2$. Medium RFI steers had lower ($P < 0.05$) FI63, FCR63, FCR126, $RFI126_1$, and $RFI126_2$ than high RFI steers. The $RFI126_1$ was correlated ($P < 0.05$) with FI126 and FCR126. Residual feed intake measurements were not correlated ($P > 0.05$) with weight and growth measurements and RFI63 did not influence ($P > 0.05$) growth and weight measurements. Ultrasound carcass measurements were not correlated ($P > 0.05$) with RFI measurements and these measurements were not influenced ($P > 0.05$) by RFI63. Carcass LMA, but not BF or IMF was found significant ($P < 0.05$) when included in the model to predicted finishing phase FI and its inclusion improved model coefficient of determination from 0.57 to 0.59. The $RFI126_2$ was correlated ($P < 0.05$) to $RFI126_1$ and RFI63. During the growing phase

as bypass amino acid level may have increased growth and improved feed efficiency. Increasing bypass amino acid level in the diet during the growing phase decreased finishing phase carcass fat content. Feeding a growing phase diet below optimum amino acid profile for growth may decrease finishing phase LMA. Feeding a growing phase diet below optimum amino acid profile for growth may improve feed efficiency during the finishing phase. As residual feed intake decreases in growing phase, finishing phase feed efficiency improved.

INTRODUCTION

United States Department of Agriculture reported that feed accounts for a significant portion of total production cost for cattle (Elstien, 2002). Decreased feed intake (FI) and increased growth through improved feed efficiency would reduce production cost and improve profitability of cattle production. The producer can alter feed efficiency by dietary manipulation or selection for superior genetics. Previous research conducted in our laboratory demonstrated that adding bypass protein to no roughage diets improved feed efficiency (Mueller et al., 2004). Limited research has been done looking at feeding no-roughage diets optimized for post ruminal flow of amino acids in growing beef steers. Our hypothesis was that optimizing bypass amino acid in no roughage diets would optimize feed efficiency and growth. Therefore growth performance of beef steers fed diets with no roughage and increasing levels of bypass amino acid were investigated.

Steers grazing native range pasture were more efficient during the finishing phase but had lower hot carcass weight, dressing percentage, longissimus muscle area, and marbling score at slaughter (Choat et al., 2003). Steers having lower rates of gain during the stocker phase had higher finishing average daily gain, lower hot carcass weights and lower dressing percentage at slaughter compared to steers having higher rates of gain during the stocker phase (Neel et al., 2007). Also in this study, steers with higher rates of gain during the stocker period had a higher USDA carcass quality grade. The increase in dietary protein level during the growing phase led to steers having a greater ribeye area at slaughter (Perry et al., 1983). Our hypothesis was that supply of bypass amino acids during the growing phase would influence finishing performance and carcass characteristics. Therefore the relationship between level of bypass amino acids fed during the growing phase, and finishing performance and carcass characteristics were measured.

The historic method used to improve feed efficiency was selection for improved feed conversion ratio (FCR). However, FCR is linked to frame size because large framed steers have lower FCR than small framed steers at the same weight (Thonney et al., 1981). Therefore selection for improved FCR will increase cattle growth and frame size which is not always desirable in beef cattle production systems (Herd et al., 2003). Residual feed intake (RFI) proposed by Koch et al. (1963) is an alternative measure of feed efficiency to FCR that accounts for energy requirements independent of growth. Genetic variation in RFI is large, the trait is moderately heritable, and research findings lend support to the hypothesis that selection for low RFI can improve feed efficiency of

beef cattle (Arthur et al., 1997; Richardson et al., 1998). Little research has been done investigating how growing phase dietary alterations influence growing and finishing phase RFI measurements, and growing phase RFI measurements relationship with performance characteristics. Our hypothesis was that level of bypass amino acid in the growing phase will influence growing and finishing phase RFI measurements and growing phase RFI measurements relationship with performance traits. Therefore the relationship between growing phase level of bypass amino acid and growing and finishing phase RFI measurements were investigated. Also the interaction between growing phase RFI measurements and level of bypass amino acids on performance measurements in the growing and finishing phase was examined.

The inclusion of 12th rib fat thickness gain and *longissmus dorsi* muscle area gain into the regression equation for the calculation of predicted and residual feed intake of bull and heifers accounted for 9% of the variation (Lancaster et al., 2009). Also, ultrasound backfat thickness was lower in low RFI compared to high and medium RFI steers (Nkrumah et al., 2004). Progeny of low RFI parents have greater change in loin eye muscle area during the RFI test and decreased fat depth at the rib and rump at the beginning of the RFI test period compared to progeny from high RFI parents (Richardson et al., 2001). Furthermore, Richardson reported that carcass fat was lower from progeny of low RFI parents compared to that of high RFI parents. Our hypothesis was that carcass composition was related to RFI; therefore the relationship between ultrasound measurements during finishing phase and RFI measurements during the growing and finishing phase was examined.

MATERIALS AND METHODS

Experimental Design, Management, and Growth of Feedlot Steers

The use of animals in this experiment was approved by the University of Missouri Animal Care and Use Committee. Eighty-seven spring-born crossbred Angus steers were used in this experiment. Steers were weaned in early November and arrived at the University of Missouri Beef Research and Teaching Farm on December 1, 2008. Upon receiving the animals, electronic ID tags (Allflex US INC., Dallas-Fort Worth Airport, TX) were attached to the exterior of the left ear to aid in tracking individual FI with the GrowSafe FI system (GrowSafe Systems Ltd., Airdrie, AB, Canada). Steers were placed on a receiving diet for 12 d prior to the feeding period to allow for acclimation to the high concentrate diet and FI system. Water and receiving diet were provided ad libitum during this period. After the receiving period two day consecutive weights were taken on December 11 and 12, 2008 to determine initial body weight (W0 = 338 ± 38 kg). Steers were stratified by W0 into 15 concrete pens (16.5'x30'). Five pens were assigned to one of three dietary treatments. Dietary treatments (Table 4.1) consisted of three diets of increasing bypass amino acid level (Low, n = 29; Medium, n = 29; High, n = 29). After 63 d on dietary treatments two day consecutive weights were taken (W63 = 440 ± 44 kg) for calculation of production traits and MMWT during the 63 d period. The first 63d on feed was termed as growing phase and production traits calculated during this phase of the feeding were average daily gain (ADG63; (W0 + W63)/63 d) and metabolic mid-

weight (MMWT63; (W0 + W63)/2)^0.75). Then steers were all placed on a finishing diet (Table 4.2) for 63 d and two day consecutive weights (W126 = 523 ± 50 kg) were taken at the end of this period to determine production traits for the period 63 to 126 d. The second 63d on feed was termed finishing phase and production traits calculated during this phase of feeding were (ADG126; ((W63+W126)/63 d) and metabolic mid-weight (MMWT126; (W63+W126)/2)^0.75).

All feed ingredients except corn and corn bran were mixed and pelleted. The resulting pellet was mixed into diet as supplement. The pelleted supplement, corn and corn bran were mixed as a total mixed ration using a truck mounted ribbon mixer. Steers were fed once daily at approximately 0800h, and the animals had ration and water available at all times.

At d 116 of the study, ultrasound measurements of 12^{th} rib fat thickness (BF), *longissmus dorsi* muscle area (LMA) and percentage of intramuscular fat (IMF) were obtained using an Aloka 500-V instrument with a 17.2-cm, 3.5-MHz transducer (Designer Genes Inc., Harrison AR). Images were collected and analyzed by beef image analysis pro software (Designer Genes Inc., Harrison AR).

Efficiency Status

Individual FI data were collected using the GrowSafe individual animal FI system (Model 5000E, GrowSafe Systems Ltd.) from d 0 to 63 (growing phase; FI63; kg) and from d 63 to d 126 (finishing phase; FI126; kg). During the growing phase each pen contained approximately six steers and one feeding bunk that restricted diet consumption

to a single animal at any given time. During the finishing phase steers from each treatment were placed in a pen (29 steers per pen) with five feeding bunks restricting access to one steer consuming feed from each bunk at a time for each feeding bunk. Feed conversion ratio was calculated for the growing (FCR 63; FI63 (kg)/ADG63 (kg)) and finishing (FCR 126; FI126 (kg)/ ADG126 (kg)) feeding periods.

One model was used to predict FI and calculate RFI during the growing phase (PFI63 and RFI63). Predicted FI was calculated using the regression (REG) procedure of SAS (Proc REG; SAS Institute, 2003) and the model included dependent variable FI63 and independent variables MMWT63, ADG63, treatment, and treatment by independent variable interactions. The independent variable treatment and its interactions were found not significant ($P > 0.05$) and removed from the regression model. The model fitted was:

$$Y_i = \beta_0 + \beta_1 ADG63 + \beta_2 MMWT63$$

where Y_i = PFI63 of animal i; β_0 = the regression intercept; β_1 = partial regression coefficient of FI63 on ADG63; and β_2 = partial regression coefficient of FI63 on MMWT63. The model fitted had an R^2 of 0.50. To calculate RFI63, $PFI63_1$ was subtracted from FI63 (Wang et al., 2006).

Two models were used to predict FI and calculate RFI during the finishing phase ($PFI126_1$, $PFI126_2$, and $RFI126_1$, $RFI126_2$, respectively). Predicted $FI126_1$ was calculated using the regression (REG) procedure of SAS (Proc REG; SAS Institute, 2003) and the model included dependent variable FI126 and independent variables MMWT126, and ADG126. The model fitted was:

$$Y_i=\beta_0 + \beta_1 ADG126 + \beta_2 MMWT126$$

where Y_i = $PFI126_1$ of animal *i*; β_0 = the regression intercept; β_1 = partial regression coefficient of FI126 on ADG126; and β_2 = partial regression coefficient of FI126 on MMWT126. To calculate $RFI126_1$, $PFI126_1$ was subtracted from FI126 (Wang et al., 2006). Predicted $FI126_2$ was calculated using the REG procedures of SAS and the model included dependent variable FI126 and independent variables ADG126, MMWT126, ultrasound carcass characteristics (12^{th} rib fat thickness (BF), intramuscular fat (IMF), and *longissmus dorsi* muscle area (LMA) and all independent variable interactions. The carcass characteristics BF and IMF and independent variable interaction were found not significant ($P > 0.05$) and removed from the model. The variables included in the model were FI126, ADG126, MMWT 126, and LMA. The model fitted was:

$$Y_i = \beta_0 + \beta_1 ADG126 + \beta_2 MMWT126 + \beta_3 LMA$$

where Y_i = $PFI126_2$ of animal *i*; β_0 = the regression intercept; β_1 = partial regression coefficient of FI126 on ADG126; and β_2 = partial regression coefficient of FI126 on MMWT126; β_3 =partial regression coefficient of FI126 LMA. To calculate $RFI126_2$, $PFI126_2$ was subtracted from FI126 (Wang et al., 2006).

Statistical Analysis

Partial correlation coefficients were calculated for RFI measurements, production trait and carcass characteristics collected during the trial using Proc CORR procedures of SAS (SAS Institute, 2003) with partial option used to adjust for treatment effects.

Variables included in the matrix were RFI measurements, production trait measurements and ultrasound carcass characteristics during the finishing phase.

The effects of the interaction of dietary treatment during the growing phase and continuous random variable RFI63 on production traits during the growing phase (W0, W63, ADG63, FCR63, FI63) and finishing phase (W126, ADG126, FCR126, FI126), RFI measurements (RFI63, $RFI126_1$) and ultrasound carcass measurements (IMF, BF, and LMA) during the finishing phase were investigated using a covariance analysis in general linear model (GLM) procedures of SAS (Proc GLM; SAS Institute, 2003) in which RFI63 was a covariate (Snedecor and Cochran, 1989). Steer was the experimental unit for all traits. The model included the dependent variables of production traits obtained during the growing and finishing phase on feed, RFI measurements, and ultrasound carcass measurements during the finishing phase and the independent variables of treatment, RFI63, and there interaction . The interaction between RFI63 and treatment was found not significant ($P > 0.15$) for all traits therefore only main effects of treatment and RFI were investigated in separate models. To examine treatment effects the model included performance and RFI measurements of both phases and carcass characteristics as dependent variables and dietary treatment as independent variable. To examine RFI63 effects the model included the same dependent variables with the independent variables of RFI63 and covariate dietary treatment. Treatment was included as a covariate to remove any effects of treatment on the traits tested in the model. To examine the relationship between RFI63 extremes of significant RFI63 effects, RFI63 was partitioned into three groups called low (RFI < 0.5 SD below the mean RFI; n = 27),

medium (RFI ± 0.5 SD above or below the mean; n = 34) and high (RFI > 0.5 SD above the mean; n = 26) (Nkumah et al., 2004). Least squares means for treatment and RFI groups was determined using least squares means statement of SAS. Least squares means of treatment and RFI group effects were analyzed and found significant at P-value of 0.05.

RESULTS AND DISCUSSION

Dietary Effects on Production and Carcass Characteristics

Feed conversion ratio, not FI during the growing phase tended ($P < 0.15$) to be influence by diet. Steers fed the High diet had ($P < 0.05$) lower FCR63 than steers fed the Low diet while steers on the Medium diet had FCR63 not different ($P > 0.15$) to those steers on the other diets (Table 4.3). Steer ADG during the growing phase, not W63 at the end of the growing phase tended ($P < 0.15$) to be influenced by diet. Steer ADG63 was greater ($P < 0.05$) for High diet steers compared Low diet steers while ADG63 of steers on the Medium diet was not different ($P > 0.15$) compared to steers on the other diets (Table 4.3). During the growing phase, increasing bypass amino acid levels in no roughage diets tended to improve FCR and increase ADG without altering feed intake. Supplementation with excess amino acids improved methionine and leucine use for protein deposition by growing cattle (Awawdeh et al., 2006). In the present study the increase in bypass amino acids during the growing phase may have improved amino acid

utilization for protein deposition which led to an increase in ADG and improvement in FCR with no change in FI during the growing phase.

Growing phase diet influenced ($P < 0.05$) FCR126. Low diet steers had lower ($P < 0.05$) FCR126 than Medium diet steers (Table 4.3). High diet steers tended ($P < 0.15$) to have and greater FCR126 than Low diet steers. Medium and High diet steers did not differ ($P > 0.15$) in FCR126. Animals feed bypass amino acids below optimum for maximum gain during the growing phase had improved feed efficiency during the finishing phase. Steers fed a high protein diet during the growing phase had the poorest gain and feed efficiency during the finishing phase compared to steers on low and intermediate diets during the growing phase (Perry et al., 1983). Byers and Moxon (1980) reported that steers on a low protein diet during the growing phase showed the greatest growth response with protein supplementation during the finishing phase compared to the steers receiving medium and high protein diets.

Ultrasound carcass fat measurements were influenced ($P < 0.05$) and LMA tended to be influenced ($P < 0.06$) by growing phase diet. High diet steers had lower ($P < 0.05$) IMF and BF compared to Low diet steers. Steers fed Medium diet had intermediate levels of BF that differed ($P < 0.05$) from High and Low diet steers. Medium diet steers had intermediate IMF that tended ($P < 0.07$) to differ from Low diet steers and differed ($P < 0.05$) from High diet steers. High and Medium diet steers had similar ($P > 0.15$) LMA that was greater ($P < 0.05$) than Low diet steers. As growing phase bypass amino acids level increases, finishing phase BF and IMF decreased. Feeding a growing phase diet below optimum amino acid profile for growth may decrease LMA compared to

growing phase diets that have optimum amino acid profile for growth. Similar to the present research Perry et al. (1983) found that increasing protein level during the growing phase caused an increase in ribeye area at slaughter. Ferrell et al. (1978) reported that carcasses from steers receiving a higher energy diet had more fat deposition than steers receiving a lower energy diet. Furthermore Ferrell showed protein content during the finishing phase had some influence on the amount of lean primal cuts. We purpose that subcutaneous and intramuscular fat content of steers was decreased in the finishing phase with feeding increasing levels of bypass amino acids during the growing phase because greater lean tissue accretion was promoted. Likewise lean tissue development decreased as bypass amino acid level in the growing phase decreased. Because energy consumption was not different between diets in the growing phase, the extra energy would have been used for fat deposition. Calves fed low diet had less lean tissue gain during the growing phase and therefore would have accreted more lean tissue during the finishing phase resulting in an improved FCR.

Relationship between Residual Feed Intake Measurement, Performance, and Carcass Measurements

Growing and finishing phase RFI was not influenced ($P > 0.05$) by diet. Growing phase residual feed intake was correlated ($P < 0.05$) with $RFI126_1$ (Table 4.5). The $RFI126_1$ was influenced ($P < 0.05$; $R^2 = 0.16$) by RFI63. Low RFI steers had similar ($P > 0.15$) $RFI126_1$ values compared to medium RFI steers. High RFI steers had greater ($P < 0.05$) $RFI126_1$ compared to low and medium RFI steers. Arthur et al. (1999) reported

that postweaning RFI was significantly correlated with cow RFI. Also RFI calculated on dairy heifers during the growing phase was genetically correlated with RFI calculated during the beginning of their first lactation (Nieuwhof et al., 1992). Previous research is similar to the present research that postweaning RFI is related to RFI tested later in the animal's life.

The comparison of RFI63 and FI63 yielded a significant ($P < 0.05$; R = 0.72) correlation (Table 4.5) and RFI63 influenced ($P < 0.05$; $R^2 = 0.52$) FI63. The FI63 for RFI groups are depicted in table 4.6. Low RFI steers had the lowest ($P < 0.05$) FI63 (8.42 ± 0.14 kg/d), high RFI steers had the greatest ($P < 0.05$) FI63 (10.25 ± 0.14 kg/d) and medium RFI steers had an intermediate FI63 (9.50 ± 0.13 kg/d), which was different ($P < 0.05$) than the other two groups. Comparison of RFI63 and FCR63 yielded a significant ($P < 0.05$; R = 0.41) correlation (Table 4.5) and RFI63 influenced ($P < 0.05$; $R^2 = 0.20$) FCR63. The FCR63 values for RFI group are depicted in table 4.6. Low RFI steers had a lower ($P < 0.05$) FCR63 (5.50 ± 0.19 kg/kg) than high RFI steers (6.53 ± 0.19 kg/kg). The medium RFI steers had an intermediate FCR63 (5.95 ± 0.17 kg/kg) that was different ($P < 0.05$) from the high RFI group and tended ($P < 0.07$) to differ from the low RFI group. Previous research by Richardson et al. (2001) reported that steers progeny of high RFI parents had greater FI values than steer progeny of low RFI parents. Also low RFI bulls and heifers consumed 17% less feed than high RFI bulls and heifers (Ribeiro et al., 2007). Low RFI steers consumed 19.1% less dry matter than high RFI steers (Gomez et al., 2007). Also Gomez et al. (2007) showed that steer FCR was positively correlated with RFI and that low RFI steers had an 18% lower FCR than high

RFI steers. Nkrumah et al. (2004) reported that high RFI steers had the greatest FCR and FI, low RFI steers had the lowest FCR and FI and medium RFI steers had an intermediate FCR and FI which was different than the other two groups. In agreement with previous research the present study showed that as RFI decreased there was a decrease in steer FCR and FI.

Comparison of RFI63 and FI126 tended to be correlated ($P < 0.06$; R = 0.20; Table 4.5). Finishing period feed conversion ratio was correlated ($P < 0.05$; R = 0.26; Table 4.5) with RFI63. The FCR126 ($P < 0.05$; $R^2 = 0.10$), not FI126 ($P > 0.06$; $R^2 = 0.04$) was influenced by RFI63. The FI126 and FCR126 values for RFI group are depicted in table 4.6. Since RFI63 did not influence FI126, no statistical analysis of RFI group was done. High RFI steers had greater ($P < 0.05$) FCR126 (7.17 ± 0.21 kg/kg) compared to low RFI steers (6.29 ± 0.21 kg/kg). Medium RFI steers had similar ($P > 0.15$) FCR126 (6.63 ± 0.19 kg/kg) compared to low RFI steers and was lower ($P < 0.05$) than high RFI steers. Nieuwhof et al. (1992) reported that feed efficiency and ME intake of lactating dairy heifer was genetically correlated to dairy heifer RFI calculated during the growing phase. Residual feed intake calculated for beef heifers postweaning was positively correlated to their mature feed efficiency and feed intake (Arthur et al., 1999). The present research was similar to previous research in that animals of low RFI have more improved feed efficiency during the subsequent test periods compared to high RFI animals.

Correlations between W0, W63, ADG63, W126, ADG126 and RFI63 were all not significant ($P > 0.15$; Table 4.5). Growing phase residual feed intake during did not

influence ($P > 0.15$) W0, W63, ADG63, W126, and ADG126. Weight and growth measurements between RFI groups are depicted in Table 4.6. Residual feed intake has been reported to be unrelated to weaning weight, postweaning weight measurements and postweaning gain (Lancaster et al., 2008; Gomez et al., 2007; Homm et al., 2007). Arthur et al. (2001) reported that RFI had no phenotypic correlation with postweaning gain and weight measurements of Angus bulls and heifers. Therefore the present study agreed with previous research that RFI was phenotypically unrelated with postweaning growth and weight measurements.

Correlation between RFI63 and IMF, BF, and LMA and were not significant ($P > 0.15$; Table 4.5). Growing phase residual feed intake during did not influence ($P > 0.15$) IMF, BF, and LMA. Ultrasound carcass measurements between RFI groups are depicted in Table 4.7. Lancaster et al. (2009) reported that RFI was related to ultrasound final BF, gain in BF, and gain in LMA during an RFI test period but not final or change in IMF and final LMA. Low RFI steers had less ultrasound BF compared to high RFI steers when data were collected during the RFI test period (Nkrumah et al., 2004). Richardson et al. (2001) reported that progeny LMA at the beginning on the RFI test period was positively and progeny change in LMA during the RFI test period was negatively related to sire estimated breeding values for RFI. In the present study ultrasound measurement was taken approximately 53 d after the end of the first RFI test period. Therefore the possible discrepancy between the present study and the previous study may be due to time ultrasound carcass measurements were made.

Carcass BF and IMF were not correlated ($P > 0.15$) with $RFI126_1$, but LMA tended ($P < 0.07$; R = 0.19) to be correlated with $RFI126_1$ (Table 4.5). Richardson et al. (2001) reported that sire estimated breeding values for RFI was positively correlated with progeny LMA at the beginning of the RFI test period. Steer LMA during the finishing period may have influenced finishing predicted FI and RFI therefore its effect was tested. Carcass characteristics were tested and LMA was found to influence ($P < 0.05$) FI prediction during the finishing phase. Inclusion of LMA in the model did increase the coefficient of determination for the prediction model of FI during the finishing phase from 0.57 to 0.59. Finishing and growing phase residual feed intake was correlated ($P < 0.05$; Table 4.6) with $RFI126_2$ and RFI63 influenced ($P < 0.05$; $R^2 = 0.14$) $RFI126_2$. Low and medium RFI steers had ($P > 0.15$) $RFI126_2$ values that were lower ($P < 0.05$) than high RFI steers (Table 4.6).

CONCLUSION

Increased bypass amino acid level in no-roughage diets during the growing phase may improve feed efficiency and increased gain. However a growing phase diet that is below animal's amino acid requirement for maximum growth may cause animal's feed efficiency to improve during the finishing phase. Increasing levels of bypass amino acids during the growing phase led to decreased subcutaneous and intramuscular fat deposition during the finishing phase. Feeding bypass amino acids below requirement for growth during the growing phase decreased LMA during the finishing phase.

As RFI decreased animals consumed less feed and were more efficient with no change in body weight during the growing phase. The RFI calculation during the growing phase was related to RFI calculation and feed efficiency during the finishing phase such that low RFI animals during the growing phase had a more improved feed efficiency and lower RFI during the finishing phase compared to steers designated as high RFI during the growing phase.

Table 4.1. Composition of diets fed to steers during the growing phase.

	Treatment[a]		
Ingredients (inclusion rate % as-fed)	Low	Medium	High
Whole Shelled Corn	60.90	57.40	52.00
Corn Bran	25.00	25.00	25.00
Pellet	14.10	17.60	23.00
Pellet Composition (inclusion rate % as-fed)			
Soyplus[b]	28.37	39.75	43.65
Blood meal (AP-301)	--------	19.88	25.10
Alimet[c]	--------	--------	0.44
Dried Distillers Grains	56.74	28.39	21.82
Dyna-K[d]	1.06	0.57	--------
Limestone	9.93	7.95	6.11
Salt	1.06	0.85	0.44
Choice white grease	1.99	1.99	1.96
Vitamin ADE premix[e]	0.43	0.34	0.26
Mineral premix[f]	0.43	0.28	0.22
Chemical Composition[g] (% DM)			
DM %	83.79	83.60	84.03
CP %	14.00	17.60	20.80
ME, Mcal/kg	3.10	3.10	3.10

[a]Dietary treatments of consist three growing steer diets of increasing bypass amino acid levels (Low, Medium, and High).
[b]Contained (DM basis) 49.84% CP, RUP 60% (%CP), RDP 40% (%CP)
[c]Beta hydroxy analog of methionine, 88% active (Novus, St. Charles, MO)
[d]Contained (as-fed basis) 50% K, 46.4% Cl.
[e]Contained (as-fed basis) 4,000,000 IU of vitamin A, 800,000 IU of vitamin D, and 1,250 IU of vitamin E/kg.
[f]Contained (as-fed basis) 10% Fe, 10% Mn, 10% Zn, 2% Cu, 1,500 ppm Se, 1,000 ppm I, and 500 mg/kg Co.
[g]Calculated using tabular values(NRC, 2000) and feed label guarantees.

Table 4.2. Composition of diets fed to steers during the finishing phase.

Ingredients (inclusion rate % as-fed)	
Whole Shelled Corn	64.96
Corn Bran	25.00
Pellet	10.04
Pellet Composition (inclusion rate % as-fed)	
Soyplus[a]	34.86
Dried Distillers Grains	44.82
Limestone	14.94
Salt	1.99
Choice White Grease	1.99
Vitamin ADE premix[b]	0.60
Mineral premix[c]	0.50
Rumensin 80[d]	0.30
Chemical Composition[e] (% DM)	
DM, %	83.79
CP, %	12.50
ME, Mcal/kg	3.20

[a]Contained (DM basis) 49.84% CP, RUP 60% (%CP), RDP 40% (%CP)
[b]Contained (as-fed basis) 4,000,000 IU of vitamin A, 800,000 IU of vitamin D, and 1,250 IU of vitamin E/kg.
[c]Contained (as-fed basis) 10% Fe, 10% Mn, 10% Zn, 2% Cu, 1,500 ppm Se, 1,000 ppm I, and 500 mg/kg Co.
[d]Rumensin mix contained 176 g of monensin/kg (Elanco Animal Health, Indianapolis, IN).
[e]Calculated using tabular values(NRC, 2000) and feed label guarantees.

Table 4.3. Least squares means (standard error) for measures of feed efficiency and production traits between steers fed diets of different levels of bypass amino acids during the growing phase.

	Treatment[a]		
Items[b]	Low	Medium	High
No. of steers	29	29	29
W0 (kg)	337.70 (7.04)	338.10 (7.04)	338.43 (7.04)
W63 (kg)	433.89 (8.09)	440.37 (8.09)	444.60 (8.09)
W126 (kg)	522.78 (9.39)	519.02 (9.56)	527.95 (9.56)
ADG63 (kg/d)	1.53 (0.06)	1.62 (0.06)	1.68 (0.06)
ADG126 (kg/d)	1.41 (0.05)	1.28 (0.05)	1.33 (0.05)
FI63 (kg/d)	9.24 (0.19)	9.53 (0.19)	9.40 (0.19)
FI126 (kg/d)	8.66 (0.20)	8.80 (0.20)	8.69 (0.20)
FCR63 (kg FI63/kg ADG63)	6.22 (0.20)	6.06 (0.20)	5.68 (0.20)
FCR126 (kg FI126/kg ADG126)	6.26 (0.20)[c]	7.07 (0.21)[d]	6.75 (0.21)[cd]
RFI63 (kg/d)	-0.03 (0.16)	0.15 (0.16)	-0.12 (0.16)
$RFI126_1$ (kg/d)	-0.22 (0.15)	0.29 (0.15)	-0.04 (0.15)

[a]Dietary treatments consist of three growing steer diets of increasing bypass amino acid levels (Low, Medium, and High).

[b]Trait abbreviations: FI63 = daily feed intake during growing phase, FCR63 = feed conversion ratio calculated using data collected during growing phase, RFI63 = residual feed intake calculated using predicted FI calculation that included FI, ADG, and MMWT calculated from data collected during the growing phase, ADG63 = average daily gain calculated using data collected from growing phase, ADG126 = average daily gain calculated using data collected during finishing phase, W0 = weight at beginning of feed trial, W63 = weight at d 63 on feed, W126 = weight at 126d on feed , FCR126 = feed conversion ratio calculated from data collected from the finishing phase, FI126 = individual feed intake during finishing phase, $RFI126_1$ = Residual feed intake calculated using predicted FI calculation that included FI, ADG and MMWT calculated from data collected from finishing phase.

[c,d]Least squares means within a row with different subscripts differ ($P < 0.05$).

Table 4.4. Least-squares means (standard errors) for ultrasound carcass measurements during the finishing phase of steers fed different levels of bypass amino acids during the growing phase.

	Treatment[a]		
Items	Low	Medium	High
No. of steers	29	29	29
Fat Thickness (cm)	1.17 (0.04)[b]	1.04 (0.05)[c]	0.81 (0.05)[d]
Longissmus dorsi muscle area (cm^2)	61.68 (2.00)[b]	67.68 (2.05)[c]	67.48 (2.05)[c]
Intramuscular Fat, %	2.47 (0.11)[b]	2.18 (0.11)[b]	1.87 (0.11)[c]

[a]Dietary treatments consist of three growing steer diets of increasing bypass amino acid levels (low, medium, and high)

[b,c,d,]Least square means within a row with different subscripts differ ($P < 0.05$).

Table 4.5. Partial correlation coefficients[a] between feed efficiency measures, production traits and ultrasound carcass characteristics during the growing and finishing phase of steers.

Traits[b]	RFI63	$RFI126_1$	$RFI126_2$
$RFI126_1$	**0.39**		
$RFI126_2$	**0.37**	**0.98**	
FCR63	**0.41**	0.11	0.09
FCR126	**0.26**	**0.47**	**0.45**
FI63	**0.72**	**0.29**	**0.27**
FI126	0.20	**0.65**	**0.64**
ADG63	0.01	0.04	0.05
ADG126	-0.08	0.00	0.00
W0	-0.01	-0.02	-0.03
W63	-0.00	0.00	-0.00
W126	-0.03	0.00	-0.00
IMF	0.07	-0.00	-0.05
BF	0.00	0.15	0.16
LMA	0.13	0.19	-0.02

[a]Correlation coefficients in bold are significant ($P < 0.05$) from 0.

[b]Trait abbreviations: FI63 = daily FI during the growing phase, FCR63 = feed conversion ratio calculated during the growing phase, RFI63 = residual feed intake calculated using predicted feed intake calculation that included FI, ADG, and MMWT data collected during growing phase, ADG63 = average daily gain calculated using data collected from growing phase, ADG126 = average daily gain calculated using data collected during finishing phase, W0 = weight at beginning of feed trial, W63 = weight at 63 d on feed, W126 = weight at 126 d on feed , FCR126 = feed conversion ratio calculated using data from finishing phase, FI126 = individual feed intake during finishing phase, $RFI126_1$ = Residual feed intake calculated using predicted FI calculation that included FI, ADG and MMWT calculated from data collected from finishing phase, $RFI126_2$ = Residual feed intake calculated using predicted FI calculation that included FI, ADG , MMWT and LMA calculated from data collected from finishing phase, IMF = ultrasound percentage of intramuscular fat, BF = ultrasound fat thickness at the 12th rib, and LMA = longissmus dorsi muscle area at the 12th rib

Table 4.6. Least-squares means (standard errors) for residual feed intake and production traits of low-, medium-, or high residual feed intake (RFI) steers.

	RFI[a]		
Items[b]	Low	Medium	High
No. of steers	27	34	26
RFI63 (kg/d)	-0.98 (0.07)[c]	-0.03 (0.06)[d]	1.05 (0.07)[e]
W0 (kg)	329.28 (7.19)	346.92 (6.40)	335.65 (7.32)
W63 (kg)	429.98 (8.29)	448.95 (7.39)	437.43 (8.45)
W126 (kg)	515.85 (9.88)	532.56 (8.78)	518.81 (9.88)
ADG63 (kg/d)	1.60 (0.06)	1.62 (0.05)	1.61 (0.06)
ADG126 (kg/d)	1.37 (0.05)	1.35 (0.05)	1.29 (0.05)
FCR63 (kg of FI/kg of gain)	5.50 (0.19)[c]	5.95 (0.17)[c]	6.53 (0.19)[d]
FCR126 (kg of FI/kg of gain)	6.29 (0.21)[c]	6.63 (0.19)[c]	7.17 (0.21)[d]
FI63 (kg/d)	8.42 (0.14)[c]	9.50 (0.13)[d]	10.25 (0.14)[e]
FI126 (kg/d)	8.50 (0.20)	8.64 (0.18)	9.03 (0.20)
$RFI126_1$ (kg/d)	-0.26 (0.15)[c]	-0.19 (0.13)[c]	0.52 (0.15)[d]
$RFI126_2$ (kg/d)	-0.19 (0.12)[c]	-0.16 (0.11)[c]	0.41 (0.12)[d]

[a]Steers were allocated to RFI group based on RFI calculated using data collected during growing phase. Low = RFI was 0.5 SD below the mean; Medium = RFI was ± 0.5 SD above or below the mean; High = RFI was 0.5 SD above the mean.
[b]RFI63 = residual feed intake calculated using predicted FI calculation that included FI, ADG and MMWT data collected during growing phase, FCR63 = feed conversion ratio calculated using data collected during growing phase, FI63 = feed intake during growing phase. W0 = weight at the beginning of the trial, W63 = weight at the end of the growing phase, ADG63 = average daily gain during the growing phase, W126 = weight at the end of the finishing phase, ADG126 = average daily gain during the finishing period, $RFI126_1$ = residual feed intake calculated using predicted FI calculation that included FI, ADG and MMWT calculated from data collected during finishing phase, $RFI126_2$ = residual feed intake calculated using predicted FI calculation that included FI, ADG, MMWT, and LMA calculated data collected from finishing phase, FCR126 = feed conversion ratio calculated using data collected during finishing phase feeding, FI126 = feed intake during finishing phase.
[c,d,e]Least square means within a row with different subscripts differ ($P < 0.05$).

Table 4.7. Least squares means (standard errors) for ultrasound carcass measurements of low, medium, or high residual feed intake (RFI) steers.

	RFI[a]		
Item	Low	Medium	High
No. of steers	27	34	26
Fat Thickness (cm)	1.01 (0.05)	0.99 (0.04)	1.03 (0.05)
Longissmus dorsi muscle area (cm^2)	63.03 (2.13)	66.19 (1.93)	67.29 (2.13)
Intramuscular Fat, %	2.17 (0.12)	2.10 (0.10)	2.28 (0.12)

[a]Steers were allocated to RFI group based on RFI calculated using data collected during growing phase. Low = RFI was 0.5 SD below the mean; Medium = RFI was ± 0.5 SD above or below the mean; High = RFI was 0.5 SD above the mean

LITERATURE CITED

Albertini, T. Z., S. R. de Medeiros, R. A. de A. Torres Júnior, and D. P. D. Lanna. 2008. Cow live weight is negatively related to feed efficiency of cow/calf pairs from birth to weaning. J. Anim. Sci. 86 E-Suppl. 2:182.

Archer, J. A., P. F. Arthur, R. M. Herd, P. F. Parnell, and W. S. Pitchford. 1997. Optimum postweaning test for measurement of growth rate, feed intake and feed efficiency in British breed cattle. J. Anim. Sci. 75:2024-2032.

Archer, J. A., P. F. Arthur, R.M. Herd, and E. C. Richardson. 1998. Genetic variation in feed efficiency and its component traits. Proc. 6th World Congr. Genet. Appl. Livest. Prod., Armidale, Australia 25:81-84.

Arthur, P. F., J. A. Archer, R. M. Herd, E. C. Richardson, S. C. Exton, J. H. Wright, K. C. P. Dibley and D. A. Burton. 1997. Genetic and phenotypic variation in feed intake, feed efficiency, and growth in beef cattle. Proc. Assoc. Advmt. Anim. Breed. Genet. 12: 234-237

Arthur, P. F., J. A. Archer, R. M. Herd, E. C. Richardson, S. C. Exton, C. Oswin, K. C. P. Dibley, and D. A. Burton. 1999. Relationship between postweaning growth, net feed intake and cow performance. Proc. Assoc. Advmt. Anim. Breed. Genet. 13:484-487.

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

Awawdeh, M. S., E. C. Titgemeyer, G. F. Schroeder, and D. P Gnad,. 2006. Excess amino acid supply improves methionine and leucine utilization by growing steers**.** J Anim Sci 84: 1801-1810.

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

Bottje, W., M. Iqbal, Z. X. Tang, D. Cawthon, R. Okimoto, T. Wing, and M. Cooper. 2002. Association of mitochondrial function with feed efficiency within a single genetic line of male broilers. Poult. Sci. 81: 546-555.

Bottje, W. G., M. Iqbal, N. R. Pumford, C. Ojano-Dirain, and K. Lassiter. 2004. Role of mitochondrial in phenotypic expression of feed efficiency. J. Appl. Poult. Res. 13:94-105.

Boveris, A., and B. Chance. 1973. The mitochondrial generation of hydrogen peroxide. Biochem. J. 134:707-716.

Byers, F. M., and A. L. Moxon. 1980. Protein and selenium levels for growing and finishing beef cattle. J. Anim. Sci. 50:1136-1144.

Choat, W. T., C. R. Krehbiel, C. G. Duff, R. E. Kirksey, L. M. Lauriault, J. D. Rivera, B. M. Captian, D. A. Walker, G. B. Donart, and C. L. Gload. 2003. Influence on grazing dormant native range or winter wheat pasture on subsequent finishing cattle performance, carcass characteristics, and ruminal metabolism. J. Anim. Sci. 81:3191-3201.

Davis, M. P., J. H. Porter, and M. S. Kerley. 2008. The assessment of complex I concentration in muscle mitochondria of crossbred steers with high and low residual feed intake. J. Anim. Sci. 86 E-Suppl. 2: 60.

Ellenberger, M. A., D. E. Johnson, G. E. Carstens, K. L. Hossner, M. D. Holland, T. M. Nett, and C. F. Nockels. 1989. Endocrine and metabolic changes during altered growth rates in beef cattle**.** J. Anim. Sci. 67:1446-1454.

Elstien, D. 2002. Estimating farm animals feed efficiency. www.ars.usda.gov/is/pr/2002/021224.htm

Ferrell, C. L., R. H. Kohlmeier, J. D. Crouse, and H. Glimp. 1978. Influence of dietary energy, protein, and biological type of steer upon rate of gain and carcass characteristics. J. Anim. Sci. 46:255-270.

Geary, T. W., E. L. McFadin, M. D. MacNeil, E. E. Grings, R. E. Short, R. N. Funston, and D. H. Keisler. 2003. Leptin as a predictor of carcass composition in beef cattle. J Anim Sci 81: 1-8.

Golden, J. W., M. S. Kerley, and W. H. Kolath. 2008. The relationship of feeding behavior to residual feed intake in crossbreed Angus steers fed traditional and no roughage diets. J. Anim. Sci. 86:180-186.

Gomez R. R., B. M. Bourg, Z. D. Paddock, G. E. Carstens, P. A. Lancaster, R. K. Miller, L. O. Tedeschi, D. K. Lunt, S. A. Moore, and D. S. Delaney. 2007. Evaluation of feed efficiency in Santa Gertrudis steers and relationship with temperament and feeding behavior. J. Anim. Sci. 85 Suppl. 454-455.

Gorocica-Buenfil, M. A., and S. C. Loerch. 2005. Effect of cattle age, forage level, and corn processing on diet digestibility and feedlot performance**.** J. Anim. Sci. 83: 705-714.

Harvey, R. W., J. D. Armstrong, E. P. Heimer, and R. M. Campbell. 1993. Feedlot performance, carcass characteristics, hormones, and metabolites in steers actively immunized against growth hormone releasing factor. J. Anim. Sci. 71:2853-2859.

Herd, R. M., J. A. Archer, P. F. Arthur, E. C. Richardson, J. H. Wright, K. C. P. Dibley and D. A. Burton. 1997. Performance of progeny of high vs. low net feed conversion efficiency cattle. Proc. Assoc. Advmt. Anim. Breed Genet. 12:742-745.

Herd, R. M., E. C. Richardson, R. S. Hegarty, R. T. Woodgate, J. A. Archer, and P. F. Arthur. 1998. Pasture intake by high versus low net feed efficient Angus cows. Anim. Prod. Aust. 22:137–140.

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

Herd, R. M., R. S. Hegarty, R. W. Dicker, J. A. Archer and P. F. Arthur. 2002a. Selection for residual feed intake improves feed conversion in steers on pasture. Aust. Soc. Anim. Prod. Proc. 24: 85-88

Herd, R. M., P. F. Arthur, J. A. Archer, and D. J. Johnston. 2002b. IGF-I is associated with genetic variation in key production traits in young angus cattle. Anim. Prod. Aust. 24: 313.

Herd, R. M., J. A. Archer, and P. F. Arthur. 2003. Reducing cost of beef production through genetic improvement in residual feed intake: Opportunity and challenges to application. J. Anim. Sci. 81(E. Suppl. 1):E9-E17.

Homm, J. W., L. L. Berger, and S. L. Rodriguez-Zas. 2007. Factors affecting residual feed intake in feedlot steers. J. Anim. Sci. 85 Suppl. 454.

Iqbal, M., N. R. Pumford, K. Lassiter, Z. Tang, T. Wing, M. Cooper, and W. Bottje. 2004. Low feed efficient broilers within a single genetic line exhibited higher oxidative stress and protein expression in breast muscle with lower mitochondrial complex activity. Poult. Sci. 83:474-484.

Iqbal, M., N. R. Pumford, Z. X. Tang, K. Lassiter, C. Ojano-Dirain, T. Wing, M. Cooper, and W. Bottje. 2005. Compromised liver mitochondrial function and complex activity in low feed efficient broilers are associated with higher oxidative stress and differential protein expression. Poult. Sci. 84: 933-941.

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

Kolath, W. H. 2006. The relationship between mitochondria and RFI. Ph. D. Dissertation. University of Missouri-Columbia.

Kolath, W. H., M. S. Kerley, J. W. Golden, and D. H. Keisler. 2006. The relationship between mitochondrial function and residual feed intake in Angus steers. J. Anim. Sci. 84:861–865.

Lalman, D. L., J. E. Williams, B. W. Hess, M. G. Thomas, and D. H. Keisler. 2000. Effect of dietary energy on milk production and metabolic hormones in thin, primiparous beef heifers**.** J. Anim. Sci. 78: 530-538.

Lancaster, P. A., G. E. Carstens, J. G. Lyons, T. H. Welsh Jr., R. D. Randel, and T. D. Forbes. 2007. Characterization of residual feed intake and relationship with serum insulin-like growth factor-I. J. Anim. Sci. 85 Suppl. 665.

Lancaster, P. A., G. E. Carstens, F. R. B. Ribeiro, M. E. Davis, J. G. Lyons, and T. H. Welsh, Jr. 2008. Effects of divergent selection for serum insulin-like growth factor-I concentration on performance, feed efficiency, and ultrasound measures of carcass composition traits in Angus bulls and heifers. J. Anim. Sci. 86: 2862-2871.

Lancaster, P. A., G. E. Carstens, F. R. B. Riberio, L. O. Tedeschi, and D. H. Crews Jr. 2009. Characterization of feed efficiency traits and relationships with feeding behavior and ultrasound carcass traits in growing bulls. J. Anim. Sci. 87:1528-1539.

Lassiter, K., C. Ojano-Dirain, M. Iqbal, N. R. Pumford, N. Tinsley, J. Lay, R. Liyanage, T. Wing, M. Cooper, and W. Bottje. 2006. Differential expression of mitochondrial and extramitochondrial proteins in lymphocyte of male broilers with low and high feed efficiency. Poult. Sci. 85: 2251-2259.

Long, C. R., T. C. Cartwright, and H.A. Fitzhugh, Jr. 1975. Systems analysis of sources of genetic and environmental variation in efficiency of beef production: cow size and herd management. J Anim. Sci. 40:409-420.

Lutz, T. R. and T. S. Stahly. 2003. Quantitative relationship between mitochondrial bioenergetics an efficiency of animal growth. J. Anim. Sci. 81 Suppl. 1. 141.

McDonagh, M. B., R. M. Herd, E. C. Richardson, V. H. Oddy, J. A. Archer and P. F. Arthur. 2001. Meat quality and the calpain system of feedlot steers following a single generation of divergent selection for residual feed intake. Aust. J. Exp. Agric. 41:1013-1021.

Moore, K. L., D. J. Johnston, H-U. Graser, and R. M. Herd. 2003. Genetic and non-genetic effects on plasma insulin-like growth factor-I (IGF-I) concentrations and

production traits in Angus cattle. Assoc. Advmt. Anim. Breed. Genet. 15:222-226

Moore, K. L., D. J. Johnston, H-U. Graser, and R. M. Herd. 2005. Genetic and phenotypic relationships insulin-like growth factor-I (IGF-I) and net feed intake, fat, and growth traits in Angus beef cattle. Aust. J. Agric. Res. 56:211-218.

Morgan, J. B., T. L. Wheeler, M. Koohmaraie, J. D. Crouse, and J. W. Savell. 1993. Effect of castration on myofibrillar protein turnover, endogenous proteinase activities, and muscle growth in bovine skeletal muscle. J Anim Sci 71: 408-414.

Mueller, A. L., W. H. Kolath, J. W. Golden, and M. S. Kerley. 2004. Evaluation of RUP amino acid levels on lean tissue growth and carcass composition of beef steers fed a roughage-free diet. J. Anim. Sci. 83(Suppl. 1):116. (Abstr.)

Neel, J. P. S., J. P. Fontenot, W. M. Clapham, S. K. Duckett, E. E. D. Felton, G. Scaglia, and W. B. Bryan. 2007. Effects of winter stocker growth rate and finishing system on: I. Animal performance and carcass characteristics. J. Anim. Sci. 85:2012-2018.

Nieuwhof, G. J., J. A. M. van Arendonk, H. Vos, and S. Kover. 1992. Genetic relationship between feed intake, efficiency and production traits in growing bulls, growing heifers and lactating heifers. Livest. Prod. Sci. 32:189-202.

Nkrumah, J. D., J. A. Basarab, M. A. Price, E. K. Okine, A. Ammoura, S. Guercio, C. Hansen, C. Li, B. Benkel, B. Murdoch, and S. S. Moore. 2004. Different measures of energetic efficiency and their phenotypic relationships with growth, feed intake, and ultrasound and carcass merit in hybrid cattle**.** J. Anim. Sci. 82: 2451-2459.

Ojano-Dirain, C., M. Toyomizu, T. Wing, M. Cooper, and W. G. Bottje. 2007. Gene expression in breast muscle and duodenum from low and high feed efficient broilers. Poult. Sci. 86:372-381.

Ojano-Dirain, C., N.R. Pumford, M. Iqbal, T. Wing, M. Cooper, and W.G. Bottje. 2005. Biochemical evaluation of mitochondrial respiratory chain in duodenum of low and high feed efficient broilers. Poult. Sci. 84: 1926-1934.

Perry, T. W., D. R. Shields, W. J. Dunn, and M. T. Mohler. 1983. Protein levels and monensin for growing and finishing steers. J. Anim. Sci. 57:1067-1076.

Ribeiro, F. R. B., G. E. Carstens, P. A. Lancaster, L. O. Tedeschi, and M. E. Davis. 2007. Relationship of feed efficiency with carcass and non-carcass tissue composition in Angus bulls and heifers. J. Anim. Sci. 85 Suppl. 455.

Richardson, E. C., R. M. Herd, P. F. Arthur, J. Wright, G. Xu, K. Dibley, and V. H. Oddy. 1996. Possible physiological indicators for net feed conversion efficiency in beef cattle. Proc. Aust. Soc. Anim. Prod. 21:103-106.

Richardson, E. C., R. M. Herd, J. A. Archer, R. T. Woodgate, and P. F. Arthur. 1998. Steers bred for improved feed efficiency ate less for the same feedlot performance. Anim. Prod. Aust. 22:213-216.

Richardson, E. C., R. M. Herd, V. H. Oddy, J. M. Thompson, J. A. Archer, and P. F. Arthur. 2001. Body composition and implication for heat production of Angus steer progeny of parents selected for and against residual feed intake. Aust. J. Exp. Agric. 41:1065-1072.

Richardson, E. C., and R. M. Herd. 2004. Biological basis for variation in residual feed intake in beef cattle. 2. Synthesis of results following divergent selection. Aust. J. Exp. Agric. 44:431–440.

Richardson, E. C., R. M. Herd, J. A. Archer, and P. F. Arthur. 2004. Metabolic differences in Angus steers divergently selected for residual feed intake. Aust. J. Exp. Agric. 44:441-452.

Sandelin, B. A., A. H. Brown Jr., C. Ojano-Dirain, M. Iqbal, M. A. Brown, W. O. Herring, M. Akin, Z. B. Johnson, and R. T. Baublits. 2004. Assessment of respiratory chain protein expression in muscle mitochondria in Angus steers with low and high feed efficiency. J. Anim. Sci. 82, Suppl. 1:416.

Sandelin, B. A., A. H. Brown Jr., C. Ojano-Dirain, M. Iqbal, W. G. Bottje, M. A. Brown, W. O. Herring, M. Akin, Z. B. Johnson, and R. T. Baublits. 2005. Different measures of energetic efficiency, ultrasound and carcass merit and their relationship with mitochondrial activity in Angus cattle. J Anim. Sci. 83, Suppl. 2:5.

Snedecor, G. W., and W. G. Cochran. 1989. Statistical Methods. 8th ed. Iowa State University, Ames, IA.

Solís, J. C., F. M. Byers, G. T. Schelling, and L. W. Greene. 1989. Anabolic implant and frame size effects on growth regulation, nutrient repartitions and energetic efficiency of feedlot steers**.** J. Anim. Sci. 67: 2792-2801.

SAS Institute, Inc. 2003. SAS user's guide: Statistics, SAS Institute, Inc., Cary, NC. Version 9.1.

Thonney, M. L., E. K. Heide, D. J. Duhaime, A. Y. M. Nour, and P. A. Oltenacu. 1981. Growth and feed efficiency of cattle of different mature sizes. J. Anim. Sci. 53: 354-362.

Voet D., and J. G. Voet. 2004. Biochemistry, Third Edition.

Wang, Z., J. D. Nkrumah, C. Li, J. A. Basarab, L. A. Goonewardene, E. K. Okine, D. H. Crews Jr., and S. S. Moore. 2006. Test duration for growth, feed intake, and feed efficiency in beef cattle using the Growsafe system. J. Anim. Sci. 84:2289-2298.

Wulf, D. M., J. B. Morgan, J. D. Tatum, and G. C. Smith. 1996. Effects of animal age, marbling score, calpastatin activity, subprimal cut, calcium injection, and degree of doneness on the palatability of steaks from limousin steers. J. Anim. Sci. 74:569-576.

Yambayamba, E. S. K., M. A. Price, and G. R. Foxcroft. 1996. Hormonal status, metabolic changes, resting metabolic rate in beef heifers undergoing compensatory growth. J. Anim. Sci. 74:57-60.

Yelich, J. V., R. P. Wettemann, H. G. Dolezal, K. S. Lusby, D. K. Bishop, and L. J. Spicer. 1995. Effect of growth rate on carcass composition and lipid partitioning at puberty and growth hormone, insulin-like growth factor-I, insulin, and metabolites before puberty in beef heifers. J. Anim. Sci. 73:2390–2405.

Yelich, J. V., R. P. Wettemann, T. T. Marston, and L. J. Spicer. 1996. Luteinizing hormones, growth hormone, insulin-like growth factor-I, insulin and metabolites before puberty in heifers fed to rates of gain. Domest. Anim. Endocrinol. 13:325-338.

VITA

Michael Patrick Davis was born in April 16, 1981 to Mike and Elaine Davis and grew up in Lamar, MO. Michael grew up on a diversified livestock and grain farm and had interest in both swine and beef cattle production. Based on these interests Michael attended the University of Missouri-Columbia and obtained a Bachelor of Science degree in Animal Science. While attending the University of Missouri-Columbia, Michael was a part of the Alpha Gama Sigma Fraternity and the University of Missouri Columbia meats and livestock judging teams. Upon completion of the degree at the University of Missouri-Columbia, Michael's interest for the cow-calf operation grew and Michael attended Oklahoma State University where Michael pursued a Master of Science in animal science under the direction of Dr. Bob Wettemann. Michael's research at Oklahoma State University dealt with the developing heifer and how nutrition influenced reproduction in beef cattle. While at Oklahoma State University Michael was a part of the animal science graduate students association. After completion of Masters of Science, Michael chose to pursue his interest for feed efficiency in beef cattle and pursue a Doctor of Philosophy degree at the University of Missouri Columbia under the direction of Dr. Monty Kerley. During this degree Michael's research interest were investigating how diet, residual feed intake and mitochondrial complex proteins are related to production traits and feed efficiency and carcass characteristics in beef cattle. Also during Michael's Doctor of Philosophy program Michael was part of the animal

science graduate student association. Upon completion of my Doctor of Philosophy program, Michael will take a post doctorial position at United States Department of Agriculture meat animal research station at Clay Center, Nebraska under the direction of Dr. Harvey Freetly.