[13] who led them through the depths?
Like a horse in open country,
they did not stumble;
[14] like cattle that go down to the plain,
they were given rest by the Spirit of the LORD.
This is how you guided your people
to make for yourself a glorious name. Isaiah 63:13-14

[2] Great are the works of the LORD;
they are pondered by all who delight in them.
[3] Glorious and majestic are his deeds,
and his righteousness endures forever.
[4] He has caused his wonders to be remembered;
the LORD is gracious and compassionate. Psalm 111:2-4

University of Alberta

GENETICS OF FEED EFFICIENCY AND FEEDING BEHAVIOR IN CROSSBRED BEEF STEERS WITH EMPHASIS ON GENOTYPE-BY-ENVIRONMENT INTERACTIONS

by

Obioha Nnamdi Durunna

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Dedication

This work is dedicated to the Almighty God for His favor, mercies and guidance throughout this project.

Abstract

This study examined whether crossbred steers had different production, feed efficiency and feeding behavior performances when they were fed a grower or finisher diet or both, in successive feeding periods. Major feed efficiency traits were residual feed intake (RFI) and gain to feed ratio (G:F) while feeding behavior traits were feeding duration (FD), head-down time (HDT) and feeding frequency (FF). Some steers received a grower diet in the first feeding period and a finisher diet in the second period (feed-swap); the control groups received only the grower or finisher diet in both periods. Compared to the control groups, about 7% more steers in the feed-swap group changed their RFI performance by 0.5 SD by the second period. Using steers in the feed-swap group (n = 331), the study observed greater ($P < 0.05$) FD, HDT and FF when the steers received the grower diet. Genetic correlations between the two feeding periods for this group were 0.78, 0.80, 0.78, 0.50, 0.91, 0.93 and 0.94 for DMI, ADG, G:F, RFI, FD, HDT, and FF, respectively. The genetic correlations may indicate the existence of genotype-by-environment interaction for DMI, ADG, RFI and G:F. The heritability estimates for the feed-swap group were greater in the grower-fed period for FD (0.25 vs 0.14) and HDT (0.14 vs 0.09) but were greater in the finisher-fed period for ADG (0.23 vs 0.08), DMI (0.34 vs 0.15), RFI (0.42 vs 0.08), G:F (0.40 vs 0.14) and feeding frequency (0.59 vs 0.56). The results indicate that the RFI, G:F, ADG and DMI measured on a grower or finisher diet may be considered as different traits for beef cattle genetic evaluations.

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List of Abbreviations

ADF: Acid detergent fiber

ADG: Average daily gain

AFD: Assigned feed disappearance

AGRP: Agouti-related peptide

ATP: Adenosine triphosphate

CCK: Cholecystokinin

CG: Contemporary group

CIM: Composite interval mapping

CP: Crude protein

DM: Dry matter

DMI: Dry matter intake

EBV: Estimated breeding value

EFI: Expected feed intake

FD: Feeding duration

FDR: False discovery rate

FE: Feed efficiency

FF: Feeding frequency

FP1: Feeding period 1

FP2: Feeding period 2

FR: Feeding rate

FSD: Feed station days

G:F: Gain to feed ratio

GE: Gross energy

GEI: Genotype-by-environment interaction

GIT: Gastrointestinal tract

HDFD: Head-down per feeding duration

HDT: Head-down time

HDV: Head-down per visit

HIF: Heat increment of feeding

IGF-1: Insulin-like growth factor 1

KR: Kleiber ratio

LH: Lateral hypothalamic area

MCH: melanin-concentrating hormone

ME: Metabolizable energy

MWT: Metabolic mid-weight

NDF: Neutral detergent fiber

NPY: Neuropeptide Y

PE: Permanent environment

PIC: Polymorphism information content

PVN: Paraventricular hypothalamic nucleus

QTL: Quantitative trait loci

RFI: Residual feed intake

RFID: Radio frequency identification

RGR: Relative growth rate

SNP: Single nucleotide polymorphism

SOTWT: Start of test weight/ Initial weight on test

TMR: Total mixed ration

UBF: Ultrasound back fat

UMB: Ultrasound marbling

UREA: Ultrasound rib eye area

VFA: Volatile fatty acids

CHAPTER 1

GENERAL INTRODUCTION

1.1 Introduction

Residual feed intake (**RFI**) also referred to as net feed efficiency is the difference between the actual intake and expected intake of individual animals based on body maintenance, production and body composition (Basarab et al. 2003; Nkrumah et al., 2004; Durunna et al., 2011). Due to its independence of growth, body maintenance or any other energy sink such as body composition, RFI is the preferred measure of feed efficiency (**FE**). The selection of animals based on their RFI status can increase total production efficiency of the beef industry especially the cow-calf sector. Herd et al. (2003) reported that females that were feed-efficient as weanlings consumed less feed as mature cows. Richardson et al. (1998) also reported that steers from highly efficient (low RFI) parents grew faster with less feed per unit body gain than those from inefficient parents.

Other measures of FE include gain to feed ratio (**G:F**), Kleiber ratio (**KR**) and relative growth rate (**RGR**). Conventionally, FE measures are input-output ratios. For example, the G:F ratio is the ratio of average daily gain to dry matter intake. The KR and RGR are not traditional measures of FE but are also considered as efficiency traits.

Most cattle are fed different diets or rations through their production life cycle. These diets may contain different proportions of forage and grains. In

Canada, most weaned calves (destined for the feedlot) are fed rations containing some roughage as a grower diet. This grower diet would improve the frame of the young calves (at a lower rate of gain) before they are placed on finishing diets. The finishing diets in the feedlot sector usually contain at least 60% of grain. These diets are formulated such that the calves reach the target finishing weight and desired level of fatness.

The rising cost of feed increases the total production cost in the beef cattle industry warranting the need for feed efficient animals to reduce costs (Herd et al., 2003; McDonald et al., 2010). Continued research on FE is encouraged by the reports of several studies, which indicated that these FE traits have a low to moderate heritability (Archer et al., 1998; Herd and Bishop, 2000; Arthur et al., 2001; Arthur et al., 2001a; Schenkel et al., 2004). Therefore, genetic improvement is possible on these traits through genetic selection.

Despite the long list of studies using different diets (Baker et al., 2002; Nkrumah et al., 2004; Brown et al., 2008; Meyer et al., 2008; Crowley et al., 2010), few studies have looked at successive feeding trials where the animals received a different diet within each trial. Possible factors limiting such multiple feeding trials may include narrow-focused research objectives, restrictive experimental designs, or high cost. However, conducting multi-environment FE trials on cattle will be more informative than single FE evaluations. Such studies will inform us about the consistency of FE over the animal's production life and across feeding regimes thereby enhancing our understanding on the subject.

Improving FE in the cow-calf and feedlot sector will reduce production cost for beef producers. About $230,000/day is possible in the feedlot sector in Canada (about 2.1 million cattle-head in Canada) if feedlot animals were more efficient by 1kg d^{-1} at a feed-cost of $0.11/kg. Reports of Richardson et al. (1998) and Herd et al. (2003) indicated that low RFI weaner heifers were efficient at mature cow stages and produced more-efficient calves as well, therefore these savings may be possible through improving RFI in the beef industry.

In view of the fact that feedlot cattle consume more than one type of diet or ration before finishing, it is pertinent to understand whether the FE status of cattle change at different production phases. This was the major objective of this study i.e. whether individual cattle might have better performance in one feeding regime than the other. The identification of individuals and their genotypes that are sensitive to certain feeding regimes will enhance genetic selection in beef breeding programs.

In addition, this study has also investigated the relationships between feeding behavior and FE traits to test the potential of behavioral traits as indicator traits for FE. Studies on feeding behavior have recently attracted more attention because of the availability of the technology to monitor and measure such traits. Previously, subjective judgments were used to make calls on the phenotypes using video recordings (Huzzey et al., 2006). This kind of assessment may be inconsistent, laborious and may introduce biases or random errors into the experimental data. The advent of automatic feeders that are able to record

individual feed intake and measures of feeding behavior avails us the opportunity to optimize the data and resources on hand.

The research conducted in this thesis was performed using beef production timelines. Several effects such as age, season, body weight, body composition were confounded with the feeding periods and may be a limitation of this study. Age, in particular, was considered to have possible influence on the animal's FE status because developmental biology indicates that certain expressions of genes occur at different developmental stages (Scherer et al., 1981).

The influence of diet, age or body weight on FE implies the existence of an interaction effect caused by these factors. The dependency of some genetic performances on the environment (such as diet, age or body weight) may further complicate our understanding about the biology of FE traits. In the presence of interactions, genotypes may have different performances in different environments. Unfortunately, the information on interactions between genes and dietary environments in beef cattle is limited or unavailable. In some genetic models, these interactions were often assumed insignificant and hence were ignored. In most of these cases, these assumptions were used to simplify the model equations or in cases where the experimental design could not accommodate interaction effects. Presence of interactions may manifest as genetic performances having opposite direction of effects in different environments (Lillehammer et al., 2008) thereby posing a problem for genetic improvement of traits in general. Predicting performance would also be difficult, thereby reducing the confidence in the animals selected as replacements.

Different approaches exist to examine the differential effects and presence of genes in different environments. In order to dissect the genetic architecture of FE and feeding behavior, genotype-by-environment interactions (**GEI**) are important. I considered a bottom-up approach in which multi-environment feeding trials (Boer et al, 2007) were conducted to generate data over three years (from 2006 to 2009) using two different cattle diets followed by a genetic analysis. A phenotypic analysis was first conducted to determine if steers fed the grower and finisher diets (successively) reranked in their FE profiles from one period to the other. A genetic analysis followed in order to determine if the reranking occurred at the estimated breeding value (**EBV**) level in the two diet environments. Finally, different groups of steers were used to determine the genetic correlation when steers were fed only the finisher diet in the two feeding periods. We used the genetic correlation (Falconer and Mackay, 1996) between the traits measured in each feeding regime as a measure of GEI.

1.2 Research hypotheses

In order to accommodate the objectives of this research the hypotheses were as follows:

1.2.1. Steers do not change their feed efficiency ranking from one period to the other when fed either grower or finisher diets, successively or when fed the same diet in two periods.

1.2.2. Genotype-by-environment interactions do not exist for intake, growth and feed efficiency traits in steers fed the grower and finisher diets.

1.2.3. The phenotypic and genetic parameters associated with feeding behavior of steers are similar from the Fall-Winter season to the Winter-Spring season irrespective of the diet fed to the steers.

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CHAPTER 2

LITERATURE REVIEW

2.1 Feed efficiency

Feeds provided to animals constitute a major cost to livestock production accounting for at least 50% of these costs (Kennedy et al., 1993). Cost of feed constitutes about 60% to 70% of egg production costs (Luiting, 1990; Aggrey et al., 2010) and 50% to 85% of pork production costs (McGlone and Pond, 2003). Up to 75% of the total energy intake in beef cows is used for body maintenance alone (Ferrell and Jenkins, 1985; Montano-Bermudez et al., 1990) whereas this value is up to 85% for the cow breeding herd (Montano-Bermudez et al., 1990). Improving the efficiency of feed utilization is an important objective for livestock producers. Measures of feed efficiency (**FE**) include gain to feed ratio (**G:F**) or its reciprocal feed conversion ratio (**FCR**), Kleiber ratio (**KR**), relative growth rate (**RGR**) and residual feed intake (**RFI**). While G:F or FCR are traditional measures of FE, KR and RGR are not, but have been adopted as measures of efficiency (Arthur et al., 2001; Nkrumah et al., 2004).

Being ratio traits, G:F or FCR and KR may have some limitations. The distribution of the phenotypes may have some slight deviations from normality (Yang et al., 2008). Predicting the future response in the trait may also be difficult given that some realized heritability estimates have been lower in swine than the use of covariance among relatives (Gunsett, 1984). In addition, differential selection pressure may be applied to either the numerator or the denominator

component of the trait (Nkrumah et al., 2007), thereby applying more selection pressure to the trait with the higher genetic variance or heritability.

2.1.1 Feed conversion ratio / Gain to feed ratio

Feed conversion ratio and gain to feed ratio are reciprocal measures of feed efficiency, relating feed intake to the production output or vice versa. In the feedlot sector, this would be the ratio of the average daily feed intake to the average daily gain and vice versa. The FCR describes the amount of feed utilized for each kg of body gain. Even though FCR does not partition energy into requirements for growth and for maintenance (Carstens and Tedeschi, Unpublished), animals with lower FCR values utilize more proportion of feed for body gain than for maintenance (Veerkamp and Emmans, 1995).

In crossbred steers, FCR has phenotypic correlations of -0.69 and 0.20 with ADG and MWT while having genetic correlations of -0.59, 0.06, 0.30, -0.29 with ADG, MWT, daily DMI and ultrasound back-fat, respectively (Nkrumah et al., 2007). Genetic correlations also exist between FCR and body composition as well as with appetite (Hoque et al., 2009a). Moderate direct heritability estimates for FCR (0.24 to 0.30) have been reported (Crowley et al., 2010). Arthur et al. (2001) showed that high genetic (-0.62) and phenotypic correlations (-0.74) exist between FCR and ADG while feed intake has positive phenotypic (0.41) and genetic (0.54) correlations with ADG. Other studies have reported similar correlations (Nkrumah et al., 2004; Crews, 2005; Lancaster et al., 2009).

The relationship among FCR, feed intake and body gain implies that two animals may have the same FCR but still have different levels of feed intake and body gain. These correlations (both phenotypic and genetic) indicate that selection for lower FCR may translate to selection of larger animals as a result of selecting individuals with higher mature weights and faster growth. Nkrumah et al. (2007) reported that FCR is confounded with maturity patterns. Arthur et al. (1999) concluded that FCR might have a low correlation with feed efficiency if the cowherd is included. The unwanted correlated response associated with FCR (in larger animals) will balance or trade-off the higher gains from calves since the cows consume more feed. Selecting higher producing animals is also an indirect selection for individuals with low FCR and there may be no need to measure the intake of such animals (Arthur et al., 1999).

2.1.2 Kleiber ratio (KR)

This is the ratio of average daily gain to the metabolic weight. The KR is a measure of growth efficiency and is independent of feed intake (Hoque et al., 2009a). Therefore, it can be used in situations where feed intake measurements are not available. Due to its high correlation with feed conversion ratio, KR is used as an indirect measure of FE (Eskandarinasab et al., 2010). Because maintenance requirement is a function of the body weight, this FE measure identifies animals with higher production relative to their body weight. Animals with higher KR values indicate higher efficiency due to lower maintenance

requirements. Such animals have more production output (e.g. Kg of average daily gain) per maintenance input.

While KR has zero or low correlations with RFI (-0.004), MWT (-0.03), ultrasound (-0.05 to 0.25) and carcass traits (-0.16 to 0.11), high phenotypic correlations exist between KR with ADG (0.85), FCR (-0.73) and relative growth rate (0.96) in crossbred cattle (Nkrumah et al., 2004). Crowley et al. (2010) reported phenotypic correlations of 0.59, -0.21, 0.84, -0.80 and 0.97 for KR with feed intake, MWT, ADG, FCR and relative growth rate, respectively. They also reported no genetic correlations between KR and feed intake whereas low to moderate genetic correlations were reported for KR with MWT (-0.34), ADG (0.75), FCR (-0.75), RFI (0.15) but high genetic correlation with RGR (0.96). Low genetic variances and heritability estimates (0.07 to 0.16) have been reported for KR in sheep (Eskandarinasab et al., 2010). Crowley et al. (2010) reported direct heritability estimates of 0.24 to 0.31 in Irish beef bulls.

2.1.3 Relative growth rate

Relative growth rate is the rate of growth of an animal relative to its weight at the end of the measuring period (Brown, Jr. et al., 1988). It is the percentage gain per day (Winder et al., 1990). The RGR is similar to the absolute growth rate (Fitzhugh, Jr. and Taylor, 1971; Brown, Jr. et al., 1988) except that the natural logarithms of the initial and final weights are used to transform geometric progressions into linear progressions. Due to the low genetic correlations between body weight and RGR (Fitzhugh, Jr. and Taylor, 1971), RGR could be used to

select for more efficient animals (faster growing) without the associated increase in body size.

The RGR has phenotypic correlations of 0.18, -0.23, 0.72, -0.75 and -0.04 with DMI, MWT, ADG, FCR and RFI, respectively (Nkrumah et al., 2004). Direct heritability estimates for RGR ranged from 0.22 to 0.33 (Winder et al., 1990; Crowley et al., 2010).

2.1.4 Residual feed intake

Residual feed intake (RFI) also known as net feed intake is the difference between the actual feed intake and the expected feed intake based on the level of production and estimated maintenance requirements. The two major components of the index for RFI are the requirements for maintenance and production but the inclusion of other energy sinks (Crews, 2005) such as body composition (Basarab et al., 2003) has been advocated and is being implemented in the calculation of RFI (Schenkel et al., 2004; Durunna et al., 2011). The index accounts for the different levels of maintenance requirements and production outputs for different animals through a linear regression approach.

Kennedy et al. (1993) reported that information from RFI is similar to that generated from a selection index that incorporated feed intake and growth as two traits selection. The RFI calculated using phenotypic regression may not be genetically independent of production. In order to eliminate the correlation, Kennedy et al. (1993) suggested that RFI should be calculated from genetic regression, which would attribute any observed genetic variation solely to feed

efficiency. The use of phenotypic RFI for genetic selection should have minimal effects on other production traits since the phenotypic and genetic correlations between genetic and phenotypic RFI are high, ranging from 0.92 to 0.98 (Nkrumah et al., 2007; Hoque et al., 2009a).

The use of RFI may be associated with some demerits. The automatic feeding equipment used to measure individual feed intake is expensive and may need routine maintenance. Apart from cost associated with measuring feed intake, selection of low RFI animals may have negative effects on body composition such as back fat thickness (Robinson and Oddy, 2004). Another unattractive feature of RFI involves its positive correlations with measures of activity, which may imply that active animals may not be selected (Cammack et al., 2005; Rauw et al., 2006b; Nkrumah et al., 2007b). However, the use of RFI as the feed efficiency measure of choice would benefit the cattle industry in several ways. Comparisons among breeds or individuals within a breed are possible since phenotypic RFI has no correlation with ADG and metabolic mid-weight. If selected as replacements, low RFI animals may reduce feed cost by 10% (Herd et al., 2003) manure production by 8%-16% (Nkrumah et al., 2006) and methane emission by 24%-28% (Nkrumah et al., 2006; Hegarty et al., 2007).

2.2 RFI in other species

The use of RFI as the measure of feed efficiency has been adopted in other species. In pigs, Gilbert et al. (2007) studied the relationship between RFI and carcass traits or meat quality traits. They reported positive genetic correlations

between RFI and back-fat thickness (0.44) but negative correlations with lean meat content (-0.55). Cai et al. (2008) and Boddicker et al. (2010) reported that progeny of selected low RFI lines had lower feed intake compared to a randomly allocated control line. Rauw et al. (2006a, b) studied the relationship between feeding behaviors and RFI and reported that the observed differences in RFI values were due to differences in intake rather than differences in feeding behaviors.

Other studies identified SNPs that were associated with RFI in pigs (Fan et al., 2010). Bunter et al. (2010) reported that IGF-1 was associated with more efficient pigs while Hoque et al. (2009b) reported weak genetic correlations (-0.20 to 0.16) between the two traits in pigs as well. Sheep have also received attention regarding RFI (Cammack et al., 2005; Knott et al., 2008). Cammack et al. (2005) reported a low heritability estimate (0.11) for RFI. They also reported genetic and phenotypic correlations of 0.61, between daily feed intake and RFI. Knott et al., (2008) calculated RFI in sheep using different models. They suggested that including a measure of body composition was necessary and would reflect a more accurate biological efficiency.

Even though few studies have focused on RFI in poultry, the trait has been reported to be moderately heritable in broilers (Aggrey et al., 2010). Su et al. (2006) investigated the relationship between feather pecking and RFI and reported that better RFI was associated with low feather pecking. Studies on RFI in aquaculture are very few. Differences in RFI among strains of the rainbow trout have been examined (Silverstein et al., 2005; Silverstein, 2006; Grima et al.,

2008) while Kause et al. (2006) examined the influence of diet on the resulting genetic parameters. In addition, mice have also received some attention with regards to the study of RFI. Being model organisms, mice have been used to throw some light into understanding the biological mechanisms behind feed efficiency (Archer and Pitchford, 1996; Archer et al., 1998). Other studies have used mice to investigate energy balance (Moody et al., 1999; Pomp and Nielson 1999; Allan et al., 2000). Moody et al. (1999) reported some QTL with a significant effect on heat loss while Allan et al. (2000) suggested the involvement of ribosomal protein L3 (RPL3) in the regulation of energy balance.

2.3 Genetic basis of RFI

Genetic improvement in a trait depends on the existing magnitude of variation in the trait within a population as well as the proportion of this variation that can be passed on from parents to offspring. Phenotypic and genetic variation exist for RFI in both growing and adult cattle (Arthur et al., 2001; Arthur et al., 2001a; Basarab and Crews, 2004) and among breeds (Schenkel et al., 2004; Crowley et al., 2010). Reports from cattle at different ages and stages of production indicate that genes account for about 14% to 58% (Fan et al., 1995; Robinson and Oddy, 2004; Schenkel et al., 2004; Crowley et al., 2010) of the total phenotypic variation in RFI. The range of the heritability shows that moderate proportion of the effects can be passed from parents to their offspring. For some of the low heritability estimates, the small sample size may have affected the accuracy of the estimates (Veerkamp et al., 1995) and/ or higher measurement error (Herd et al., 2003).

Recent whole genome association studies support the genetic basis of RFI. These studies have shown that some SNP are associated with RFI (Nkrumah et al., 2007a; Sherman et al., 2008). Given that the SNPs associated with RFI were found in different regions of the genome, Moore et al. (2009) inferred that many polymorphic variants might be contributing to the variation in RFI. Furthermore, several SNPs detected in functional regions of the genomes indicate the potential effect of such regions on RFI. Barendse et al. (2007) reported that the proximity of some SNPs to unique micro-RNA might suggest that such micro-RNA have regulatory functions specifically for RFI. Other SNPs were detected in introns and exons of genes involved in energy usage, apoptosis, cell progression, ion channels and flux, transcription, translation growth, development, appetite, body-mass homeostasis, etc. The multiple processes that are thought to affect RFI may bring up a complex network of genes. Some of the genes may have pleiotropic effects on several traits because similar QTL locations that influence RFI, DMI, FCR and ADG simultaneously have been detected (Nkrumah et al., 2007a).

2.4 Reasons for differences in feed efficiency in cattle

Apart from systematic effects (such as quantity and type of feed, breed, management, environment, etc.) that may influence feed efficiency of animals, individuals from the same breed still differ in their feed efficiency performance (Herd et al., 2004). Possible differences among individuals for feed efficiency may be due to biology or physiology even if they have similar weights. However, the majority of the biological mechanisms behind these differences in feed

efficiency between animals with similar growth rate and body weight are poorly understood. A better understanding of the physiological and biological mechanisms may promote the identification of easier-to-measure traits that may be used as indicators of feed efficiency and thus reduce the need for feed intake measurements.

Arthur et al. (1999) and Herd et al. (2004) discussed major contributors to the differences in RFI. These factors may be classified into variations due to feed intake, digestion and dry matter digestibility, energy partitioning, body composition and metabolism, visceral tissue, ion transport and mitochondrial respiration. Others include physical activities and feeding pattern as well as thermoregulation

2.4.1 Feed intake

Daily feed intake in cattle may be up to 4% equivalent of body weight and it is the visible factor driving the quest for feed efficient animals. Differences between the most efficient and least efficient animals could be up to 3.77kg/day (Basarab et al., 2003). Such differences could translate to daily savings or costs of $0.41/animal (as fed) on a finishing phase at $0.11/kg or $0.26/animal on a grower diet at $0.07/ kg.

Animals classified into the low, medium or high RFI groups may have similar average age, weight or body composition but different levels of feed intake. These differences in feed intake among these groups are consistent across several studies with the least efficient animal (high RFI) having a significantly greater DMI than

animals in either the medium or low RFI groups. Nkrumah et al. (2007) reported steers' average intake of 9.53kg/d, 10.56kg/d and 11.63kg/d, for the low, medium and high RFI-classes, respectively; Crowley et al. (2010) also reported similar phenotypes for the RFI-classes while Lancaster et al. (2009) reported DMI of 8.76kg/d, 9.48kg/d and 10.34kg/d for the low, medium and high RFI classes in heifers.

2.4.2 Digestion and dry matter digestibility

Digestibility of feed fed to cattle is determined by the amount consumed, digestibility of the feed itself and the passage rate of the feed through the gastrointestinal tract (**GIT**). Retention time of feed in the gut is positively correlated with digestibility (Colucci et al., 1982) and may be under genetic control (Hegarty, 2004). Even though DMI has a positive correlation with passage rate, it has a negative relationship with retention time (Colucci et al., 1982; Melaku et al., 2005). Basarab et al. (2003) reported that extra feed intake might cause lower rates of metabolism of the extra feed ingested, heavier visceral organ weights and higher heat increment of feeding (HIF).

Given the correlation between feed intake and RFI, there should be differences among RFI groups for dry matter digestibility. Increased intake above maintenance affects digestibility negatively (Herd et al., 2004) thereby affecting the proportion of the gross energy available for maintenance and growth. This would reduce the amount absorbed by the GIT and increase the resultant waste products. The differences observed among RFI groups for digestibility were not

conclusive. While some studies have reported subtle to significant differences among groups (Channon et al., 2004; Nkrumah et al., 2006; Richardson et al., 1996), others have reported no statistically significant differences among the RFI classes (Richardson et al., 2004; Cruz et al., 2010). Reports have indicated that phenotypic and genetic variation exists for dry matter digestibility (Oddy, 1993; Richardson et al. 1996). Digestion may account for as much as 19% of the total variation in RFI (Herd et al., 2004; Richardson and Herd, 2004)

2.4.3 Energy partitioning

There is genetic variation in an animal's ability to partition energy for maintenance and for growth (Montano-Bermudez et al., 1990). In cattle, between- and within-breed differences also contribute to inherent variation that exists in the allotment of energy for maintenance or for growth (Jenkins et al., 1991; Jenkins and Ferrell, 2004). Maintenance requirements should fulfill the body needs for basal metabolism, necessary movements, body heat production, protein synthesis and turnover, fat synthesis and turnover and upkeep of body organs. Animals that use more feed intake for maintenance are likely to be inefficient than those that allot more for production purposes. Basarab et al. (2003) and Nkrumah et al. (2006) showed that inefficient animals expended a greater part of the extra metabolizable energy intake as heat and lesser quantity was retained.

Reports have shown that RFI has a linear relationship with the components in the energy system. In relation to digestible energy, RFI is positively (0.33) correlated with dry matter fecal output but negatively correlated with apparent

digestibility (-0.33) in steers (Nkrumah et al., 2006). These authors reported that high and medium RFI steers produced more feces than low RFI steers while low RFI steers produced less methane than medium or high RFI groups. They reported that DMI had a positive correlation with methane production (0.38) but negatively correlated with digestible energy (-0.46), metabolizable energy (-0.48) and retained energy (-0.53). Nkrumah et al. (2006) also showed that low RFI steers produce approximately 16,100 L/head less methane per year in comparison to high RFI steers. The authors suggested that mechanisms behind the differences in methane production may be due to the heritable nature of methane production. This may agree with Hackstein et al. (1996) who reported that the placement of methanogenic and non-methanogenic species on different phylogenetic trees may suggest that methane production was under genetic control. Other possible reasons for the differences in methane production include differences in digestibility and ruminal retention time.

RFI was positively correlated with heat production (0.68) and energy retention (0.67) in beef steers (Nkrumah et al., 2006). The study showed that low RFI steers produced less heat than high (21%) or medium (10%) RFI steers and had greater retained energy than the high or medium RFI steers. The lower heat production was probably due to lower feed intake from the low RFI steers. The study indicated that the medium and high groups had similar HIF, which were significantly higher than that of the low group. The HIF may account for about 9% of total variation in RFI (Herd et al., 2004).

The degree of maturity and the sex of the animal have also been linked to the ability to partition energy (Webster, 1993). Older animals tend to partition a major part of ME intake into fat rather than protein. Webster (1980) also reported that sex plays a role in efficiency given that bulls lose more heat (20%) than steers making them less efficient than steers at low levels of feed intake/energy but more efficient at feeding levels above maintenance.

2.4.4 Body composition and metabolism

Individuals with higher fat content may have lower maintenance requirements than lean animals (Arthur et al., 1999). This is because of the greater energetic efficiency (considering synthesis and degradation) of fat than protein. Protein is more energetically efficient to synthesize, however, its maintenance is more costly due to more frequent turnover. The proportion of energy lost as heat with protein accretion (53% energy) is much higher than the energy (24%) associated with fat accretion (Owens et al. 1995). DiConstazo et al. (1990) also showed that it costs over 9-fold more to maintain 1kg of protein (804 kJ) than a similar weight of fat (86kJ). Subcutaneous fat deposition is also more energetically efficient than intramuscular fat deposition (Herd et al., 2004).

The variation in body composition accounts for about 5% of the overall feed intake (Richardson et al., 1999; Basarab et al. 2003). Genetic variation may exist in the rate of degradation of protein (Arthur et al., 1999) given that lines selected for weaning weight (high and low lines) in lambs and cattle were negatively correlated with protein degradation even though both lines had similar rates of

protein synthesis (Oddy, 1993; Oddy et al. 1998). The efficiency of body weight gain is affected by the rate of water, protein and fat accretion (Basarab et al., 2003). The authors reported that low RFI steers accreted lesser body fat and energy than medium or high RFI steers but also had more body water accretion than the two groups. They also reported that high RFI steers retained about 1/3 of the extra energy as waste fat. The rate of fat deposition in low RFI steers was slower than in high RFI steers.

Richardson and Herd (2004) reported a possible genetic association between protein turnover and RFI. Some studies have also reported that inefficient animals (high RFI) were associated with high creatinine:urea ratio and high levels of plasma protein (Tatham et al., 2000; Richardson and Herd, 2004). Urea is an indicator of protein breakdown and has a negative relationship with protein accretion and lean growth. However, a positive genetic and phenotypic relationship between urea concentrations and RFI exists in steers (Richardson et al., 2004). It is known that feed intake is positively correlated with urea concentrations. Reduced protein degradation improves the rate of protein gain (Herd et al., 2004). The authors also reported a negative correlation (-0.33) between RFI and percent whole body protein relative to body size. They noted that more efficient steers were able to deposit more protein with less degradation or turnover.

Some other factors such as the relative levels of leptin and IGF-1 have been associated with the differences in the efficiency of fat or protein deposition. The level of leptin has a positive correlation with fatness. Richardson and Herd (2004)

reported a positive association between the levels of leptin and RFI. On the other hand, the levels of IGF-1 was shown to be positively correlated with RFI and body weight gain (Davis and Simmen, 2006; Lancaster et al., 2008) indicating that efficient animals had lower IGF-1 levels. Lancaster et al. (2008) found significant negative correlations between the levels of IGF-1 and RFI in cattle fed a roughage diet but did not observe any correlation in those fed a grain-based diet.

2.4.5 Visceral tissue, ion transport and mitochondrial respiration

Fat and lean tissues are not the only tissues involved in metabolic activities and energy requirements. Others include the heart, liver, GIT and mammary tissues. Because of high maintenance requirements, high feed intake may result in heavier visceral organ weights (Basarab et al., 2003; Herd et al., 2004). Ferrell and Jenkins (1985) suggested that the high-energy requirements in these visceral organs for basal metabolism might be due to high protein turnover or re-synthesis in such tissues. These tissues are larger in the dairy breeds than in the beef breeds (Jenkins et al., 1986). This means that differences within breeds for maintenance requirements would partly depend on the relative size of the visceral organs (Hersom et al., 2004). Low RFI steers had lower weight for liver, intestine (small and large), stomach, kidney and trim fat (Basarab et al., 2003). There were significant differences between the visceral organs of animals placed on high energy diets and those on low energy diets (McLeod and Baldwin, 2000).

The GIT, liver, spleen, pancreas and mesenteric fat depots comprise the tissues of the splanchnic bed. In ruminants, these splanchnic tissues along with

their associated connective tissues and blood vessels make up about 15 to 20 % of the total body mass (Seal and Parker, 2000). The estimated oxygen consumption of these tissues is high especially in the GIT and liver. As a result of digestion, the GIT accounts for the largest proportion of oxygen consumption (Seal and Reynolds, 1993; Cant et al, 1996). Huntington et al. (1988) reported that oxygen consumption has a positive association with feed intake. Oxygen use by tissues indirectly causes some damage to cell components, shorter life span, ageing and loss of vitality (Tolkamp and Ketelaars, 1992). Richardson and Herd et al. (2004) implied that low RFI steers would have a lower oxygen intake than high RFI steers.

The efficient utilization of oxygen seems to be mainly influenced by the enzymes involved in the transport of ions, specifically- Na^+/ K^+-ATPase. The Na^+/ K^+-ATPase is responsible for 1/3 of the cell's energy expenditure as well as for 2/3 of the energy expenditure in neurons (McBride and Kelly, 1990). Evidence has shown that Na^+/ K^+-ATPase accounts for up to 61% of the total oxygen consumption in the GIT (McBride and Milligan, 1985). The pattern and efficiency of these biochemical events may define the efficiency status of any animal.

Efficient production of ATP in the mitochondria may also be necessary for the efficiency of feed utilization in animals. The electron carriers within the electron transport chains of the mitochondria undergo oxidation and reduction as they donate and receive electrons. In the process, about 2 to 4% of the oxygen utilized by the mitochondria may be converted to reactive oxygen species (**ROS**) instead of water as a result of electron leakage (Chance et al., 1979; Bottje and Carstens,

2009). A greater respiratory control is indicative of a more efficient electron transfer through the electron transport chain. This inefficiency may damage cellular components including the mitochondria (Starkov, 2008). The relationship between these ROS and feed efficiency has been reported in chickens where the less efficient chickens had more electron leakage than the more efficient ones (Bottje et al., 2002; Tinsley et al., 2010). Kolath et al. (2006) reported a significant difference in the respiratory control ratio between low and high RFI steers where the low RFI steers had a greater respiratory control. On the other hand, the authors observed greater hydrogen peroxide (indicative of electron leak) in the skeletal muscle mitochondria of low RFI steers as well. They did not find any difference between the low and high RFI steers for mitochondrial function but reported a greater rate of mitochondrial respiration in the low RFI steers.

2.4.6 Physical activity and feeding patterns

Reports show that there is a strong correlation between level of physical activity and feed efficiency. These activities include locomotion, feeding, chewing, rumination etc. They may account for about 5% of total variation in RFI. Animals that are more active have more maintenance requirements; thereby resulting in greater heat production (Herd et al., 2004). Similar reports exist for poultry (Katle, 1991; Luiting et al., 1994) and cattle (Richardson et al., 2001) where increases in feed intake were associated with increasing level of activities. In sheep, eating activities increase heart rate and heat production (Webster et al.,

1977). The report in cattle indicates that the level of activity accounts for about 10% of the overall variation in RFI (Richardson et al., 2001).

The feeding pattern in cattle may depend on the type of diet offered. Cattle consume concentrates or pelleted diets more quickly than forages (Forbes, 1995). The literature on feeding behavior in cattle is growing (Sowell et al., 1998; Nkrumah et al., 2006; Nkrumah et al., 2007b; Golden et al., 2008; Kelly et al., 2010a, b). Richardson and Herd (2004) as well as Nkrumah et al. (2007b) reported that inefficient steers spent more time eating at the bunks. The authors observed that the animals went to feed earlier and that their feeding patterns had a faster decline than the efficient steers. Richardson and Herd (2004) also reported that the high-RFI steers stood longer than the efficient steers. Standing has a greater energy cost than lying and increases the daily muscle energy expenditure in ruminants by up to 30% (Lobley, 1990). Adam et al. (1984) reported that the time an animal spends eating has a more significant energy cost than the amount of feed ingested.

2.4.7 Thermoregulation

Metabolic processes and feeding related activities produce heat. Differences in heat producing abilities may be related to diet (Takeuchi et al., 1995), breed (Carvalho et al., 1995) or physiological state of the animal (Fuquay, 1981). Energy is conserved when animals maintain a thermoneutral environment. There may be need for the body to generate additional heat in cold climates or minimize heat production in hot climates. The hypothalamus controls heat production and

heat loss by receiving information from the warm and cold receptors located in the skin and in the central nervous system (Hammel et al., 1963; Webb, 1995). The body uses thermogenesis in periods of cold either by the oxidation of brown fat also called non-shivering thermogenesis (Himms-Hagen, 1983) or the contraction of skeletal muscle or shivering thermogenesis (Rose and Ikonomopoulou, 2005).

On the other hand, when the temperature is above the comfort zone of the animal, mechanisms are called upon to reduce body heat production. Animals display initial behavioral responses in order to accommodate various ranges of thermal stimuli. However, if the behavioral responses fail, the body automatically invokes thermoregulatory mechanisms (Sakurada et al., 2000) in order to ameliorate the discomfort. Mechanisms available for reducing body heat include evaporative and non-evaporative means, as well as through removal of urine, faeces and milk (Fuquay, 1981). Evaporative energy loss is the principal route of energy loss in animals through heat exchange from the lungs (Herd et al., 2004). Evaporative mechanisms are deployed by converting surface body fluids (sweat, saliva, etc) into water vapor while the non-evaporative heat loss is evident in vasodilation of the blood vessels (Webb, 1995) which occurs by conduction, convection and radiation. Cattle under heat stress would generally increase respiration and expose their tongues (Carvalho et al., 1995). Some evaporative mechanisms include sweating, saliva spreading and panting (Robertshaw, 1985).

The relationship between RFI and thermoregulation could be derived indirectly by investigating the relationship between RFI and heat production

(Nkrumah et al., 2006) as well as between RFI and mitochondrial respiration (Kolath et al., 2006). RFI was positively correlated (0.68) with daily heat production in steers (Nkrumah et al., 2006). The authors reported significant differences among the low (129kcal/kg), medium (143 kcal/kg) and high (164 kcal/kg) RFI-classes for daily heat production. Similar observations were reported for French large white pigs (Barea et al., 2010).

2.4.8 Microbial population

The population of rumen microbes (methanogens, bacteria, protozoa, fungi, etc) may influence the performance of steers through their influence on methane production (Zhou et al., 2009). The energy cost to the animal (because of the production of methane) occurs when the methanogens use the hydrogen produced during fermentation for methanogenesis. Fermentation is the production of volatile fatty acids (**VFA**), CO_2, methane, hydrogen etc. from the breakdown of carbohydrates in the rumen and is usually accompanied by deamination of amino acids (Hobson, 1972). The methanogens receive a constant supply of hydrogen by attaching themselves to entodinimorphid protozoa. These microbial communities in the rumen are affected by changes in diet (Maczulak et al., 1993) and are able to adapt to the new diet ingredients (Kamra, 2005).

Some plant-derived feed materials contain anti-nutritional compounds that limit the growth of some microbes. Some of these compounds include tannins, lignins, saponins and mimosine. While some rumen microflora are tolerant to certain levels of tannins, extended feeding of materials containing tannins

influences the rumen to favor only population of microbes that are able to handle these compounds. Some saponins affect fermentation negatively by reducing the acetate:propionate ratio as well as the total VFA produced in the rumen but some saponins such as Yucca extract (Wang et al., 1998) are able to favor fermentation by reducing the proportion of protozoa in the rumen which also increases the population of bacteria.

Other rumen microbes include the fungi and bacteriophages. Fungi in the rumen help in fibre degradation. Feeding fibre to ruminants tends to promote fungi growth since it has longer retention time unlike pelleted feed (Kamra, 2005). Bacteriophages also have large a population in the rumen. Klieve and Swain (1993) detected large numbers in the rumen and suggested that they may be responsible for lysis of bacteria in the rumen. Bacteriophages may be animal-specific even for group-penned animals under same diet (Kamra, 2005). However, changes in the feed composition may reduce feed efficiency because of non-specific bacteriophage activity (Klieve and Swain, 1993; Kamra, 2005).

2.5 Other biological mechanisms influencing feed intake, feed efficiency and feeding behavior

Initial studies on energy balance and feeding behavior in animals originated from the involvement of the brain in the regulation of feed intake, starvation and weight regulation. Different studies have implicated various parts of the nervous and digestive system in the regulation of feed intake in animals. Eating is coordinated by the interactions between the central nervous system and the

peripheral organs. Certain regions of the brain such as the hypothalamus and brainstem process information coming from the GIT and body energy stores (Richards and Proszkowiec-Weglarz, 2007). The paraventricular hypothalamic nucleus (PVN) and lateral hypothalamic area (LH) are regions of the brain that regulate feeding, energy expenditure and hormone secretion (Nakazato et al., 2001; Olszewski et al., 2003). According to Chandrashekar et al. (2006), taste preference during feeding is detected by receptors in the mouth, which convey information to the brainstem (nucleus tractus solitarius and lateral parabrachial nucleus).

Many factors regulate satiety, which include presence of nutrients, chemicals or signals (neural, humoral, etc) from the GIT to the brain. The signals (peptides, nutrients, neural) from the GIT regulate taste perception, meal size and satiety while leptin, insulin and glucocorticoids regulate the connection between intake and body weight as well as fat deposition (Ahima and Osei, 2001). For example, a gut peptide, Cholecystokinin (CCK), secreted by gut endocrine cells, has been shown to reduce meal size depending on its level in the gut (Della-Fera and Baile, 1980; Furuse et al., 1991; D'Alessio, 2008). In addition, the hepatic and GI receptors also regulate satiety in the presence of carbohydrate, fat or protein metabolites (Ahima and Osei, 2001).

Neuropeptide Y (NPY), orexin (hypocretin), melanin-concentrating hormone (MCH) and agouti-related peptide (AGRP) also mediate the regulation of appetite by stimulating feed intake while at the same time inducing lipogenic enzymes in the liver and white adipose tissues (Schwartz et al., 2000). It has been shown that

disrupting the MCH gene in mice led to hypophagia and leanness (Shimada et al., 1998). Energy expenditure during fasting, exercise or lactation, as well as deficiency of leptin or insulin causes the secretion of NPY in order to stimulate feeding. On the other hand, melanocortins, corticotrophin-releasing hormone (CRH), thyrotropin-releasing hormone (TRH), cocaine-and amphetamine-regulated transcript (CART) inhibit feed intake in response to increased brain adiposity signaling (Schwartz et al., 2000).

Leptin is mainly produced in the adipose tissues and affects several feeding behaviors, which include adaptation to fasting, regulation of meal size, and suppression of feeding. There is a direct relationship between body energy stores and the levels of leptin, insulin and glucocorticoids in the body (Dallman et al., 1995; Sesmilo et al., 1998). Leptin acts as a signal to the hypothalamus and other regions of the brain in the regulation of intake and energy balance and may be involved in the taste pathway. Leptin levels are reduced during food deprivation (Marie et al., 2001; Liefers et al., 2005). As feeding increases, the level of leptin increases as well, thereby reducing appetite and increasing energy expenditure. Leptin deficiency in humans and mice is associated with hyperphagia, obesity and metabolic abnormalities (Montez et al., 2005). Sex steroids such as androgen and estrogen also regulate leptin production. Androgens stimulate appetite thereby increasing body mass while estrogen decreases intake and reduces body weight (Considine, 2001). Insulin inhibits the biosynthesis of NPY thereby inhibiting food intake (Silverstein and Plisetskaya, 2000; Sato et al., 2005). Deficiency of insulin, unlike leptin, does not cause obesity (Schwartz et al., 2000) but the

disruption in the insulin receptor gene led to a significant increase in feed intake in mice (Masaki et al., 2004).

Insulin-like growth factor 1 (IGF-1) is an endocrine hormone that regulates glucose metabolism, amino acid metabolism, protein accretion and growth (Jones and Clemmons, 1995) while ghrelin is found in the peripheral tissues as well as in the central nervous system (Olszewski et al., 2003). Nakazato et al. (2001) reported that injection of ghrelin or GHRP-6 increased food intake in male wistar rats in satiated or fasted conditions. The GHRP-6 (a synthetic hexapeptide) increased feed intake and releases growth hormone by binding to the secretagogue receptor (GHR-S).

The relationships between some of these hormones and measures of intake, growth and feed efficiency have been studied in several livestock species. Some researchers have investigated the possible role of IGF-1 in pigs (Bunter et al., 2002) and in cattle (Moore et al., 2005). Some studies have also conducted divergent selection of different lines using serum IGF-1 concentrations. Positive genetic correlations between postweaning IGF-1 concentrations and RFI were 0.39 (Johnston et al., 2002), 0.57 (Moore et al., 2005) but negative genetic correlations (-0.12) have also been reported by Wolcott et al., (2006). Lancaster et al. (2008) reported positive phenotypic correlations in bulls and heifers between final IGF-1 concentrations and ADG (0.14 to 0.19), lean meat yield (0.09 to 0.45) but had negative phenotypic correlations with FCR (-0.49 to -0.14). They reported inconsistent correlations between IGF-1 concentrations with DMI (-0.24 to 0.10) and RFI (-0.40 to 0.03). On the other hand, Kelly et al. (2010b) reported that IGF-

1 was not related to any measure of feed efficiency in heifers but was positively correlated with ADG (0.26). No significant correlation was also observed between IGF-1 with DMI, FCR or RFI (Kelly et al., 2010a).

Ehrhardt et al. (2000) reported that the serum leptin levels in calves and lambs were related to their plane of nutrition. In crossbred steers, Nkrumah et al. (2007c) reported heritability estimate of 0.34 for serum leptin concentrations. Leptin was correlated with DMI (0.43) and FCR (0.48) but not with RFI (Kelly et al., 2010a). Nkrumah et al. (2007c) reported phenotypic correlations of 0.15, -0.44 and -0.24 for serum Leptin concentrations with DMI, FCR and RFI, respectively. Serum leptin levels were genetically correlated with phenotypic-RFI (0.74) and daily feed intake (0.26) in Duroc pigs (Hoque et al., 2009b). The authors also reported positive genetic correlations between IGF-1 concentrations at 8 weeks of age with phenotypic-RFI and daily feed intake but these correlations were negative with the IGF-1 concentrations at 105kg of body weight. Plasma insulin was not related to DMI, ADG, FCR nor RFI in beef heifers (Kelly et al., 2010a).

2.6 Analysis of quantitative traits

Quantitative traits are traits whose phenotypes do not follow simple Mendelian inheritance at any single locus, but rather follow a distribution. Most economically relevant traits are quantitative traits and are influenced by multi-genes and environment or the interaction between the genes and the environment. Because of these influences, different genotypes may have the same phenotype (Lander and Schork, 1994) or similar genotypes may give rise to different

phenotypes. Genetic studies conducted on quantitative traits could examine estimated breeding values (EBV), heritability estimates, correlation coefficients among traits, etc. Several models can be used to estimate the breeding value of an individual depending on the nature of the trait, its frequency of collection or the individual the estimate is meant for.

The animal model is commonly used to obtain EBVs for each individual animal. In simple single trait animal models (Wood et al., 1991; Sun et al., 2009; Tarres et al., 2010), each animal has a single observation for each trait. The components for this model are the fixed effects and the additive genetic effect for each animal (random effect). When repeated records are available for a trait, a repeated records model (Van Vleck and Gregory, 1992) is used. The phenotypic correlation between different measurements represents the repeatability of the trait while the genetic correlation is assumed unity. This model has a permanent environmental component that includes those effects that affect all successive records of the animal. Effects such as good management may favor performance while the loss of a quarter in a dairy cow would reduce performance.

The multi-trait or multivariate model (Lassen et al., 2007; Nobre et al., 2003) can analyze more than one correlated trait simultaneously while incorporating the genetic and environmental correlations between traits. The multi-trait model is better than the single trait (univariate) model because it uses more information collectively. Using the correlated information from traits increases the accuracy of prediction of the EBV of the traits. A multi-trait model could reduce selection bias (Pollak et al., 1984) when there are missing data.

2.7 Correlations among traits

Phenotypic or genetic correlations indicate the relationship among different traits. Phenotypic correlations between two traits indicate the co-variation that exists between the two traits in a population. The co-variations are due to genetic correlation or environmental correlation between traits or both. Genetic correlation exists when similar sets of genes affect the two traits (pleiotropy) or as a result of gametic linkage disequilibrium among genes (Falconer and Mackay, 1996). The signs carried by correlations indicate the direction of the effects of the genes; it is positive if the genes affect the trait in the same direction and negative if they act in opposite directions.

Many studies have looked at the correlations that exist among various production traits in beef cattle. Estimates of phenotypic correlations for feed intake with ADG (0.6) and MWT (0.65) are generally high and positive, showing that both ADG and MWT account for a large proportion of the differences in feed intake (Nkrumah et al., 2007). Nkrumah et al. (2007) also reported a moderate phenotypic correlation of 0.41, 0.20 and 0.35 between DMI with ultrasound backfat thickness, ultrasound marbling and ultrasound lean meat area, respectively. Similar phenotypic correlations have been reported by other researchers (Herd and Bishop, 2000; Arthur et al., 2001; Lancaster et al., 2009).

The RFI trait has moderate to high correlations with FCR ranging from 0.42 to 0.86 (Basarab et al., 2003; Tedeschi et al., 2006). Phenotypic RFI also has positive correlations with marbling (0.15), dissectible carcass fat (0.14), gain in

ultrasound backfat thickness (0.22), gain in ultrasound marbling (0.22), empty body fat gain (0.26), metabolizable energy intake (0.80), retained energy (0.28) and heat production (0.56). However, it is negatively correlated with carcass lean meat yield (-0.21) and empty body protein (-0.14) (Basarab et al., 2003). Genetic RFI, however, had no genetic correlation with ultrasound backfat thickness but is moderately genetically correlated with carcass grade fat but negatively correlated with LM area (-0.69) and lean meat yield (-0.43) (Nkrumah et al., 2007). Tedeschi et al. (2006) reported a moderate relationship of 0.42 between RFI (unadjusted for body composition) and empty body fat (EBF). This positive correlation shows that inefficient animals are fatter than efficient ones at similar production and maintenance levels. The genetic correlations between RFI and body weight measured in cattle were different from zero (Kennedy et al., 1993; Arthur et al., 2001a). Even though phenotypic RFI may not be genetically independent of weight and average daily gain, there is a high correlation between the phenotypic and genetic RFI (Arthur et al., 2001a).

2.8 Correlations among environments or genotype-by-environment interaction

Livestock breeders or producers are in the quest for animals that will suit their production and marketing environments (James, 2009). The differential performance of genotypes in different environmental conditions is called genotype-by-environment interaction (GEI). The GEI has also been described as

the non-parallelism of phenotypic response across environments (Eeuwijk et al., 2004; Malosetti et al., 2004).

For most quantitative traits, the performance of the genotype depends on the environment. Most studies in cattle have assumed absence of GEI, subsequently, any interaction that may exist between genotypes and the environments were ignored. This assumption is not always true since some dependencies of genotypes on the environments have been reported (Kearney et al., 2004a; Kearney et al., 2004b; Fahey et al., 2007). Interactions could be due to heterogeneity of genotypic variances among environments or lack of correlation between genotypic performances in different environments (Montaldo, 2001). There may be need for a specific breeding program when the genetic correlation is less or equal to 0.6 (Mulder, 2006) in order to improve the trait in each environment.

According to Hammami et al. (2009), there are 3 main methods for estimating GEI, namely interaction model, character state model and reaction norm model.
The interaction model for analyzing a GEI can be conducted through analysis of variance as:

$y_{ijk} = \mu + G_i + E_j + GE_{ij} + e_{ijk}$

where y is the performance of genotype i in environment j, μ is the overall mean, G_i is the mean of the i*th* genotype effect over all environments, E_j is the mean of the j*th* environment effect over all genotypes and GE_{ij} is the mean GEI effect which is a measure of departure from the additivity of the G_i and E_j.

The character state model refers to the use of genetic correlations to determine if a trait measured within two periods or two environments should be considered as the same trait or not (Falconer and Mackay, 1996). The character state model used in this thesis is the most appropriate given that the environments are discrete and it also has the best interpretation for GEI (Hammami et al., 2009).

Furthermore, the reaction norm analysis has also been used to detect GEI in non-discrete environments having some sort of continuous distribution (Knap and Su, 2008). The reaction norm approach estimates the genetic correlation between the intercept (mean performance of genotype) and slope (environmental sensitivity) of the trait under investigation. The reaction norm model expresses the phenotype as a polynomial function of the environment value where it is assumed that genes affect the polynomial coefficients.

Although GEI can be classified in several ways, the most practical way of classification would be in terms of scale or rank (Fahey et al., 2007; James, 2009). Scale type interactions are due to differences in the level of production. Interactions due to changes in magnitude usually have a high correlation (close to unity) and may be removed by data transformation (James, 2009). Rank type interactions have much lower correlations. Several researchers have used the genetic correlations approach of Falcon and MacKay (1996) to compare different traits measured across different ages (Arthur et al., 2001), sexes (Tilsch et al., 1989; Oikawa et al., 1999), breeds (Lin and Togashi, 2002) or diets (Kearney et al., 2004a; Kearney et al., 2004b). The variances (Maniatis and Pollott, 2002) and

variance ratios (such as heritability estimates) can also be examined in each environment.

Genotype-by-environment interactions have been reported in various livestock species such as sheep (Maniatis and Pollott, 2002; Pollott and Greeff, 2004; Steinheim et al., 2008), goats (Louca and Hancock, 1977; Mavrogenis et al., 1984; Baker et al., 2004), pigs (Brascamp et al., 1985; Knap and Su, 2008; Merks, 1989) and chickens (Ali et al., 2001; Deeb and Cahaner, 2002; Bekele et al., 2009). In most of these cases, mild GEI was reported. In cattle, genetic correlations between the measurements obtained in weaner bulls versus yearling bulls were high for weight and feed intake and low for RFI (Arthur et al., 2001a) leading the authors to conclude that RFI measured in weaners should be considered as a different trait from those measured in yearlings. They suggested that since muscle is deposited early in life and fat deposition later in life, then different genes may be acting at those times. Significant breed by location interactions for crossbred cattle was reported for pregnancy rate, rate of unassisted calving and weaning weight (Olson et al., 1991). Breed-by-sex interaction has also been reported for birth weight (Chase, Jr. et al., 2004) while breed-by-feeding rate interaction was reported for some growth and efficiency traits (Jenkins and Ferrell, 2004).

Very few researchers have investigated variance components estimated from animals fed different diets. Crews et al. (2003) reported a greater phenotypic variance for RFI when steers were fed a grower diet than when they were fed the finishing diet. They suggested that selection of steers fed growing a diet will lead

to a greater genetic improvement since both the heritability and genetic variance were greater at the grower-fed period than that at the finisher-fed period. In a different study, Archer et al. (1997) reported that phenotypic variance for RFI reduces over time. Arthur et al. (2001a) reported a greater heritability estimate for RFI measured during the weaning phase (0.32) than that measured during the yearling phase (0.25).

From the foregoing, it is important to examine the influence of feeding period on the FE and feeding behavior performances of feedlot steers fed different diets. The results will inform us whether these traits measured in successive feeding regimes are influenced by the same set of genes. For genetic evaluation purposes, this study will indicate whether they are similar traits or not, thereby indicating the importance of collecting more phenotypes at different feeding phases.

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CHAPTER 3

FEED EFFICIENCY RERANKING IN BEEF STEERS FED GROWER AND FINISHER DIETS[1].

3.1 INTRODUCTION

Many studies have investigated phenotypic measures of feed efficiency (**FE**) in beef cattle (Koch et al., 1963; Arthur et al., 2001a) but limited information exists on these measures taken at different times in an animal's life or on rations differing in energy content. Few studies have investigated the effect of diets differing in energy density on the FE performance of group-fed cattle (Fan et al., 1995) but none has looked at the FE ranking of beef cattle fed different diets successively. The lack of information on multiple FE measurements may be due to the increased cost associated with multiple measures and with conducting longer trials using the same animals. This information is necessary to improve lines of efficient cattle at all ages and all feeding regimes thereby helping beef producers in any sector reduce their feeding costs. The evidence available suggests that one of such measures of FE, residual feed intake (**RFI**), measured in cattle at young ages is highly correlated with those measured later in life (Arthur et al., 2001b; Archer et al., 2002). Goonewardene et al. (2004) reported high rank correlations between RFI measured at 63-d, 84-d and 105-d test periods on the same animals.

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Feedlot steers often receive a backgrounding or grower diet before receiving a high energy feedlot diet. It is not known whether animals that are efficient on a backgrounding feeding regime or grazing pasture would also be efficient on a high grain feeding regime. Knowledge about this relationship is important for selection decisions regarding which animals to use as replacements and when to measure or evaluate animals for FE. Consequently, our objective was to investigate if steers change their FE rankings from a grower feeding regime to a finisher feeding regime. The null hypothesis tested was that an animal's FE rank would not be different between these two feeding regimes.

3.2 MATERIALS AND METHODS

3.2.1 Animals and Management

All animals were located at the University of Alberta ranch at Kinsella, Alberta and were cared for according to the Canadian Council on Animal Care (CCAC, 1993) guidelines. A total of 490 steers were used in the three-year trial (2006-2009). These steers were born in the spring of 2006, 2007 and 2008 from multiple sires mated to hybrid dams on pasture. The hybrid dams were crosses between Angus or Charolais bulls and composite dams generated from three composite cattle lines designated Beef Synthetic 1 (BS1), Beef Synthetic 2 (BS2) and Dairy × Beef Synthetic (DBS) (Goonewardene et al., 2003). The three composite dam lines had different original breed compositions. The BS1 line was composed of 16.5% Angus, 16.5% Charolais, 20% Galloway and 47% of other beef breeds. The BS2 line was composed of 60% Hereford and 40% of other beef

breeds while the DBS line was made up of 60% dairy breeds (Brown Swiss, Holstein and Simmental) and 40% beef breeds (Angus and Charolais). The sires used were either hybrid or Angus bulls. The hybrid sires were selected bulls from crosses between Angus or Charolais bulls and the hybrid dams.

The steers (born in the spring) grazed with their dams until weaned in October of each year. All animals had been vaccinated for infectious bovine rhinotracheitis, parainfluenza-3 virus, bovine viral diarrhea, bovine respiratory syncytial virus, *haemophilus somnus*, *pasteurella multocida* and clostridial diseases four weeks before arriving at the feeding facility. Upon arrival, each steer was treated with a pour-on parasiticide, Ivomec (Merial, Baie d'Urfe, Canada), that controls warble larvae, mites, lice and horn fly. Each steer was identified with a radio frequency transponder button (half duplex RFID, Alflex USA, Inc., Dallas/Ft. Worth Airport, TX 75261-2266) in its right, or left ear. The transponder button was located five to six cm from the base of the ear, in the middle, with the transponder button on the inside part of the ear.

The test facility was a fenced area divided into two, each containing one of the two test-groups of steers. The design of the test facility was such that the lying area was at one end and where they were offered feed was at the other end. For each group, the distance between the two ends was about 50 m with the water trough located in the middle of the two ends. Feed and clean drinking water were offered *ad libitum* throughout the test periods. Each group had access to ten GrowSafe System feeding bunks which were housed in a shed. The lying area for each group was a large outdoor pen with wheat straw as bedding. Wheat straw

was used as a bedding material because of its poor nutritive quality. Fresh wheat straw was added when the old straw bedding was wet; however, the effect of potential straw intake on our results, especially the finisher-fed period, is unknown.

There were two feeding periods in each of the three years. The first feeding period (**FP1**) was during the Fall-Winter season while the second feeding period (**FP2**) was during the Winter-Spring season. Each year (except the first year), the animals were divided into two groups. In the first year, all steers (n = 175) were in the feed swap group and were fed a grower diet in FP1 followed by the finisher diet in FP2. In years two and three, the feed-swap groups had 84 steers and 72 steers, respectively. The control groups were fed the same diet in the two periods; finisher diet in the second year (n = 88) and grower diet in the third year (n = 71).

The composition of the grower diet on an as-fed basis was 74% oats, 20% smooth brome hay and 6% feedlot supplement (see Table 3- 1) while the finisher diet contained 10% alfalfa pellets, 28.3% oats, 56.7% barley and 5% feedlot supplement. Weekly samples of feed were collected and pooled into monthly samples and were subsequently analyzed for DM, CP, crude fat, NDF and ADF. Dry matter was determined by an overnight oven-drying to a constant weight at 110^{o}C. Crude protein was measured by determining the N content in feed using the Kjeldahl procedure (AOAC, 1980). Neutral detergent fiber was determined according to the procedure of Van Soest et al. (1991) while acid detergent fiber was determined according to AOAC (1997). The NDF and ADF were determined using the ANKOM 200 fiber analyzer (Ankom Technology Corp.,Fairport, NY).

The steers were adjusted to their trial diets during a pre-test adjustment period of 21 to 30 days. This initial adjustment period enabled the animals to acclimate to the GrowSafe System feeding units and test diets. At the end of FP1, a two-week adjustment period was allowed before the commencement of feed intake data collection in FP2. During this period, the grower diet (for the feed-swap group) was gradually adjusted to the finisher diet.

3.2.1 Data Collection

Table 3- 2 shows the number of animals, lengths of the different periods and data integrity checks for all years and test groups. Data collected from the feed-swap groups over the three years were pooled for subsequent data analyses. Fourteen steers were excluded from the data analyses due to incomplete phenotypic data.

In the first year, the test ran from November 1, 2006 to May 2, 2007. The second and third years ran from November 6, 2007 to May 1, 2008 and November 2, 2008 to May 1, 2009, respectively. Details are shown in Table 3- 2. Although a minimum of 63 to 70 days (Archer et al., 1997; Wang et al., 2006) of reliable data is required for RFI calculations, the number of days exceeded the requirement to make up for days that were excluded due to temporary malfunctions in the feeding system, power outages, or days with low data integrity values. The weights of all steers were measured once every 2 wk throughout the test periods while ultrasound back-fat (**UBF**) thickness was measured at the beginning and at the end of the feeding period with an Aloka 500V real-time ultrasound with a 17.5 cm

3.5MHz probe (Overseas Monitor Corporation Ltd., Richmond, British Columbia, Canada). Feed intake was measured daily on each steer using the GrowSafe feeding system (GrowSafe Systems Ltd., Airdrie, Alberta, Canada). The system consisted of radio frequency identification tag on each animal, 20 feeding nodes located in a covered feeding shed, a data logging reader panel and a computer which contained the data acquisition software. Each feeding node consisted of a feed tub on two load bars and an antenna embedded in the rim of each tub.

The antenna detects and identifies each animal through radio waves emitted by the transponder encased in the ear tag. Subsequent feeding and behavioral data are recorded as the animal is feeding from the bunks. Data generated from the feeding units are stored in the data logging reader panel and are transferred wirelessly to the personal computer located about 100 meters away. The GrowSafe data acquisition and analysis software in the computer converts the data into readable formats for subsequent analyses. For data integrity and quality control purposes, the GrowSafe system has an internal audit system that calculates the daily assigned feed disappearance (**AFD**) for each node by dividing the total daily feed delivered to each tub by the daily sum of individual animal feed intakes as attributed by the GrowSafe System for a specific tub. The AFD (Table 3- 2) should be sufficiently high (> 95%) for each day's data to be included for data analysis. Data collected on the days that had low AFD were excluded from all analyses. The low AFD were due to power outages, heavy winds, heavy rains or snow, or temporary malfunctions in the system. Other data integrity shown in Table 3- 2 includes the correlation between DMI and metabolic mid-weight

(**MWT**), ADG, ultrasound back-fat and expected feed intake. The correlations are used to examine the data for known relationships among the variables. Serious deviations from the allowable limits of the correlations would question the integrity of the data. This also includes the proportion of the variation in DMI accounted by ADG, MWT and UBF.

3.2.3 Trait Derivations and Statistical Analysis

The ADG, initial weight and mid-test body weight of each animal were computed from the regression coefficients of each animal's linear growth path using the PROC REG procedure in SAS (Version 9.2, SAS Inst., Inc., Cary, NC). The mid-test body weight was converted to metabolic mid-weight (MWT) by $BW^{0.75}$. Daily feed intake (as fed) was obtained as the average feed intake for valid test-days. This was multiplied by the dry matter content of the feed to derive the DMI for each steer. The DMI observed was standardized across diets and years to 10MJ ME kg^{-1} DM. The ME of each diet was estimated with the CowBytes ration balancing software (Alberta Agriculture and Rural Development, Edmonton, Canada). Expected DMI was obtained as a regression of standardized DMI on ADG, MWT and UBF using PROC GLM of SAS. The residuals from the equation (shown below) were output as RFI, which was calculated within contemporary groups defined by year of test, feeding group and feeding period. The equation is shown below:

$$\boldsymbol{DMI = ADG + MWT + UBF + CG + RFI}$$

where DMI is the standardized dry matter intake, ADG is the average daily gain over the test period, MWT is the mid-test metabolic weight, UBF is the final ultrasound back-fat measurement, CG is the contemporary group classification and RFI indicates the residuals (Basarab et al., 2003)

Other FE measures were calculated for each animal within contemporary groups. The G:F ratio was calculated as the ratio of daily ADG to DMI. Kleiber ratio was calculated as the ratio of ADG to MWT (Tedeschi et al., 2006). In addition to calculating FE measures within each period and year, across period within year (**FP1&FP2**), FE measures were also calculated for each animal.

The steers were grouped into three classes based on the FE (ie RFI, G:F or KR) standard deviation of each contemporary group. They were classified as 'Low' (< 0.5SD), 'Medium' (± 0.5SD) and 'High' (> 0.5SD). The objective of this approach was to have three RFI classes and approximately equal number of steers in each RFI class. Assuming a normal distribution, we know that 68 percent of the steers would be ± 1 SD from the mean. Therefore, about 34 percent of the steers would be about ± 0.50 SD from the mean; the actual SD to obtain one third in each group is not 0.5 SD but this would be close. The classification would also help us to identify steers that changed FE-classes. A class-change occurs when the FE class of any steer is different in each of the two periods. We also looked into the proportion of steers that changed their RFI by 0.25 SD, 0.5 SD and 1 SD in FP2. To determine the extent to which ranks changed within each group of steers, the Spearman's rank correlation statistic between FP1 and FP2 was calculated. The Pearson correlation statistic was used to determine the relationship among FE

measures taken in the two periods. Part-whole correlations (Pearson) between the within and across-period FE measures were also calculated. The part-whole correlations identified the similarities between the within FE measures and the FE measured from the entire trial. Equality of correlations was tested using transformed Z-scores (Stockburger, 1996). The FE measures in FP1 and FP2 were tested for equal variances within each test group using PROC TTEST of SAS. Least square differences among test group means were tested with the GLM procedure in SAS using the PDIFF option in a model which included year of test, RFI-class and age-on-test as a linear covariate.

The proportion of steers that changed their FE class from one feeding period to the other was compared to the proportion that maintained the same FE class using a chi-square test executed using PROC FREQ of SAS. Using the same procedure, we compared the proportion of steers that changed from the low FE-class to the high FE-class with those that changed from the high class to the low class.

Furthermore, the difference between RFI in FP1 and FP2 were calculated to identify the extent of change each steer made in FP2. The differences (**D**) were classified into 3 groups based on steers that changed by 1 SD or 0.56 kg DM d^{-1} of RFI giving –ve$\Delta\Delta$ = (D < -0.56 kg DM d^{1}), +ve$\Delta\Delta$ = (D > +0.56 kg DM d^{1}), NeutralΔ = (D ± 0.56 kg DM d^{1}). Least square differences among group means were tested with the GLM procedure in SAS using the PDIFF option. These differences may explain the reasons behind the changes in RFI from FP1 to FP2.

3.3 RESULTS

Table 3- 2 shows the average age, number of days-on-test as well as some integrity checks for the data collected on each feeding regime. The ADG, MWT and UBF used to compute RFI for the pooled feed-swap group accounted for 58% and 57% of the variation in DMI in FP1 and FP2, respectively. Corresponding values for the finisher-fed group and the grower-fed group were 71% and 36%, and 60% and 52%.

3.3.1 Differences in Feed Efficiency among Test Groups

Table 3- 3 shows the results for the different periodic FE and its components obtained for the three test groups. In FP1, the mean DMI, ADG, MWT and KR for the feed-swap group were similar ($P > 0.05$) to that of the grower-fed group but different from that of the finisher-fed group. There was no difference ($P > 0.05$) in RFI among all groups. The G:F was similar between the feed-swap and the finisher-fed group but the G:F of the feed-swap group was greater than ($P < 0.05$) the grower-fed group. However, in FP2, ADG, DMI and KR were different ($P < 0.05$) among all three groups of steers. The G:F was not different between the two control groups but the feed-swap group was different ($P < 0.05$) from either of them. The grower-fed group had the lowest G:F in FP1 and FP2 while the finisher-fed group had the greatest in FP1. This implies that the grower diet supported the least growth in both periods while the steers that received the finisher diet in FP1 (early) grew faster.

The RFI variance in FP1 was different ($P < 0.05$) from that in FP2 for the three groups (Table 3- 3) but the variances were greater in FP2 than in FP1. For each of the feed-swap and finisher-fed groups, the G:F variances were different between FP1 and FP2 within the feed-swap and the finisher-fed groups but the KR variances in the two feeding periods were similar ($P > 0.05$).

3.3.2 Feed Efficiency Reranking

For all test groups, there were unequal proportions of steers in the low, medium and high classes with more steers in the medium-FE class than either the high-FE or the low-FE class. For RFI and G:F (Table 3- 4), a greater proportion of steers in the feed-swap group changed their FE class from FP1 to FP2. On the other hand for RFI, the proportion of steers that changed their FE class was not different from those that maintained the same FE class. The two proportions (change vs no-change) were different when evaluated with G:F and KR. Similar proportions of steers in the two control groups changed or maintained the same FE class from FP1 to FP2. Within each of the three groups, the proportion that switched from the low to the high class (Table 3- 5) was not significantly different ($P > 0.05$) from the proportion that switched from the high class to the low class. On the other hand, a small proportion of the steers maintained the same efficiency class (from FP1 to FP2) across all FE measures evaluated in the different test groups. About 5.4%, 3.4% and 8.5% maintained same class for the four FE measures in the feed-swap, finisher-fed and grower-fed groups, respectively.

In either FP1 or FP2, majority of the steers were in the medium class. While some steers maintained the same class (low or high) in both feeding periods, others changed from the medium class (in FP1) to either the high or low classes in FP2 and vice versa. On the other hand, 17, 5 and 0 steers switched from the low to the high RFI class for the feed-swap, finisher-fed and grower-fed groups, respectively while 12, 3 and 6 steers switched from high to low RFI class for the feed-swap, finisher-fed and grower-fed groups, respectively. We do not know the reasons behind the switches and these steers may require further investigation into reasons for such transitions. Considering the SD changes in FP2, the proportion of steers that changed their RFI measure by 1SD were 31%, 30% and 23% for the feed-swap group, finisher-fed group and grower-fed group, respectively. Corresponding values for the 0.5 SD and 0.25 SD were 58%, 51% and 51%, and 79%, 69% and 77% for the feed-swap group, finisher-fed group and grower-fed group, respectively.

Further evidence of reranking is observed in the correlation coefficients between FE measured in FP1 and FP2. The Pearson correlations (data not shown) were similar but higher than the Spearman correlations. A low rank (Spearman) correlation within a group indicates that most steers changed their relative positions in FP2. The FE rank correlation for all test groups were below 0.5 but the feed-swap group (Table 3- 6) had lower rank correlations between FP1 and FP2 than the control groups (Tables 3- 7 and 3- 8). Greater rank correlations for the two control groups indicate that the FE ranks of steers in FP1 and FP2 were similar. The RFI rank correlations between FP1 and FP2 were greatest within the

feed-swap and finisher-fed groups. The grower-fed group had greater and more consistent correlations across the four FE measures.

Table 3- 9 shows the part-whole Pearson correlation coefficients between the FE calculated from entire feeding period (FP1&FP2) with each FE calculated in FP1 and FP2. For the feed-swap and the grower-fed groups, the FE from FP1&FP2 had a greater correlation with the FE calculated from FP2 than that from FP1. The finisher-fed group had a greater correlation between the FP1&FP2-FE and the FE in FP1 indicating that the FE measured during FP1 was more similar to the FE measured during the entire feeding period (FP1 and FP2 combined).

Tables 3-10 showed the differences among the steers based on a classification of 0.56 kg DM d^{-1}, respectively while Figure 3- 1 shows the scatter plots of the RFI in FP1 and FP2. The classification based on the 0.56 kg DM d^{-1} (Table 3- 11) did not show any difference ($P > 0.05$) between the two extreme groups for initial body weight, ADG, FF, UBF, UREA and UMB but DMI and G:F were different in both periods between the extreme groups.

3.4 DISCUSSION

In the design of this experiment, practices obtainable in the commercial beef sector were considered. Steers are usually fed a grower diet before they are transitioned to a finisher diet. It is very unlikely and impractical to feed high energy diets before low energy diets and this option was not considered in the study design. Using feed-efficient animals in the cow-calf and feedlot production

systems would reduce the cost of production and produce less greenhouse gases such as methane thereby having a less negative impact on the environment than inefficient steers (Nkrumah et al., 2006; Hegarty et al., 2007). Most studies on FE have focused on single-period measurements on a single diet (Arthur et al., 2001a, b; Nkrumah et al., 2004). Archer et al. (2002) evaluated FE measured on heifers at postweaning and as mature cows while Christopher and Marston (unpublished) compared the RFI rankings of heifers fed low and then high energy-dense diets at the Kansas State University.

Measuring FE twice showed class changes in all the test groups implying that diet and the feeding period affect the FE performance of steers. The effect of the feeding regime is observed in the greater number of steers that changed their efficiency class when the diets were switched. Steers in the feed-swap group that were efficient under both diets may perform well under diverse feeding regimes and may be sought-after in an integrated beef sector. Those that maintained their RFI classes in both periods, whether efficient or not, could offer a platform for understanding the genetic mechanisms surrounding FE.

Having so few animals maintain the same class across the four FE measures may have selection consequences. While some animals may be considered very efficient using a particular FE measure, they become less efficient when evaluated with another FE measure. It then implies that different animals may be considered for selection depending on the FE measure of choice. For example, a producer that does not have access to automatic feeding system to compute RFI may select a different set of efficient animals using G:F.

The switch from one efficiency class to another for the feed-swap group may be attributed to some factors that may limit any animal's ability to adjust to a new feed. Guan et al. (2008) reported that an animal's ability to utilize feed is associated with the population of rumen microbes. Feeding a concentrate or high-energy diet after a low energy diet, changes the pH and the population of rumen microbes in cattle reducing the cellulolytic bacteria but on the other hand, reduced intake (Calsamiglia et al., 2008). Apart from rumen microbes, individual animal variations may also be caused by the feeding rate or ruminal activities (Hegarty, 2004). For these reasons, different animals may perform differently on various diets (Russell et al., 1992) or different periods, thereby determining the FE class of an animal.

Higher growth rates may have contributed to the changes in the efficiency classes observed in the feed-swap group. The steers within this group may have experienced higher growth rate in FP2 than other groups due to compensatory growth. Drouillard et al. (1991) observed greater finishing performance when diets of steers were energy-restricted. Similar trend was observed when McCarthy et al. (1985) studied feedlot cattle fed different energy-dense diets. Those fed low-high diets had higher body gains in the finishing period than those fed high-high diets. Compensatory gains have been reported in heifers fed a high energy-dense diet after an initial period of less energy-dense diet (Barash et al., 1994).

Feeding the finisher diet in FP1 of the finisher-fed group may have also contributed to the switches in their FE classes in the subsequent period. The greater DMI and ADG in FP1 for the finisher-fed group compared to the feed-

swap or grower-fed groups may be driven by the rumen-fill. Such greater intake may avail the steers with more energy for metabolic processes. Differences may exist among animals in their abilities to utilize greater metabolizable energy at an early age. Steers that partitioned more protein during this period may have a different efficiency performance from those that partitioned more fat. This may eventually affect their maintenance requirement and subsequent efficiency performance in FP2.

It is important to consider the variability underlying phenotypic RFI (Crews, 2005), therefore the changes in RFI (from FP1 to FP2) by 0.5 SD or more could be regarded as important shifts in FE status. The steers that had such shifts could provide insight into mechanisms underlying reranking. It is not surprising that a large percentage of steers changed their RFI in FP2 by 0.25 SD, which is a small margin. Majority of such changes may have arisen from random errors which occurred during body weight measurement of the steers or during the estimation of ADG. Errors in body weight measurements would affect the metabolic mid-weight as well as the ADG, thereby resulting in inaccurate estimates. These would subsequently affect the RFI estimated within any period and may cause reranking from one period to another by a small margin. The gut fill of the steers at the time of measurement may also influence individual body weights and cause greater variation in body weights (Archer and Bergh, 2000). Steps were taken to control these random errors. The steers were weighed first in the morning before they were fed to avoid disrupting feeding patterns (Archer et al., 1997) and this pattern was maintained throughout the trials. Further errors were minimized by taking

multiple body weight measurements (Koch et al. 1963) and using linear regression to estimate ADG (Archer and Bergh, 2000). Frequent monitoring of the GrowSafe System, conducting data integrity checks as well as excluding days that may contain invalid feed intake data minimized other random errors that may have arisen from measuring intake. Considering the animals that changed their RFI from FP1 to FP2 by 0.2 kg DM d^{-1} and 0.5 kg DM d^{-1} may point out that the main differences between the efficient and inefficient groups were due to DMI, and ADG. Therefore, the factors that affect these traits may be the underlying elements influencing their efficiency status.

Another evidence of reranking is observed in the low to moderate correlation estimates between FE measured in FP1 and FP2. These correlation estimates for all FE measures in all test-groups may show that majority of the steers performed differently on the different diet-types and different periods. A low correlation estimate may indicate that efficient animals in FP1 may not be efficient in FP2 or vice versa. The low correlation estimates observed in the two control groups may point out that the FE ranking of an animal may be affected by time or feeding period. That the correlations observed in the control groups were not different from that observed in the feed-swap may show that both diet and feeding period may have contributed to the reranking and variation. The grower-fed group had greater and more uniform correlations than other groups; however, the reasons behind these are unclear. Christopher and Marston (unpublished) reported no correlation between RFI measured in the two feeding periods, which contrasts our findings. Their results were probably due to a low number of subjects (n = 26).

The phenotypic correlations between RFI in FP1 and FP2 obtained here may indicate that both RFI measures are different traits in each environment. Even though RFI had greater correlations between FP1 and FP2 than other FE measures a lot needs to be understood about the characteristics of RFI.

The low RFI correlations for the feed-swap group were similar to those obtained from other species. Studies in mice reported low correlations between RFI measured at postweaning and at mature stages. Archer et al. (1998) reported a phenotypic correlation of 0.29 between the RFI measured at the same stages in mice. On the other hand, the phenotypic correlations for the control groups were similar to the findings of Arthur et al. (2001b) who reported values of 0.43 for RFI.

The reranking reported for phenotypic FE in this study may question the appropriate time to measure the trait especially for individuals intended to be used as replacements. Even though early identification of efficient individuals is important for genetic improvement of FE in the beef industry, reranking may become a hindrance. The part-whole correlation may clarify some important points. The greater correlations between FP1&FP2 with FP2 in the feed-swap and grower-fed groups may show that conducting the FE evaluations in FP2 seem to give a better efficiency potential of each animal. At this time the steers were 290 d on average indicating that FE evaluations may be more appropriate at an older age when the animals are close to their mature weight. Apart from the effect of feeding period, the type of diet may also affect the level at which an animal

expresses its FE potential. The result from the finisher-fed group suggests that the efficiency of an animal may be determined earlier by offering a high-energy diet.

Our results were similar to those reported by Goonewardene et al. (2004) indicating that RFI measured later in a feed test was better correlated to the overall FE of animals. They reported greater Pearson correlation estimates for the part-whole correlations for RFI. The reasons behind the greater correlation are unclear but may be due to the use of different feed ingredients having different nutrient values. In addition, the sample size (n = 10) for their study was small and may bias results.

3.5 CONCLUSION

We set out to investigate if diet type influences the FE ranking of beef cattle by looking at the FE-class changes and correlation estimates between the two feeding regimes. The majority of the steers did not maintain their previous FE classes in FP2. A greater proportion of steers in the feed-swap group changed their RFI measure in FP2 by 0.25 SD, 0.5 SD or 1 SD. The correlation estimates between the two feeding periods for all test groups were low but were lower for the feed-swap group. We observed that switching diets as well as feeding period or stage of maturity affects the FE and FE-ranking of steers. Residual feed intake had the greatest correlation between the two periods for majority of the groups. Given that reranking exists, we suggest that finisher diet is still ideal for RFI evaluation in feedlot animals. We also suggest that RFI evaluation on lower energy diets should be examined in an effort to understand the relationships

between FE and feeder profitability. More studies are needed to understand the mechanisms surrounding the reranking in all groups.

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Table 3- 1. The ingredients (as-fed) and composition of the grower and finisher diets

Feed Composition	Grower diet	SD (n = 5)[a]	Finisher diet	SD (n = 5)[a]
Alfalfa Pellets	0.0	-	10.0	-
Oats grains	74.0	-	28.3	-
Barley grains	0.0	-	56.7	-
Grass Hay (Smooth brome)	20.0	-	0.0	-
Feedlot-32 Supplement [1]	6.0	-	5.0	-
ME content, MJ/kg	10.9	-	12.1	-
Chemical composition, % of DM				
DM	85.5	0.8	87.0	0.2
CP	13.0	0.5	13.5	0.4
Crude fat	4.3	0.4	3.3	0.3
ADF	17.9	1.8	10.3	0.6
NDF	39.4	3.1	29.5	4.7

[a]Five subsamples were analyzed for each component.

[1] Contained 440 mg/kg of Monensin, 1.6 mg/kg of Selenium, 5.0% Ca, 0.58% P, 0.76% K, 16 mg/kg I, 80 mg/kg Fe, 170 mg/kg Cu, 480 mg/kg Mn, 485 mg/kg Z, 4.3 mg/kg Co, 1.98% Na, 0.17% S, 0.38% Mg, 80500Iu/kg Vitamin A, 8000 Iu/kg Vitamin D, 1111 Iu/kg.

Table 3- 2. Integrity checks for the data collected on each feeding regime for the 3 groups for the 3 years[1]

	Feed-swap group						Control groups			
							Finisher-Fed		Grower-Fed	
Data check[2]	Year1-FP1	Year1-FP2	Year2-FP1	Year2-FP2	Year3-FP1	Year3-FP2	Year2-FP1	Year2-FP2	Year3-FP1	Year3-FP2
Number of animals	175	175	84	84	72	72	88	88	71	71
Mean age, d	193	-	195	-	200	-	195	-	201	-
Total days on test	83	93	90	71	79	82	90	71	79	82
Number of days excluded	1	28	24	7	1	1	5	5	1	2
Number of days included	82	65	66	64	73	81	85	66	73	80
Average feed disappearance (AFD),%	98.8	96.6	98.2	97.1	99.1	97.9	99.4	97.3	99.1	98.0
Total feed station days (FSD)	1,061	1,860	900	710	1,406	820	900	710	1,406	820
Feed station days < 95% AFD	29	627	115	117	22	64	19	128	22	69
Percentage of FSD < 95% AFD	2.7	33.7	12.8	16.5	1.6	7.8	2.1	18.0	1.6	8.4
Feed station days < 90% AFD	19	241	60	27	5	12	8	17	5	6
Pearson correlations										
Correlation between DMI and MWT	0.73	0.65	0.59	0.68	0.72	0.78	0.70	0.55	0.67	0.68
Correlation between DMI and ADG	0.58	0.48	0.46	0.57	0.61	0.69	0.63	0.41	0.52	0.33
Correlation between DMI and EFI	0.82	0.71	0.69	0.73	0.86	0.86	0.84	0.60	0.78	0.72
Correlation between DMI and UBF	0.40	0.32	0.46	0.29	0.60	0.50	0.39	0.12	0.40	0.33
Coefficients of determination										
Variation in DMI ~ ADG,MWT	0.64	0.48	0.42	0.54	0.71	0.75	0.70	0.36	0.58	0.48
Variation in DMI ~ ADG,MWT,UBF	0.67	0.50	0.49	0.54	0.74	0.76	0.71	0.36	0.60	0.52

[1] The feed-swap group was fed the grower in period 1 (FP1) followed by the finisher diet in period 2 (FP2), the Finisher-fed group was fed the finisher diet in both periods while the Grower-fed group was fed the grower diet in both periods.

[2] Feed station days (FSD) is calculated as the product of the days on test and the number of feeding nodes or bunks; MWT = metabolic mid-weight; UBF = Ultrasound back-fat; EFI = Expected feed intake.

Table 3- 3. Means and standard deviation of traits

	Feed-swap group				Finisher-fed group				Grower-fed group			
	Period 1, Grower		Period 2, Finisher		Period 1, Finisher		Period 2, Finisher		Period 1, Grower		Period 2, Grower	
Trait[1]	Means	SD	Means	SD	Means	SD	Means	SD	Means	SD	Means	SD
Initial BW, kg	260	31.6	381	39.0	259	29.6	413	35.8	268	30.4	392	35.4
Final BW, kg	364	37.1	539	50.2	398	34.7	535	43.0	357	34.2	516	40.6
DMI, kg/d	7.5	0.9	10.3	1.3	8.3	0.9	10.0	1.2	7.8	0.8	10.3	1.1
ADG, kg/d	1.2	0.2	1.8	0.3	1.5	0.2	1.6	0.3	1.2	0.2	1.5	0.2
MWT	74	6.0	99	6.9	77	5.4	102	6.1	74	5.6	98	6.0
RFI, Kg DM/d	0.00	0.56	0.00	0.95	0.00	0.59	0.00	0.93	0.00	0.57	0.00	0.79
G:F	0.15	0.02	0.14	0.02	0.15	0.02	0.14	0.02	0.14	0.02	0.13	0.02
KR (x100)	1.7	0.3	1.8	0.2	2.0	0.3	1.6	0.3	1.6	0.3	1.5	0.2

The feed-swap group was fed the grower in period 1 followed by the finisher diet in period 2, the Finisher-fed group was fed the finisher diet in both periods while the Grower-fed group was fed the grower diet in both periods.

[1] MWT = metabolic mid-weight; RFI = residual feed intake; KR = Kleiber ratio.

Table 3- 4. Proportion of the steers that changed or maintained the same feed efficiency class between periods

	Feed-swap group				Finisher-fed group				Grower-fed group			
	Changed		No-Change		Changed		No-Change		Changed		No-Change	
Feed Efficiency Measure[1]	n	%	n	%	n	%	n	%	n	%	n	%
Residual feed intake	181	54.7[a]	150	45.3[a]	45	51.1[a]	43	49.9[a]	36	50.7[a]	35	49.3[a]
Gain to feed ratio	204	61.6[a]	127	38.4[b]	52	59.1[a]	36	40.9[a]	38	53.5[a]	33	46.5[a]
Kleiber ratio	188	56.8[a]	143	43.2[b]	50	56.8[a]	38	43.2[a]	36	50.7[a]	35	49.3[a]

[a-b]Within each group, different superscripts indicate that the proportion of changed vs No-change are different at $P < 0.05$.

Table 3- 5. The proportion of steers that changed between the low and high classes

Feed Efficiency Measure [1]	Feed-swap group				Finisher-fed group				Grower-fed group			
	Low-to-High		High-to-Low		Low-to-High		High-to-Low		Low-to-High		High-to-Low	
	n	%	n	%	n	%	n	%	N	%	n	%
Residual feed intake	16	55.2[a]	13	44.8[a]	4	57.1[a]	3	42.9[a]	0	0	5	100
Gain to feed ratio	24	54.5[a]	20	45.5[a]	7	77.8[a]	2	22.2[a]	4	50[a]	4	50[a]
Kleiber ratio	15	48.4[a]	16	51.6[a]	3	42.9[a]	4	57.1[a]	3	42.9[a]	4	57.1[a]

[a-b] Within each group, different superscripts indicate that the proportion of changed vs No-change are different at $P < 0.05$.

Table 3- 6. Spearman rank correlations among the feed efficiency measures for the group fed the grower diet in FP1 and finisher diet in FP2[1]

Trait[2]	RFI2	G:F1	G:F2	KR1	KR2
RFI1	0.33***	-0.46***	-0.11	0.04	0.10
RFI2		-0.05	-0.57***	0.11*	-0.01
G:F1			0.20***	0.81***	0.20***
G:F2				0.15**	0.72***
KR1					0.31***

[1]Feed efficiency measures with suffix '1' were measured in the first feeding period while those with suffix '2' were measured in the second feeding period.
[2]RFI = residual feed intake (kg/d); KR = Kleiber ratio; G:F = Gain to feed ratio
*P < 0.05; **P < 0.01; ***P < 0.001

Table 3- 7. Spearman correlations for the control group fed the finisher diet in FP1 and FP2[1]

Trait[2]	RFI2	G:F1	G:F2	KR1	KR2
RFI1	0.42***	-0.52***	-0.35***	0.02	-0.17
RFI2		0.02	-0.49	0.31	-0.05
G:F1			0.29**	0.78***	0.34**
G:F2				0.06	0.86
KR1					0.22*

[1]Feed efficiency measures with suffix '1' were measured in the first feeding period while those with suffix '2' were measured in the second feeding period.
[2]RFI = residual feed intake (kg/d); G:F = Gain to feed ratio; KR = Kleiber ratio
*P < 0.05; **P < 0.01; ***P < 0.001

Table 3- 8. Spearman correlations for the control group fed the grower diet in FP1 and FP2[1]

Trait[2]	RFI2	G:F1	G:F2	KR1	KR2
RFI1	0.44***	-0.46***	-0.14	-0.01	0.0
RFI2		-0.16	-0.41***	0.07	0.06
G:F1			0.38***	0.84***	0.42***
G:F2				0.31**	0.84***
KR1					0.46***

[1]Feed efficiency measures with suffix '1' were measured in the first feeding period while those with suffix '2' were measured in the second feeding period.
[2]RFI = residual feed intake (kg/d); G:F = Gain to feed ratio; KR = Kleiber ratio
*P < 0.05; **P < 0.01; ***P < 0.001

Table 3- 9. **The Pearson correlations between combined-period FE with periodic-FE**

Trait[1]	Feed-swap group		Finisher-fed group		Grower-fed group	
	FP1[2]	FP2[2]	FP1[2]	FP2[2]	FP1[2]	FP2[2]
RFI	0.74[a]	0.83[b]	0.85[a]	0.78[a]	0.72[a]	0.87[b]
G:F	0.52[a]	0.59[a]	0.80[a]	0.59[b]	0.76[a]	0.84[a]
KR	0.61[a]	0.71[b]	0.79[a]	0.63[b]	0.79[a]	0.81[a]

FP1 indicates the first feeding period while FP2 is the second feeding period

[a-b]Within each group different superscripts indicate that both correlation coefficients are different at $P < 0.05$.

[1]RFI = residual feed intake (kg/d); G:F = Gain to feed ratio; KR = Kleiber ratio

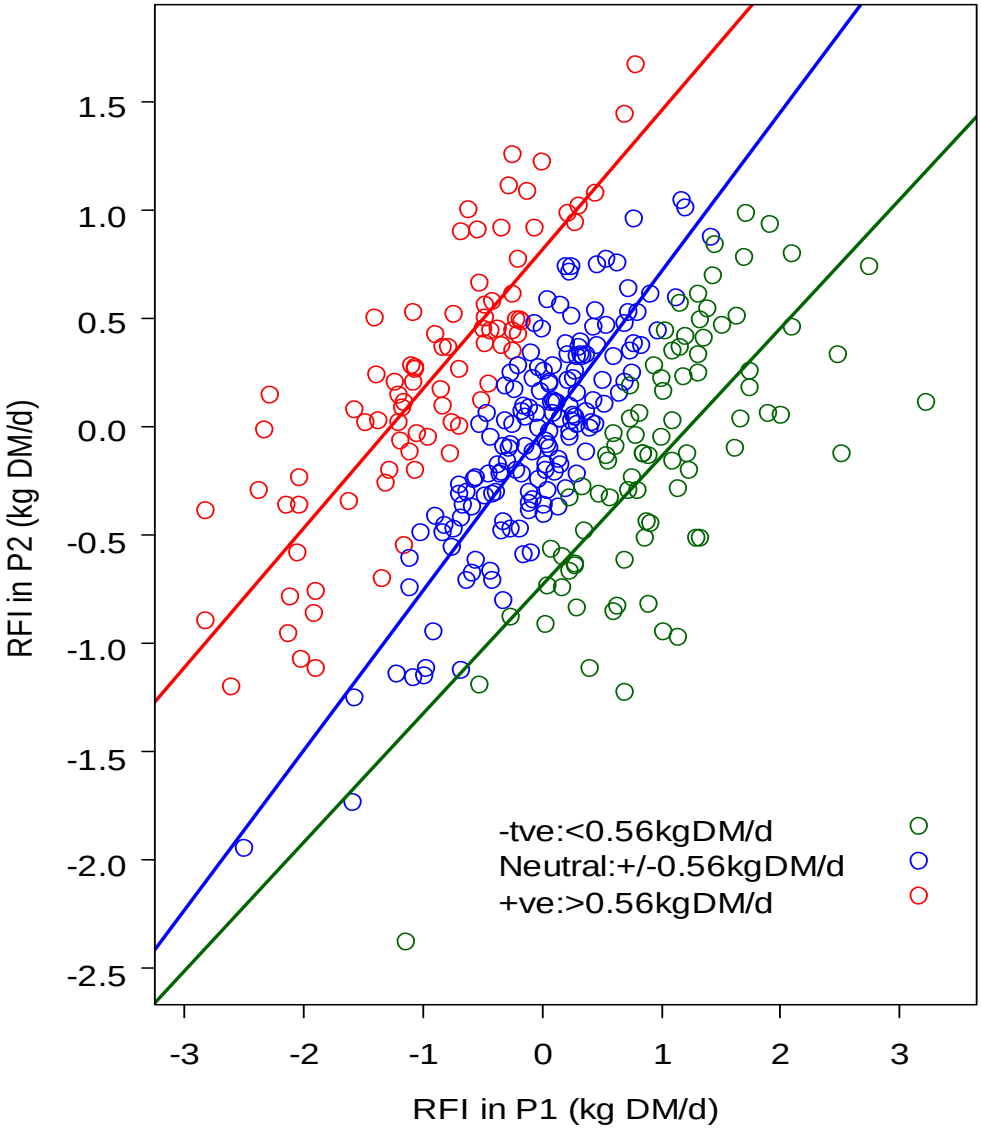
[2]Indicates the part-whole correlation between the feed efficiency trait in the period specified and the feed efficiency measured for the entire (FP1 + FP2) feeding period.

Table 3- 10. Least squares means of steers (Feedswap group) in different classes based on change in RFI by 1SD or 0.56 kg DM d^{-1}

	First feeding period				Second feeding period			
Trait	–veΔΔ (n=85)	NeutralΔ (n=162)	+veΔΔ (n=84)	P-Value	–veΔΔ (n=85)	NeutralΔ (n=162)	+veΔΔ (n=84)	P-Value
Initial body weight, kg	262.57 ± 3.38	256.48 ± 2.41	259.77 ± 3.32	0.309	382.71 ± 4.22	379.51 ± 3.01	387.27 ± 4.15	0.302
Average daily gain, kg d^{-1}	1.25 ± 0.02	1.25 ± 0.02	1.28 ± 0.02	0.503	1.86 ± 0.03	1.80 ± 0.02	1.82 ± 0.03	0.167
Dry matter intake, kg d^{-1}	7.80 ± 0.09^{a}	7.47 ± 0.07^{b}	7.46 ± 0.09^{b}	0.007	9.66 ± 0.12^{a}	10.24 ± 0.09^{b}	11.22 ± 0.12^{c}	<0.0001
Gain to feed ratio	0.15 ± 0.002^{a}	0.15 ± 0.002^{ab}	0.16 ± 0.002^{b}	0.003	0.16 ± 0.002^{a}	0.14 ± 0.001^{b}	0.13 ± 0.002^{c}	<0.0001
Residual feed intake, kg DM d^{-1}	0.22 ± 0.06^{a}	-0.04 ± 0.04^{b}	-0.13 ± 0.06^{b}	0.0001	-0.95±0.08^{a}	-0.03±0.05^{b}	1.01±0.07^{c}	<0.0001
Ultrasound backfat thickness, cm	0.47 ± 0.02	0.46 ± 0.01	0.43 ± 0.02	0.170	0.83 ± 0.02	0.82 ± 0.02	0.81 ± 0.02	0.869
Ultrasound rib eye area, cm^2	58.42 ± 0.74	58.21 ± 0.53	57.94 ± 0.72	0.895	74.88 ± 0.79	74.61 ± 0.56	74.80 ± 0.77	0.955
Ultrasound marbling	4.12 ± 0.06	4.15 ± 0.04	4.03 ± 0.06	0.238	5.02 ± 0.07	5.07 ± 0.05	5.02 ± 0.07	0.771

$^{a-b}$Within each feeding period, different superscripts indicate that both correlation coefficients are different at $P < 0.05$.

Figure 1: Steers' RFI in period 1 and period 2 (0.56 kg DM d^{-1})



Each point indicates the coordinates of each steer's RFI in P1 and P2. The red points reflect the steers that declined in RFI (became inefficient) in P2 by at least 0.56 kg DM d^{-1} while the green points indicate steers that improved in RFI (became efficient) by at least 0.56 kg DM d^{-1}. The blue points show the steers that changed by less than 0.56 DM d^{-1} in P2.

CHAPTER 4

GENETIC PARAMETERS AND GENOTYPE-BY-ENVIRONMENT INTERACTION FOR FEED EFFICIENCY TRAITS IN STEERS FED GROWER AND FINISHER DIETS[2].

4.1 INTRODUCTION

Recently, many researchers have conducted feeding trials in order to examine feed utilization in beef cattle (Okine et al., 2001; Crews et al., 2003; Nkrumah et al., 2004; Golden et al., 2008) but most of these studies were conducted in feedlots using energy-dense finisher diets. However, a common practice in North American beef production is that young cattle are often backgrounded with less energy-dense diets prior to the finishing period. If the goal of beef production is enterprise feed efficiency, then it is important to identify feed efficient animals across all beef production segments.

Despite the number of studies conducted on feed efficiency traits, little is known about the genetic parameters under different feeding regimes or the consistency of feed efficiency measures throughout the beef production cycle. In addition, most of the genetic parameters for feed efficiency traits in cattle were estimated under the assumption of independence of genetic and environmental effects in their model estimations. Durunna et al. (2011) reported the existence of phenotypic reranking for residual feed intake (RFI), G:F and Kleiber ratio, however, the existence of genetic reranking for these traits is still unclear. It is

[2] A version of this chapter has been published online. Durunna et al. 2011a. J. Anim. Sci. doi: 10.2527/jas.2010-3516

important to know whether the steers that were efficient in the feedlot were also efficient on previous diets prior to the finisher diet. Ignoring differential genetic performance (if they exist) may lead to inaccurate estimation of overall genetic performance. An early evaluation of these animals while they are on other diets might give some indication of their final efficiency status thereby facilitating the identification of animals with consistent performances across different feeding regimes.

Based on the foregoing, we used growing beef steers to determine whether (1) similar genetic variation exists when a grower diet or a finisher diet is fed, (2) the genetic relationships between the feed efficiency traits measured under the grower-fed and finisher-fed periods are close to unity, i.e. if the traits measured are not affected by genotype-by-environment interactions (GEI).

4.2 MATERIALS AND METHODS

All animals were located at the University of Alberta ranch at Kinsella, Alberta and were cared for according to the Canadian Council on Animal Care (CCAC, 1993) guidelines.

4.2.1 Animals and Management

A total of 490 steers were used in the three-year trial from 2006 to 2009. These steers were born in the spring of 2006, 2007 and 2008 from 46 sires mated to 357 crossbred dams on pasture. The steers were crosses between hybrid, Angus

or Charolais bulls and hybrid dams generated from three composite cattle lines (Goonewardene et al, 2003).

The steers grazed with their dams until they were weaned. All animals had been vaccinated four weeks prior to arriving at the feeding facility. The vaccinations were for infectious bovine rhinotracheitis, parainfluenza-3 virus, bovine viral diarrhea, bovine respiratory syncytial virus, *Haemophilus somnus*, *Pasteurella multocida* and clostridial diseases. Upon arrival, each steer was treated with Ivomec (Merial, Baie d'Urfe, Canada), which controls warble larvae, mites, lice and horn fly. Each steer was also identified with a radio frequency transponder button (half duplex RFID, Alflex USA, Inc., Dallas/Ft. Worth Airport, TX 75261-2266) in its right, or left ear. The transponder button was located five to six cm from the base of the ear, in the middle, with the transponder button on the inside part of the ear.

The composition of the grower diet on a 100% as-fed basis was 74% oats, 20% hay and 6% feedlot supplement while the finisher diet contained 10% alfalfa pellets, 28.3% oats, 56.7% barley and 5% feedlot supplement. The ME content of the grower diet was 2.6 Mcal/kg while that of the finisher diet was 2.9 Mcal/kg. The crude protein contents were 13% and 13.5% for the grower and finisher diets, respectively. The steers were adjusted to their trial rations during a pre-test adjustment period of 21 to 30 days, and 14 days between feeding regimes. The initial adjustment period enabled the animals to acclimate to the GrowSafe feeding units and test rations.

There were two feeding regimes in each of the three years. The first feeding regime (**FP1**) was during the Fall-Winter season while the second feeding regime (**FP2**) was during the Winter-Spring season. In the first year, all steers (n = 175) were in the feed-swap group. This group was provided with a grower diet in FP1 followed by the finisher diet in FP2. In the second and third years, the animals were divided into two (feed-swap and control) groups. The feed-swap groups for the second (n = 84) and third (n = 72) years were also fed a grower diet in FP1, then the finisher diet in FP2. In total, there were 331 steers were in the feed-swap group. The control groups were fed the same diet throughout the two feeding regimes where the finisher diet was fed in the second year (n = 88) while the grower diet was fed in the third year (n = 71). Therefore, the steers in the control groups had repeated records on each diet.

4.2.2 Data collection

In the first year, the entire test ran from November 1, 2006 to May 2, 2007 while the second and third years ran from November 6, 2007 to May 1, 2008 and November 2, 2008 to May 1, 2009, respectively. The weights of all steers were measured once every 2 wk throughout the test periods. Ultrasound back-fat (**UBF**) thickness was measured at the beginning and at the end of each feeding regime. It was measured with an Aloka 500V real-time ultrasound, which has a 17.5 cm 3.5MHz probe (Overseas Monitor Corporation Ltd., Richmond, British Columbia, Canada). Feed intake of each steer was measured daily using the GrowSafe automatic feeding system (GrowSafe Systems Ltd., Airdrie, Alberta,

Canada). Briefly, the system used for data collection consisted of 20 feeding nodes (located in a covered feeding shed), a data-logging reader panel and a computer that contained the data acquisition software. Each feeding node had a feed tub on two load bars and an antenna embedded in the rim of each tub. The daily assigned feed disappearance (**AFD**) for each node was used for data integrity and checking purposes. The AFD was calculated as the ratio of the total daily feed delivered to each tub to the daily sum of individual animal feed intakes as attributed by the GrowSafe System for a specific tub. The AFD should be sufficiently high (> 95%) for each day's data to be included for data analysis. Data collected on the days that had low AFD were excluded from all analyses.

4.2.3 Genotyping and sire identification

Because the mating were made in a multi-sire pasture, sire identification was performed via genotyping. Ear tissues or blood samples or both were collected from all steers for DNA extraction. The Invitrogen-PureLink 96 kit (Invitrogen Canada Inc. Mainway, Burlington, Ontario, Canada) was used for DNA extraction from ear tissues while the QuickGene DNA whole Blood kit (Fujifilm Medical System U.S.A. Inc. Stamford, CT, U.S.A.) was used for DNA extraction from blood. The DNA from all steers and potential sires in all mating groups were genotyped with the Illumina BovineSNP50 BeadChip. A subset of the SNPs (n = 28,364) out of 51,000 SNPs was used for parentage determination. The SNP selection criteria were based on 100% SNP frequency, at least 95% animal call rate and a 0.1 minor allele frequency. Sire-progeny calls or sib-group calls were

made by comparing the number of genotype mismatches among the steers and potential sires. For any locus, a mismatch was flagged if neither allele for one animal matches either allele for the other animal (for e.g. AA and BB are mismatches while AA and AA or AB are not). Sire-progeny calls were made based on the fewest number of mismatches between a potential sire and steer. All steers assigned to a sire, were compared to each other by averaging the number of mismatches between each steer and all its assigned siblings. The average number of SNP mismatches for sire-progeny calls was 5 while sib-groups had an average mismatch of 722 SNPs. If a sire's genotype was unavailable or if certain steers do not have a putative sire, the average sibling mismatch score was used to assign such steers into sib groups whereby the best possible sib-group was determined by comparing each steer to every other sibling group.

4.2.4 Trait derivations and Statistical Analysis

The ADG, initial body weight and mid-test body weight of each animal were computed from the regression coefficients of each animal's linear growth path using the PROC REG procedure in SAS (Version 9.2, SAS Inst., Inc., Cary, NC). The mid-test body weight was converted to metabolic mid-weight (**MWT**) by $BW^{0.75}$. Each steer's average daily feed intake (100% as-fed) was multiplied by the dry matter content of the feed to derive the DMI. The DMI was standardized across diets and years to 10 MJ ME kg^{-1} DM. Expected DMI was obtained as a regression of the standardized DMI on ADG, MWT and UBF using the PROC GLM of SAS. The RFI was calculated as the actual standardized DMI minus the

expected DMI. The G:F ratio was calculated for each steer as the ratio of daily ADG to DMI.

4.2.5 Genetic Evaluation and Genotype-by-environment Interaction

Estimated breeding values, genetic and phenotypic correlations were derived for the steers (n = 331) in the feed-swap group using a bivariate animal model implemented in ASReml (Gilmour et al., 2008). The model equation is shown below with the breed-of-sire and year-of-test as fixed effects while the age at the beginning of the test was used as a linear covariate. Feeding duration (a measure of activity) was included as an additional covariate in the analysis of RFI in order to account for differences in feeding behavior (Basarab et al., 2011; Durunna et al. 2011a).

$$\begin{bmatrix} \boldsymbol{y}_1 \\ \boldsymbol{y}_2 \end{bmatrix} = \begin{bmatrix} \boldsymbol{X}_1 & 0 \\ 0 & \boldsymbol{X}_2 \end{bmatrix} \begin{bmatrix} \boldsymbol{b}_1 \\ \boldsymbol{b}_2 \end{bmatrix} + \begin{bmatrix} \boldsymbol{Z}_1 & 0 \\ 0 & \boldsymbol{Z}_2 \end{bmatrix} \begin{bmatrix} \boldsymbol{a}_1 \\ \boldsymbol{a}_2 \end{bmatrix} + \begin{bmatrix} \boldsymbol{e}_1 \\ \boldsymbol{e}_2 \end{bmatrix}$$

where $\mathbf{y}_1$ and $\mathbf{y}_2$ are the vectors of phenotypic measurements for traits measured in the grower-fed (length = $N_1 \times 1$) and finisher-fed (length = $N_2 \times 1$) periods, respectively; $\mathbf{X}_1$ and $\mathbf{X}_2$ are incidence matrices relating the fixed effects to records y_1 and y_2, respectively; $\mathbf{b}_1$ and $\mathbf{b}_2$ are vectors of fixed effects (year and sire-breed) in the grower-fed and finisher-fed periods respectively;. $\mathbf{Z}_1$ and $\mathbf{Z}_2$ are incidence matrices relating the phenotypic observations to the vectors of polygenic (**a**) effects for the grower-fed and finisher-fed periods, respectively. $\mathbf{e}_1$ and $\mathbf{e}_2$ are vectors of random residuals in the grower-fed and finisher-fed periods, respectively.

The expectations and variances were

$$E\begin{bmatrix} y_1 \\ y_2 \end{bmatrix} = \begin{bmatrix} X_1 & 0 \\ 0 & X_2 \end{bmatrix} \begin{bmatrix} b_1 \\ b_2 \end{bmatrix}$$

and

$$V\begin{bmatrix} a_1 \\ a_2 \\ e_1 \\ e_2 \end{bmatrix} = \begin{bmatrix} A\sigma^2_{a1} & A\sigma_{a21} & 0 & 0 \\ A\sigma_{a21} & A\sigma^2_{a2} & 0 & 0 \\ 0 & 0 & I\sigma^2_{e1} & I\sigma_{e12} \\ 0 & 0 & I\sigma_{e21} & I\sigma^2_{e2} \end{bmatrix}$$

a and **e** were assumed to be normally distributed with mean of zero and (co)variances $A\sigma^2_a$, $I\sigma^2_e$ for a and e, respectively. A is the additive relationship matrix, σ^2_a and σ^2_e are the additive genetic and residual variances, respectively. I is an identity matrix with order equal to the number of animals.

Estimates of permanent environmental (**PE**) effects were derived by including the animals that received the same diet in the two successive feeding periods (control groups). Subsequently, the total number of records for the grower-fed group was 473 from 402 steers while there were 507 records in the finisher-fed group from 419 steers. A repeated animal model was implemented in ASReml (Gilmour et al., 2008) for DMI, ADG, RFI and G:F. The model was

$$y = Xb + Z_1a + Z_2p + e$$

where **y** is the vector of phenotypic observations, **X** is a design matrix relating the observations in y to particular levels of the fixed effects vector **b**. Z_1 and Z_2 are incidence matrices relating the observations in y to the vectors of polygenic (**a**) effects and the PE effects (**p**), respectively. **e** is a vector of random residuals. a, p and e were assumed to be normally distributed with mean of zero and

(co)variances $A\sigma^2_a$, $I_n\sigma^2_p$, $I_n\sigma^2_e$ for a, p and e, respectively. A is the additive relationship matrix, σ^2_a, σ^2_p, and σ^2_e are the additive genetic, permanent environment and residual variances, respectively. I_n is an identity matrix with order equal to the number of animals. It was assumed that the polygenic effects and the PE effects were independent. The PE effects were calculated as the ratio of PE variance to the total phenotypic variance while the heritability was calculated as

$$h^2 = \frac{\sigma_a^2}{\sigma_a^2 + \sigma_p^2 + \sigma_e^2}$$

Falconer and Mackay (1996) indicated that the genetic correlation between traits estimated in two different environments gives an indicator of the genotype-by-environment interaction. The character-state model (Hammami et al., 2009) was based on this method. The GEI was obtained from the bivariate analysis using the feed-swap group.

4.3 RESULTS AND DISCUSSION

4.3.1 Genetic Parameters

Inclusion of the UBF in the model containing ADG and MWT increased the R^2 by up to 7% (Durunna et al. 2011). Tests for homogeneity of variances were not statistically significant ($P > 0.05$) for the traits in FP1 but were significant ($P < 0.5$) in P2. We did not transform the variables in FP2 because a bivariate animal model could account for heterogeneous variances (Henderson, 1984). In addition,

Boldman and Freeman (1990) observed that sire evaluations were less sensitive to unequal variances and they concluded that ignoring the existence of heterogeneous variances may be better than log transformation. We do not know the reasons behind this heteroscedasticity in the second feeding regime nor its eventual consequences, but animals' performances may be wrongly ranked if the variances increase with the mean performance of the group (Boldman and Freeman, 1990). However, Dimov et al. (1995) reported that interplay between the genotypes and the environments may not be responsible for the heteroscedasticity.

The phenotypic variances and heritability estimates for the grower-fed and finisher-fed groups from the bivariate analyses were shown in Table 4- 1. There were greater phenotypic variances in the finisher-fed group for DMI, ADG, and RFI while G:F had greater phenotypic variance in the grower-fed regime. The results from the univariate analyses (for the two groups) are shown in Table 4- 2. The bivariate and univariate results showed that heritability estimates of DMI, ADG, RFI and G:F were greater in the finisher-fed regime than in the grower-fed regime. The PE effects were greater in the grower-fed regime for ADG, RFI and G:F by 0.10, 0.08 and 0.35, respectively. However, DMI had greater PE effects in the finisher-fed regime than in the grower-fed regime.

There were greater genetic variances (data not shown) in the finisher-fed group than in the grower-fed group and may have contributed to the observed heritability estimates. Genetic and phenotypic variances for production traits have been investigated under different environments (Nauta et al., 2006; Haile-Mariam

et al., 2008). Nauta et al. (2006) reported greater phenotypic variances for milk yield traits in a conventional production environment than in an organic environment in which the feed contains at least 60% DM from forages. Also in agreement with our findings, Kearney et al. (2004) reported greater genetic variances and heritability estimates for production traits in herds of dairy cows fed a conventional feed, compared to those grazed on forages. Cienfuegos-Rivas et al. (1999), however, reported lower genetic variance in milk yield of Holstein cows in Mexican environments vs. in US environments. Cerón-Muñoz et al. (2004) pointed out that smaller genetic variances do not always translate to smaller heritability estimates but will also depend on the size of the residual variances. We do not know the reasons behind the low genetic variances and heritability in the grower-fed group. There may be (unknown) influential factors that need to be considered. The estimates from the finisher-fed group were similar to values in the literature.

The available reports on heritability estimates for growth and efficiency traits were inconsistent with age or production phase. Archer et al. (2002) reported greater additive genetic variance in the cows than in the post-weaned calves. Their heritability estimates agreed with the finisher-fed group in this study for DMI (0.28 vs. 0.34). They reported a greater value for ADG (0.33) while the results here were greater for G:F or feed conversion ratio (FCR) and RFI. Genetic variances for growth and efficiency traits were greater at the yearling stage of Charolais bulls than in the weaner stage for RFI, FCR and daily feed intake (Arthur et al., 2001). However, the authors reported greater heritability estimates

at the weaner stage for ADG (0.31), daily feed intake (0.46) and FCR (0.42). The greater heritability estimates for the weaner calves was probably due to greater genetic variance observed at that age. Fan et al. (1995) reported a heritability estimate of 0.16 for ADG in Hereford bulls, which was lower than the estimate from the finisher-fed group.

The greater genetic variance in the finisher-fed group compared to the grower-fed group may imply that the grower diet or the feeding period may have introduced some unknown influence that limited the genetic evaluation or growth potential in that group. On the other hand, it may suggest possible effect of age in the expression of genes. Even though the initial age on test was included as a fixed effect, there may be other unaccounted effects due to age or weather conditions. Other confounding factors such as body size may have also limited our findings. The experimental design used in this study could not separate the effects due to age or body size from those due to diet. Further studies may be required to investigate the effect of age in order to give more insight into the biology of feed efficiency.

Investigating the permanent environmental effect (Table 4- 2), showed that the grower-fed group had greater environmental influence than the finisher-fed group. Choy et al. (2002) reported that nutrition poses a permanent environmental effect. Mujibi et al. (2010) reported that season of testing also influences the performance of crossbred steers. The heritability estimates from this analysis were generally greater than those obtained from the bivariate model. Even though the

sample size was larger, separating the PE effect might have improved the analysis of the grower-fed group.

4.3.2 Genotype by Environment Interaction

Previous reports have indicated the existence of reranking in steers fed the grower and finisher diets in successive regimes (Crews et al., 2003; Durunna et al., 2011). The presence of GEI causes the reranking of animal performances across different environments (Nauta et al., 2006). Baker et al. (2002) used the interaction model to examine the presence of GEI for Angus and Hereford bulls performance-tested on pasture or high concentrate diet. They reported an absence of significant interactions.

The phenotypic and genetic correlations among DMI, ADG, G:F and RFI measured during the grower- and finisher-fed regimes are shown in Table 4- 3. There were larger standard errors for the genetic correlations, which may be due to large variability or insufficient sample size. The large standard errors (especially) in the grower-fed regime would limit our conclusions from this study. Genetic correlations between the grower-fed and the finisher-fed groups were different from unity for DMI, ADG, G:F and RFI.

Genetic correlation greater than 90% may indicate absence of GEI showing that performances were uniform across the different environments (Crews et al., 2003). While the genetic correlations for DMI, ADG and G:F were moderately high (0.78 to 0.80), it may suggest that the trait measured in the two feeding periods may be different traits and may be influenced by different sets of genes.

The genetic correlation for RFI was much less, an indicator of differential performances over different environments.

The phenotypic correlations between G:F and RFI were negative in both periods. The results within the finisher-fed steers were similar to those reported by Nkrumah et al. (2007). RFI had no phenotypic relationship with ADG but the genetic relationship was not zero in the finisher-fed period. The relationship between RFI measured in the two feeding regimes was positive. The RFI in the grower-fed period had a low phenotypic correlation with DMI measured in the finisher-fed period.

The magnitude of genetic correlations between the traits expressed in different environments of interest have been used by several researchers to determine the existence of GEI in milk production traits in cattle (Nauta et al., 2006; Haile-Mariam et al., 2008), growth traits in chickens (N'Dri et al., 2007), and carcass traits in pigs (Merks, 1986). Archer et al. (2002) reported a lower genetic correlation for G:F (0.20) compared to the results in this study. Their reports indicated serious GEI for G:F. N'Dri et al. (2007) reported important GEI for growth trait parameters used for indirect selection for feed conversion ratio in 'Label Rouge' chickens while Merks (1986) reported that genotype-by-batch and genotype-by-sex interactions did not exist for feed conversion ratio in pigs. Crews et al. (2003) reported a genetic correlation of 0.55 between the net feed efficiency measured during the growing and finishing phases of steers. This value was similar to the results in this study (ignoring the large standard errors) even though the compositions of the diets were slightly different in the two studies. They also

fed the steers for a longer time (especially in FP2) than reported here. Arthur et al. (2001) reported greater genetic correlations between weaner and yearling bulls fed the same diet for body weight (0.95), daily feed intake (0.90), feed conversion ratio (0.42) and RFI (0.75). The high estimate for body weight agrees with the conclusion of Hartmann (1990) that GEI does not have much impact on body weight. This study obtained lower estimates for DMI but almost double of their estimate for G:F.

Fan et al. (1995) reported breed-by-diet interactions for residual feed consumption and gross feed efficiency in postweaned Angus and Hereford bulls fed high and medium energy diets where the Angus bulls had greater residual feed consumption but lower gross feed efficiency on the high-energy diet than the Hereford bulls. Zwald et al. (2003) reported low genetic correlations among genotypes classified by temperature, herd size and peak milk yield. Kearney et al. (2004) reported low product-moment and rank correlations for milk yield (0.59, 0.62), fat yield (0.63, 0.64) and protein yield (0.66, 0.66) between herds of cattle reared in grazing and confined production environments, respectively. Cienfuegos-Rivas et al. (1999) reported low rank correlations (< 0.7) in sire breeding values for milk yield in their daughters measured in Mexican and US herd environments. Differences in sire performances in different environments may also be due to heterogeneous genetic variances within a population, small sample size or preferential treatment given to sib-groups (Maniatis and Pollott, 2002).

The consequence of ignoring these rerankings (where they exist) may result in higher feed costs within the feeding phase where the genotypes were more sensitive to the diet. Other consequences may include reduced benefits from global marketing of products (Cerón-Muñoz et al., 2004), disregard for the need for a separate breeding program (Nauta et al., 2006) and reduced genetic progress as a result of lower accuracy of genetic evaluations (Zwald et al., 2003). A solution for differential RFI performance may be selective breeding (Nauta et al., 2006), where only the parents of animals that are efficient in both feeding regimes may be used for subsequent breeding. Alternatively, animals may also be selected based on the environment of best performance. Even though the results here place less emphasis on the feed efficiency on roughage-based diets for feedlot steers, feed efficient cows in the cow-calf sector are extremely important because of their level of feed intake throughout the beef production cycle.

4.4 CONCLUSION

To maximize benefits, improvement in feed efficiency should occur at all phases of beef production, which are marked by the type of feed given to animals. Cattle that are efficient at all phases regardless of the type of diet given to them would be more desirable. This study has reported the existence of genotype-by-environment interactions for DMI, ADG, RFI and G:F in beef steers fed grower and finisher diets in successive feeding regimes. From these results, the efficiency status of a steer may be dependent on the feeding regime. Because of the presence of GEI for RFI, it is of the opinion of the authors that steers should be evaluated

across diets or seasons. Nevertheless, where selection is difficult for animals with excellent performance across feeding regimes (generalists), choosing parents whose progeny are efficient in the finishing phase may be more cost effective than those that are more efficient on the growing phase. This is due to the higher cost (per kg) of the finisher diet than the grower diet. However, this strategy may place less importance on high forage diets and may ignore the importance of efficiency of feed utilization in the cowherd. It should be noticed that although effect of age on the test animals could not be separated from the effect of diet in this study, the confounding will exist in most commercial production settings. However, further research may be required to examine the contribution of age to the overall reranking of steers for feed efficiency traits. Finally, the authors advocate further comprehensive feeding trials in order to provide more insight into the mechanisms surrounding GEI in cattle.

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Table 4- 1. Phenotypic variances and heritability estimates from bivariate analyses for the grower-fed and finisher-fed groups.

	Grower-fed group		Finisher-fed group	
Trait[1]	σ^2_p	h^2	σ^2_p	h^2
ADG	0.04 ± 0.003	0.08 ± 0.13	0.07 ± 0.006	0.23 ± 0.14
DMI	0.68 ± 0.05	0.15 ± 0.14	1.42 ± 0.11	0.34 ± 0.16
RFI	0.29 ± 0.02	0.08 ± 0.11	0.78 ± 0.06	0.42 ± 0.16
G:F	0.00044 ± 0.00004	0.14 ± 0.15	0.00035 ± 0.00003	0.40 ± 0.17

[1] RFI = residual feed intake

Table 4- 2. Genetic parameters from univariate analysis including permanent environmental (PE) effects in the grower-fed and finisher-fed steers.

	Grower-fed group		Finisher-fed group	
Trait[1]	Heritability	PE effect	Heritability	PE effect
DMI	0.30 ± 0.15	0.30 ± 0.15	0.43 ± 0.14	0.35 ± 0.14
ADG	0.06 ± 0.08	0.38 ± 0.12	0.17 ± 0.10	0.28 ± 0.12
RFI	0.19 ± 0.12	0.18 ± 0.14	0.36 ± 0.13	0.10 ± 0.15
G:F	0.07 ± 0.09	0.40 ± 0.13	0.26 ± 0.12	0.05 ± 0.14

[1] RFI = residual feed intake

Table 4- 3. The phenotypic (above the diagonal) and genetic correlations (below the diagonal) among the traits measured in the two feeding periods.

Trait[1]	DMI-grower	ADG-grower	G:F-grower	RFI-grower	DMI-finisher	ADG-finisher	G:F-finisher	RFI-finisher
DMI-grower	1	0.55 ± 0.04	-0.20 ± 0.05	0.62 ± 0.04	0.63 ± 0.03	0.27 ± 0.05	-0.26 ± 0.05	0.23 ± 0.05
ADG-grower	0.69 ± 0.97	1	0.70 ± 0.03	-0.00 ± 0.06	0.45 ± 0.05	0.38 ± 0.05	0.01 ± 0.06	0.06 ± 0.05
G:F-grower	-0.73 ± 0.93	0.63 ± 0.60	1	-0.55 ± 0.04	0.01 ± 0.06	0.17 ± 0.05	0.22 ± 0.05	-0.12 ± 0.05
RFI-grower	-0.34 ± 0.74	NE	-0.24 ± 1.2	1	0.32 ± 0.05	0.05 ± 0.06	-0.18 ± 0.06	0.39 ± 0.05
DMI-finisher	0.78 ± 0.27	0.47 ± 0.64	-0.33 ± 0.74	-0.28 ± 0.76	1	0.55 ± 0.04	-0.27 ± 0.05	0.68 ± 0.03
ADG-finisher	-0.20 ± 0.65	0.80 ± 0.79	0.70 ± 0.47	-0.50 ± 0.54	0.35 ± 0.33	1	0.65 ± 0.03	-0.00 ± 0.06
G:F-finisher	-0.90 ± 0.42	NE	0.78 ± 0.43	-0.26 ± 0.41	-0.55 ± 0.28	0.56 ± 0.26	1	-0.62 ± 0.04
RFI-finisher	0.37 ± 0.56	-0.31± 0.98	-0.33 ± 0.61	0.50 ± 0.48	0.59 ± 0.26	-0.15 ± 0.48	-0.67 ± 0.26	1

[1] RFI = residual feed intake; NE = Not estimable due to negative variances

CHAPTER 5

PHENOTYPIC AND GENETIC RELATIONSHIPS AMONG MEASURES OF FEEDING BEHAVIOR WITH FEED INTAKE, AND FEED EFFICIENCY IN STEERS FED GROWER AND FINISHER DIETS[3].

5.1 INTRODUCTION

The relationships among feed intake and feeding behavior traits (feeding duration (**FD**), headdown time (**HDT**) and feeding frequency (**FF**) or visits) have been reported in cattle (DeVries et al., 2005; Nkrumah et al., 2007; Azizi et al., 2009; Bingham et al., 2009). Feeding behavior traits can account for up to an additional 35% of the total variation in DMI to those contributed by ADG, metabolic mid-weight (**MWT**) and ultrasound fat measurements (Lancaster et al., 2009). This means that they can potentially provide additional information that will give us a better understanding of the biological and physiological mechanisms surrounding residual feed intake (**RFI**) variation (Lancaster et al., 2009). In addition, Nkrumah et al. (2007) added that measures of feeding behavior could be used as indicator traits for feed efficiency performance.

Growing calves are fed different feed compositions but most literature on feeding behavior traits in feedlot cattle have been carried out using the finisher diet. Gibb et al. (1998) reported that feeding behavior for individual animals were usually consistent throughout a test period. Nevertheless, not much is known about the consistency of feeding behavior across feeding regimes especially for

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steers that transition from a backgrounding diet to a finishing diet. In addition, measures of feeding behavior may help to explain how animals adapt to different diets (Abijaoude et al., 2000). The objectives of the study were to examine (1) whether feeding behavior was the same when feedlot steers were fed a grower versus a finisher diet; (2) whether differences in steers' feeding behavior traits were consistent among the different efficiency classes regardless of the feeding period and (3) whether the feeding behavior traits measured in different feeding periods have a genetic correlation of unity.

5.2 MATERIALS AND METHODS

5.2.1 Animals and Management

Crossbred steers (n = 331) were used in a 3-yr feeding trial conducted at the University of Alberta ranch at Kinsella, Alberta from 2006 to 2009. The steers were cared for according to the Canadian Council on Animal Care (CCAC, 1993) guidelines. The steers were born in the spring of 2006, 2007 and 2008 from 44 crossbred sires mated to 265 crossbred dams on pasture. The crossbred dams were crosses between Angus or Charolais bulls and composite dams generated from three synthetic cattle lines namely Beef Synthetic 1(BS1), Beef Synthetic 2 (BS2) and Dairy × Beef Synthetic (DBS) (Goonewardene et al., 2003). The crossbred sires were bulls selected from crosses between crossbred, Angus or Charolais bulls and the crossbred dams.

Upon arrival at the test facility, each steer was tagged with a radio frequency transponder button (half duplex RFID, Alflex USA, Inc., Dallas/Ft. Worth Airport, TX 75261-2266) in its right, or left ear which was located 5 to 6 cm from the base of the ear, with the transponder button on the inside part of the ear. Feed and clean drinking water were offered *ad libitum* throughout the test periods. There were two feeding periods each year. The first feeding period (**FP1**) ran from November to January. The minimum number of days on test was 79 days. During this period, the steers received a grower diet composed of approximately 74% oats, 20% hay and 6% feedlot supplement. The grower diet had an ME content of approximately 2.6 Mcal/Kg. In the second feeding period (**FP2**) that ran from February to May (minimum number of days = 71). The steers received a finisher diet that contained approximately 10% alfalfa pellets, 28% oats, 57% barley and 5% feedlot supplement while the ME content was approximately 2.9 Mcal/Kg. There were 175, 84 and 72 steers, respectively for test-years 1, 2 and 3, respectively. The steers were adjusted to their trial rations during a pre-test adjustment period of at least 21 days. This initial adjustment period enabled the animals to acclimate to the GrowSafe feeding units and test rations. At the end of the first period, a 14 d adjustment period was allowed before the commencement of feed intake data collection for the FP2. During this period, the diet was adjusted from the grower to the finisher diet.

5.2.2 Data Collection

The weights of all steers were measured once every 2 wk throughout the test periods. Ultrasound back-fat (**UBF**) thickness was measured at the beginning and at the end of the feeding period with an Aloka 500V real-time ultrasound with a 17.5 cm 3.5MHz probe (Overseas Monitor Corporation Ltd., Richmond, British Columbia, Canada). Feed intake measurements were taken with the GrowSafe feeding system (GrowSafe Systems Ltd., Airdrie, Alberta, Canada). The system consists of radio frequency identification (**RFID**) tag on each animal, 20 feeding units located in a covered feeding shed, a data logging reader panel and a computer that contained the data acquisition software. Each feeding unit consisted of a feed tub balanced on two load bars, and an antenna embedded in the rim of each tub.

The antenna detects and identifies each steer via electromagnetic waves. The system then records the amount of feed consumed as well as feeding behavior as each steer eats from any feed bunk. Data generated from the feeding units are stored in the data logging reader panel. The data are transferred wirelessly to the personal computer located about 100 meters away. The GrowSafe data acquisition and analysis software in the computer converts the data into readable formats for subsequent analyses. For data integrity and quality control purposes, the GrowSafe system has an internal audit system that calculates the daily assigned feed disappearance (**AFD**) for each feeding node. The system reconciles the total daily feed delivered to each bunk with the sum of the daily consumption of each steer. The AFD should be sufficiently high (> 95%) for each day's data to be

included for data analysis. Data collected on the days that had low AFD were excluded from all analyses.

5.2.3 Trait Derivations, Statistical and Genetic Analyses

All traits were calculated within each feeding regime. The ADG, initial body weight and mid-test body weight of each animal were calculated from the regression coefficients of each animal's linear growth path using the GLM procedure in SAS (Version 9.2, SAS Inst., Inc., Cary, NC). The mid-test body weight was converted to metabolic mid-weight (**MWT**) by $BW^{0.75}$. Daily feed intake (as-fed) was the average feed intake for valid test-days. This was multiplied by the dry matter content of the feed to derive the DMI for each steer. The DMI was standardized across diets and years to 10MJ ME kg^{-1} DM. Expected DMI was obtained as a regression of standardized DMI on ADG, MWT and UBF using PROC GLM of SAS. The ME of each diet was estimated with the CowBytes ration balancing software (Alberta Agriculture and Rural Development, Edmonton, Canada). The residuals from the equation (shown below) were assigned as RFI,

$$Y_j = \beta_0 + \beta_1 ADG_j + \beta_2 MWT_j + \beta_3 UBF_j + e_j$$

where for each animal, Y_j is the standardized DMI, β_0 is the regression intercept, β_1 is the ADG regression coefficient, β_2 is the MWT regression coefficient, β_3 is the UBF regression coefficient, e_j indicate the residuals (RFI). Each steer was assigned to an RFI-class based on 0.5 standard deviations above or below the

mean. There were three RFI-classes namely 'Low' (RFI < 0.5 SD), 'Medium' (± 0.5 SD) and 'High' (> 0.5SD) from the mean.

Apart from feed intake, the measures of feeding behavior collected on a daily basis by the GrowSafe System include FD, HDT and FF collected within feeding events. A Feeding event is an uninterrupted detection of a steer's transponder (Basarab et al., 2003). Feeding interruptions could be the presence of another steer at the same bunk or if the difference between the last two RFID reads on the same steer was greater than 300 s. The total number of individual feeding events is the FF. The FD was the total time spent within each feeding event. It was the difference between the first and last RFID reads for any steer for any feeding event. It could also be regarded as the length of time animals spent in feeding-related activities at the bunk. These may include eating, chewing, licking, socializing, etc (Nkrumah et al., 2007). The HDT was calculated as the number of times the RFID of a particular steer was read by the system multiplied by the scanning time (1 s). The feeding rate (**FR**) is the ratio of total daily DMI to the total daily FD. The headdown per feeding duration (**HDD**) was the ratio of the total daily HDT to the total daily FD while the headdown per visit (**HDV**) was the ratio between the total daily HDT and the total daily feeding frequency. The HDD and HDV indicate the intensity of feeding activities at the bunks.

The feeding behavior traits (FD, HDT, FF) were progressively included in the model containing ADG, MWT and UBF, to identify extra variation in DMI accounted by the feeding behavior traits. Differences between the observations for feeding behavior traits in the grower-fed and the finisher-fed periods were

subsequently analyzed using the PDIFF option and the Tukey test in SAS GLM procedure where the fixed effects were year-of-test and the breed of sire while the age at the beginning of test was a linear covariate.

Genetic analyses were implemented in ASReml (Gilmour et al., 2008) using a series of bivariate animal models which included year-of-test and breed of the sire as fixed effects. The age at the beginning of the test was used as a linear covariate. The model is shown below

$$\begin{bmatrix} \boldsymbol{y}_1 \\ \boldsymbol{y}_2 \end{bmatrix} = \begin{bmatrix} \boldsymbol{X}_1 & 0 \\ 0 & \boldsymbol{X}_2 \end{bmatrix} \begin{bmatrix} \boldsymbol{b}_1 \\ \boldsymbol{b}_2 \end{bmatrix} + \begin{bmatrix} \boldsymbol{Z}_1 & 0 \\ 0 & \boldsymbol{Z}_2 \end{bmatrix} \begin{bmatrix} \boldsymbol{a}_1 \\ \boldsymbol{a}_2 \end{bmatrix} + \begin{bmatrix} \boldsymbol{e}_1 \\ \boldsymbol{e}_2 \end{bmatrix}$$

where $\mathbf{y}_1$ and $\mathbf{y}_2$ are the vectors of phenotypic measurements for traits measured in the grower-fed (length = $N_1 \times 1$) and finisher-fed (length = $N_2 \times 1$) periods, respectively; $\mathbf{X}_1$ and $\mathbf{X}_2$ are incidence matrices relating the fixed effects to records y_1 and y_2, respectively; $\mathbf{b}_1$ and $\mathbf{b}_2$ are vectors of fixed effects (year and sire-breed) in the grower-fed and finisher-fed periods respectively;. $\mathbf{Z}_1$ and $\mathbf{Z}_2$ are incidence matrices relating the phenotypic observations to the vectors of polygenic (**a**) effects for the grower-fed and finisher-fed periods, respectively. $\mathbf{e}_1$ and $\mathbf{e}_2$ are vectors of random residuals in the grower-fed and finisher-fed periods, respectively.

The expectations and variances were

$$E\begin{bmatrix} \boldsymbol{y}_1 \\ \boldsymbol{y}_2 \end{bmatrix} = \begin{bmatrix} \boldsymbol{X}_1 & 0 \\ 0 & \boldsymbol{X}_2 \end{bmatrix} \begin{bmatrix} \boldsymbol{b}_1 \\ \boldsymbol{b}_2 \end{bmatrix}$$

and

$$V\begin{bmatrix} a_1 \\ a_2 \\ e_1 \\ e_2 \end{bmatrix} = \begin{bmatrix} A\sigma^2_{a1} & A\sigma_{a21} & 0 & 0 \\ A\sigma_{a21} & A\sigma^2_{a2} & 0 & 0 \\ 0 & 0 & I\sigma^2_{e1} & I\sigma_{e12} \\ 0 & 0 & I\sigma_{e21} & I\sigma^2_{e2} \end{bmatrix}$$

a and **e** were assumed to be normally distributed with mean of zero and (co)variances $A\sigma^2_a$, $I\sigma^2_e$ for a and e, respectively. 'A' is the additive relationship matrix, σ^2_a is the variance of the random polygenic effect, I is an identity matrix with order equal to the number of animals. Heritability was calculated using variance components obtained from the bivariate analyses

$$h^2 = \frac{\sigma_a^2}{\sigma_a^2 + \sigma_e^2}$$

Genetic correlations were determined as the ratio between the genetic covariance and the product of the genetic standard deviations in both feeding periods. The phenotypic correlations were determined in similar manner but with phenotypic parameters.

5.3 RESULTS

Table 5- 1 shows the least square means for the traits studied during the grower-fed and finisher-fed regimes. Even though the finisher-fed regime had greater ($P < 0.001$) DMI, ADG, MWT and UBF, the grower-fed regime had greater ($P < 0.0001$) FD, HDT, FF, HDV and HDFD than the finisher-fed regime. The FR was greater in FP2. Including FD, HDT or FF increased the R^2 of the model containing ADG, MWT and UBF (Table 5- 2). In the grower-fed regime,

the base model was improved by additional 4% and 6% when FD and HDT, respectively, were included. During the finisher-fed phase, R^2 improved by 6%, 9% and 13%, respectively for the FF, FD and HDT.

There was no difference ($P > 0.13$) among the three RFI-classes in either the grower-fed or the finisher-fed regimes for ADG, MWT, and UBF, as expected (Table 5- 3). Within the grower-fed and finisher-fed groups, all RFI-classes were significantly different ($P < 0.03$) from each other for FD and HDT. However, there were no differences ($P > 0.68$) among the RFI-classes for FR. In the grower-fed regime, there was no difference between the low RFI-class and medium RFI-class or between the medium RFI- and high RFI-classes for FF, but the low RFI-class steers had fewer ($P = 0.002$) visits than the high RFI-class. There was also no difference between the medium and the high class for HDD but they were significantly different from the low RFI-class. There were no differences among the three RFI-classes for HDV. For the same grower-fed regime, steers in the low RFI-class had the lowest values for all measures of feeding behavior while those in the high RFI-class had the greatest. There were also significant differences ($P < 0.006$) among the three RFI-classes within the finisher-fed regime for HDV and HDD. Steers in the low RFI-class for these measures had lower values than the medium or high classes while the low class had significantly fewer ($P < 0.0007$) FF than either the medium or the high-RFI class.

Table 5- 4 shows the phenotypic relationships between the feeding behavior traits and DMI for the grower-fed and finisher-fed periods. All the feeding behavior traits in the grower-fed period were positively (at least 0.50) correlated

with those measured during the finisher-fed period. In both periods, FD had positive phenotypic correlations with HDT, FF and DMI but had a negative correlation with FR. The HDT had a positive correlation with FF and DMI but a negative correlation with FR in both periods as well. The relationship between FR and FF was positive but was greater during the grower-fed period. The FR had a low and negative relationship with DMI in both periods. Large variability in the grower-fed period may have prevented convergence of the remainder of bivariate analyses for RFI. During the finisher-fed period, RFI was correlated with FD (0.41 ± 0.05), HDT (0.52 ± 0.04) and FF (0.19 ± 0.06) but unrelated to FR (-0.06 ± 0.06)

The genetic correlations (Table 5- 5) between the feeding behavior traits measured in the grower-fed period and the finisher-fed period were high and positive. The standard errors were generally larger than those from the phenotypic correlations. The genetic correlations between the grower-fed period and the finisher-fed period for FD, HDT and FF were greater than 90%. The FR had lower genetic correlations (between the two feeding periods) but the values were greater than 85%. During both periods, FD had positive genetic correlations with HDT and FF but the correlations with FR and DMI were negative. The HDT was negatively correlated with FR and DMI in both periods as well. Positive correlations were observed between HDT and FF in both periods but FR was correlated (negatively) with DMI in the grower-fed period alone. During the finisher-fed period, RFI was correlated with FD (-0.57 ± 0.55), HDT (-0.50 ± 0.85), FR (0.18 ± 0.31) and FF (-0.29 ± 0.36)

Apart from FD and HDT, the heritability estimates (Table 5- 6) of FR and FF were greater (numerically) in the finisher-fed period than in the grower-fed period. The phenotypic variances were greater during grower-fed period than in the finisher-fed period.

5.4 DISCUSSION

Various studies have incorporated radio frequency technology to examine and monitor animals' health, feed intakes and feeding behavior (Nkrumah et al., 2007; Basarab et al., 2003; DeVries et al., 2003; Gibb et al., 1998; Sowell et al., 1998). The GrowSafe system is a validated tool for feed intake and feeding behavior data collection and its results agree with visual measurements (DeVries et al., 2003). Most reports of the relationship between feeding behavior and feed intake or feed efficiency have used finishing diets. This is the first study (to the best of our knowledge) that has examined the relationship among intake, RFI and feeding behavior traits when two different diets were fed successively to a cohort of beef steers. Understanding the relationships between feeding behavior traits measured under different diet regimes may inform us about their performances under actual production timelines. The effect of some factors such as age, body weight or season of feeding may not be excluded from this study because these steers were older and larger in the second period (finisher diet). This study had focused on feeding activities typical in the beef industry where steers meant for finishing receive a backgrounding diet before an energy-dense finisher diet.

This study supports the findings of Lancaster et al. (2009) who reported that including feeding behavior traits (meal duration and meal frequency) in a model containing ADG, MWT and ultrasound trait improves the proportion of DMI explained by the explanatory variables. Other reports indicate that DMI (in cows) is affected by feeding behavior, which may be influenced by external factors such as management, environment, health and social activities (Azizi et al., 2009; DeVries et al., 2005; Grant and Albright, 2001). As much as 33% of total ME derived from some forages can be expended in feeding activities such as eating, chewing and ruminating (Lancaster et al., 2009).

The longer FD, longer HDT, greater FF and reduced feed intake observed in the grower-fed regime may be associated with the particle size of the grower diet. Zebeli et al. (2009) reported that the length and size of feed particles may have some influence on animals' feed intake. Other studies have also associated long particle lengths with low DMI (Bradford and Allen, 2007; Zebeli et al., 2008). Greter et al. (2008) reported that feed intake decreased with the addition of straw while Zebeli et al., (2009) suggested that lower DMI might have arisen from longer mean retention time of the digesta.

The inclusion of hay in the grower diet may have also favored sorting, which might increase feeding-related activities such as longer eating-time. Similar observations were reported by Lancaster et al. (2009) where the bulls fed a less energy-dense diet containing cottonseed hulls had greater meal duration (118 mins vs. 85min) and meal frequency (8.66 vs. 7.74) than the bulls fed the energy-dense diet without the cottonseed hulls. Zebeli et al. (2009) also reported that

dairy cows sorted against long particle lengths while Greter et al. (2008) found that sorting increased in dairy heifers with increasing levels of straw in the diet. The addition of straw (Greter et al., 2008) or hay (Bae et al., 1981) in diets increases the feeding time in cows as well. In goats, Abijaoude et al. (2000) reported that longer eating and ruminating time were associated with feeding a greater amount of forage to goats. On the other hand the amount of digesta in the reticulo-rumen and the rate at which the forages are broken down by mastication or in the rumen may also influence feeding related activities (Lindstrom and Redbo, 2000).

In addition to a larger body size, the greater FR observed in the finisher-fed period may have contributed to the greater overall intake of the steers during this period. On the contrary slower eating rate was attributed to longer chewing and rumination time in dairy heifers fed a diet containing straw (Greter et al., 2008; Robles et al., 2007). Golden et al. (2008) reported no differences in the average daily eating rate between efficient and inefficient crossbred Angus steers. Other reports have shown that increased average meal size in high producing cows contributed to the greater DMI even though the FD was shorter (Azizi et al., 2009; Dado and Allen, 1994). Animals may use shorter eating time to control ruminal disorders (Abijaoude et al., 2000) that may result from rapid ingestion of concentrates (Krause and Oetzel, 2006).

The reports on FF and diet type were inconsistent. Contrary to the findings in this study, Zebeli et al. (2009) reported increasing frequency of visits per meal with reducing feed particle size. Friggens et al. (1998) reported that feeding a high

concentrate total mixed ration (TMR) was associated with fewer visits and greater intake per visit than cows fed a low concentrate TMR. Azizi et al. (2009) investigated feeding behavior differences in primiparous and multiparous cows with different levels of milk yield (high and low). Their study found no difference in feeding visits and FD between the high and low milk yield levels in either the primiparous or mulitparous group. Miron et al. (2004) did not find any significant difference for bunk visits in cows fed soy hulls or barley grains supplements.

Competition at the bunks may influence feeding behavior traits. However, there were no observed indicators of competition at the bunks in this study. The steers were fed *ad libitum* and were provided with sufficient feeding bunks throughout the test. Proudfoot et al. (2009) reported no effect of competition on daily FD, bunk visits, FR and feed intake in primiparous dairy cows. Nevertheless, competition increased the frequency of visits in multiparous cows, and also reduced FD and DMI in the week before calving. After calving, the cows compensated for competitiveness by increasing the FR.

The results from this study for the finisher-fed period were similar to those reported by Nkrumah et al. (2007) for FD and HDT. The FF for the low, medium and high RFI-classes (according to their reports) were 27 visits d^{-1}, 30 visits d^{-1} and 32 visits d^{-1}, respectively. They reported significant differences among all RFI classes. The study did not find any difference between the medium-RFI and high-RFI classes. The authors used meal events as the basis for calculating the feeding behavior traits while calculations in this study were based on feeding events. A meal event in the Growsafe system is usually longer than a feeding event because

a feeding event is limited to feeding sessions at any particular bunk at any time while meal events may occur at several bunks. A meal event could consist of several feeding events. From other reports, Kelly et al. (2010) also did not find any difference among the FD for high, medium and low-RFI heifers but Golden et al. (2008) reported that inefficient steers had more daily eating bouts than the efficient ones, nevertheless, the results may be biased because they used very few animals (< 10) in each class.

The relationship between the feeding behavior traits and RFI classes may imply that these measures of feeding behavior may be used as indicator traits for feed efficiency. In agreement with the results from this study, Nkrumah et al. (2007) reported that feed-efficient steers had fewer observations of feeding behavior than inefficient steers. These results support the suggestion that low RFI steers use less energy in their feeding activities. In addition to other physiological differences, efficient steers minimize energy expenditure through various mechanisms that may avail them with greater metabolizable energy for growth and production.

Lancaster et al. (2009) reported no difference among the efficiency classes for FR but found significant differences among the low, medium and high classes, respectively, for meal duration (92 min d^{-1}, 99 min d^{-1}, 107 min d^{-1}) and HDT (42 min d^{-1}, 45 min d^{-1}, 49 min d^{-1}). For FF, the low (7.3 visits d^{-1}) and medium (7.6 visits d^{-1}) classes were not significantly ($P > 0.05$) different from each other but were significantly ($P < 0.05$) different from the high class (8.2 visits). Their reports were lower than the FF reported here.

Contrary to most reports on measures of feeding behavior, Bingham et al. (2009) reported greater HDT in the low-RFI Brangus heifers (152 min/d) compared to those in the high-RFI class (124 min/d). They found no difference in the meal duration as well as the meal frequency between the high and low-RFI classes. On the other hand, they found significant ($P < 0.001$) differences in FR between the high (50 g/min) and low-RFI (42 g/min) classes. The meal durations reported by Bingham et al. (2009) were greater than most reports in the literature, including this study. They explained that heifers attend feed bunks more frequently and spend more time at the bunks than steers (Schwartzkopf-Genswein et al., 2002).

The correlations between those measured in the grower-fed period and finisher-fed period will indicate if the performance on a grower-fed period could be used to predict a subsequent performance on another diet-regime. Genetic correlations indicate whether the traits are influenced by the same set of genes. When the same trait is measured in two environments, the genetic correlation also indicates whether they are the same trait or not (Falconer and McKay, 1996) and whether the environmental factors (e.g. feeding regime) influence the performance of the steers.

Kelly et al. (2010) reported zero phenotypic correlations between FD and DMI while Robinson and Oddy (2004) reported positive phenotypic correlations. The negative correlation between DMI and FR was unexpected in this study. It could imply that steers which ate slowly (per feeding event) eventually ate more DM in a day than steers that had faster rate of intake per feeding event. Nkrumah

et al. (2007) reported 0.49, 0.50, and 0.18 as correlations between RFI and FD, HDT and FF, respectively. These were very similar to the phenotypic correlations obtained in the finisher-fed period. Lancaster et al. (2009) reported 0.23, 0.36, and 0.53 as phenotypic correlations between DMI with meal duration, headdown duration and FR, respectively; DMI and meal frequency were uncorrelated while the correlations between RFI with meal duration, headdown duration, and meal frequency were 0.41, 0.38, and 0.26, respectively. Similar to previous studies (Golden et al., 2008; Lancaster et al., 2009), the phenotypic correlations between RFI and FR from this study were not different from zero for the finisher-fed period. Robinson and Oddy (2004) reported a low correlation (0.14) between RFI and FR. The results from the finisher-fed periods also disagreed with the conclusions of Bingham et al. (2009) that FR has a strong relationship with RFI. This could be due to a number of differences. They used heifers for their study which may indicate major biological differences from steers. In addition, their sample size (n = 18/group) was relatively small and they recorded feeding behavior using video cameras. The correlation between DMI with FD, HDT and FF, suggests that FD or HDT and FF may be included as covariates (measures of animal activity) in the model for calculating RFI.

The genetic correlations between the two feeding periods for FD, HDT and FF indicate that the feeding behavior traits evaluated in both feeding regimes were identical traits. On the other hand, FR may not be regarded as identical trait because of the lower genetic correlation between the two feeding periods. It may also indicate that there may be animal-by-feeding regime interaction for FR.

The results here do agree with the reports of Nkrumah et al. (2007) and Gibbs et al. (1998) that measures of feeding behavior in cattle are generally consistent. Unlike the previous studies, the findings here provide more evidence in this regard since the same animals were measured twice for the 'same' trait. The correlations between DMI and measures of feeding behavior support the findings of Nkrumah et al. (2007) that feeding behavior traits in cattle may be connected with pathways regulating hunger and satiety. The authors reported a negative genetic correlation between DMI and FF (-0.74), however the results here were lower. Compared to the genetic correlation reported by Nkrumah et al. (2007) for DMI with FD (0.56) and HDT (0.59), our results were lower and negative for both feeding periods. Robinson and Oddy (2004) did not observe any genetic correlation between DMI and feeding time (0.03)

Apart from FD and HDT, FR and FF were more heritable when the finisher diet was fed. The heritability obtained in this study were lower than those of Nkrumah et al. (2007) for FD (0.28) and HDT (0.33) while the FF (0.38) was lower in their study. They obtained heritability estimates for each measure of feeding behavior as the average estimate of pair-wise bivariate analyses with other traits which might have caused the disparity between their results and those obtained during the finisher-fed period. Robinson and Oddy (2004) also obtained larger heritability estimates for feeding time (0.36) and eating rate (0.51) but their heritability estimate for FF was lower.

Further studies may be required to investigate how these measures of feeding behavior relate to general steer activities. This will advance our understanding

about the proportion of total animal activity represented by these measures of feeding behavior. It is also important to investigate other measures of feeding behavior such as the pressure exerted by animals during feeding in an effort to gain better understanding of the unexplained portions of the variation in feed intake and feed efficiency.

5.5 CONCLUSION

Regardless of the feeding regime, including feeding behavior traits to a model containing ADG, MWT and UBF, improved the proportion of variation accounted in DMI. In general, this study found that feeding behavior phenotypes were numerically larger for FP1 compared to FP2. The differences between the RFI-classes were consistent regardless of the feeding regime. Efficient steers consistently had fewer observations of feeding behavior than inefficient steers. The measures of feeding behavior, may be used (to an extent) as indicator traits for feed efficiency. Finally, genetic correlations between FD, HDT and FF measured on the grower-fed and finisher-fed periods provide evidence that these pairs are identical traits.

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Table 5- 1: **Least square means of production and feeding behavior traits between the grower-fed and the finisher-fed periods.**

Trait[1]	Grower-fed period	Finisher-fed period	SE	P-Value[2]
Feeding duration, min d^{-1}	112	70.3	1.02	< 0.0001
Head-down time, min d^{-1}	63.9	31.7	0.90	< 0.0001
Feeding rate, kg/hr	4.93	5.60	0.12	< 0.0001
Feeding frequency, visits d^{-1}	34.3	22.3	0.51	< 0.0001
HDV, min $visit^{-1}$	2.57	1.68	0.06	< 0.0001
HDD	0.56	0.44	0.01	< 0.0001
DMI, Kg d^{-1}	7.6	10.4	0.06	< 0.0001
ADG, Kg d^{-1}	1.25	1.82	0.01	< 0.0001
RFI, Kg d^{-1}	0.00	0.00	0.05	1.00
MWT, Kg of $BW^{0.75}$	74	99	0.4	< 0.0001
UBF, cm	0.46	0.82	0.01	< 0.0001

[1]HDV=Head-down time $visits^{-1}$, HDD=Head-down time/Feeding duration; RFI= Residual feed intake; MWT = metabolic mid-weight; UBF = Ultrasound back-fat thickness

[2]The P-value of the difference between the least square means in both periods

Table 5- 2. The R^2 accounted by different models for DMI

Model[1]	Grower-fed period	Finisher-fed period
β_0+ β_1ADG+ β_2MWT+ β_3UBF	0.59	0.54
β_0+ β_1ADG+ β_2MWT+ β_3UBF+ β_4FD	0.63	0.63
β_0+ β_1ADG+ β_2MWT+ β_3UBF+ β_4HDT	0.65	0.67
β_0+ β_1ADG+ β_2MWT+ β_3UBF+ β_4FF	0.59	0.60
β_0+ β_1ADG+ β_2MWT+ β_3UBF+ β_4HDT+ β_5**FF**	0.66	0.67
β_0+ β_1ADG+ β_2MWT+ β_3UBF+ β_4HDT+ β_5***FD***	0.65	0.67
β_0+ β_1ADG+ β_2MWT+ β_3UBF+ β_4FD+ β_5**FF**	0.63	0.64
β_0+ β_1ADG+ β_2MWT+ β_3UBF+ β_4HDT+ β_5***FD***+ β_5**FF**	0.66	0.68

[1] β_0 is the intercept, β_1- β_5 are regression coefficients for the different traits, MWT = metabolic mid-weight; FD = feeding duration; HDT = head-down time; FF = feeding frequency; Feeding behaviors in bold were not significant in the grower-fed period ($P > 0.05$); Feeding behaviors in italics were not significant in the finisher-fed period ($P > 0.05$); Feeding behaviors in bold and italics were not significant in both periods ($P > 0.05$).

Table 5- 3. Differences among the feed-efficiency classes for the feeding behavior traits in the grower and finisher-fed periods.

	Grower-fed period			Finisher-fed period		
Trait[1]	Low	Medium	High	Low	Medium	High
Duration, min d^{-1}	104 ± 2.05^{a}	111 ± 1.76^{b}	118 ± 1.95^{c}	63 ± 1.47^{a}	72 ± 1.16^{b}	78 ± 1.48^{c}
Head-down, min d^{-1}	53.3 ± 1.74^{a}	63.9 ± 1.49^{b}	69.9 ± 1.65^{c}	24.3 ± 1.19^{a}	33.7 ± 0.94^{b}	40.2 ± 1.19^{c}
Feeding frequency, visits d^{-1}	32.2 ± 0.95^{a}	34.9 ± 0.82^{ab}	36.6 ± 0.91^{b}	19.9 ± 0.55^{a}	22.5 ± 0.43^{b}	22.9 ± 0.55^{b}
Feeding rate, Kg/hr	4.99 ± 0.21^{a}	4.97 ± 0.18^{a}	5.19 ± 0.20^{a}	5.51 ± 0.16^{a}	5.51 ± 0.12^{a}	5.43 ± 0.16^{a}
HDV, min $visit^{-1}$	2.35 ± 0.12^{a}	2.46 ± 0.10^{a}	2.63 ± 0.12^{a}	1.41 ± 0.08^{a}	1.80 ± 0.06^{b}	2.10 ± 0.08^{c}
HDFD	0.51 ± 0.01^{a}	0.57 ± 0.01^{b}	0.59 ± 0.01^{b}	0.37 ± 0.01^{a}	0.46 ± 0.01^{b}	0.51 ± 0.01^{c}
RFI, Kg d^{-1}	-0.67 ± 0.03^{a}	0.01 ± 0.02^{b}	0.59 ± 0.03^{c}	-1.15 ± 0.05^{a}	0.02 ± 0.04^{b}	1.14 ± 0.05^{c}
DMI, Kg d^{-1}	7.01 ± 0.07^{a}	7.48 ± 0.06^{b}	8.18 ± 0.07^{c}	9.52 ± 0.11^{a}	10.3 ± 0.08^{b}	11.3 ± 0.11^{c}
MWT, Kg of $BW^{0.75}$	75 ± 0.6^{a}	73 ± 0.5^{a}	75 ± 0.6^{a}	100 ± 0.7^{a}	98 ± 0.58^{a}	99 ± 0.7^{a}
ADG, Kg d^{-1}	1.27 ± 0.02^{a}	1.23 ± 0.02^{a}	1.28 ± 0.02^{a}	1.84 ± 0.03^{a}	1.81 ± 0.02^{a}	1.81 ± 0.03^{a}
UBF, cm	0.45 ± 0.02^{a}	0.46 ± 0.01^{a}	0.46 ± 0.02^{a}	0.82 ± 0.02^{a}	0.84 ± 0.02^{a}	0.80 ± 0.02^{a}

[a-c]Within each period, different superscripts indicate differences among feed-efficiency classes at $P < 0.05$.

[1]HDV = Head-down time $visits^{-1}$, HDFD = Head-down time/Feeding duration; RFI = Residual feed intake; MWT = Metabolic mid-weight; UBF = Ultrasound back-fat thickness.

Table 5- 4. The phenotypic correlations among feeding behavior traits and DMI in the grower-fed (above the diagonal) and the finisher-fed periods (below the diagonal).

		Grower-fed period				
	Trait[1]	FD	HDT	FR	FF	DMI
Finisher-fed period	FD	**0.62 ± 0.03**	**0.79 ± 0.02**	**-0.34 ± 0.05**	**0.14 ± 0.06**	**0.38 ± 0.05**
	HDT	**0.83 ± 0.02**	**0.61 ± 0.04**	**-0.27 ± 0.05**	**0.20 ± 0.05**	**0.32 ± 0.05**
	FR	**-0.21 ± 0.06**	**-0.28 ± 0.05**	**0.50 ± 0.04**	**0.77 ± 0.02**	**-0.13 ± 0.06**
	FF	**0.55 ± 0.04**	**0.44 ± 0.05**	**0.58 ± 0.04**	**0.54 ± 0.04**	**-0.07 ± 0.06**
	DMI	**0.34 ± 0.05**	**0.35 ± 0.05**	**-0.13 ± 0.06**	**-0.05 ± 0.06**	**0.63 ± 0.03**

[1]FD = Feeding duration; HDT = Head-down time; FR = Feeding rate; FF = Feeding frequency

Table 5- 5. The genetic correlations among feeding behavior traits and DMI in the grower-fed (above the diagonal) and the finisher-fed periods (below the diagonal).

		Grower-fed period				
	Trait[1]	FD	HDT	FR	FF	DMI
Finisher-fed period	FD	**0.91 ± 0.26**	**0.98 ± 0.24**	**-0.15 ± 0.35**	**0.43 ± 0.35**	**-0.56 ± 0.56**
	HDT	**0.95 ± 0.25**	**0.93 ± 0.37**	**-0.51 ± 0.62**	**0.50 ± 0.76**	**-0.64 ± 0.86**
	FR	**-0.09 ± 0.38**	**-0.34 ± 0.41**	**0.87 ± 0.16**	**0.81 ± 0.10**	**-0.51 ± 0.46**
	FF	**0.54 ± 0.28**	**0.18 ± 0.43**	**0.79 ± 0.12**	**0.94 ± 0.11**	**-0.98 ± 0.38**
	DMI	**-0.43 ± 0.44**	**-0.44 ± 0.55**	**0.03 ± 0.29**	**-0.47 ± 0.27**	**0.78 ± 0.27**

[1]FD = Feeding duration; HDT = Head-down time; FR = Feeding rate; FF = Feeding frequency

Table 5- 6. Heritability ± SE of the feeding behavior traits in the grower-fed and finisher-fed periods.

Trait[1]	Grower-fed		Finisher-fed	
	σ^2_p	h^2	σ^2_p	h^2
Feeding duration,	405.2 ± 32.9	0.25 ± 0.16	216.5 ± 17.0	0.14 ± 0.11
Head-down time	317.0 ± 25.6	0.14 ± 0.15	157.9 ± 12.4	0.09 ± 0.10
Feeding rate	3.77 ± 0.31	0.35 ± 0.16	2.16 ± 0.19	0.67 ± 0.19
Feeding frequency	81.15 ± 7.08	0.56 ± 0.19	27.10 ± 2.35	0.59 ± 0.18

CHAPTER 6

ESTIMATION OF PHENOTYPIC AND GENETIC PARAMETERS FOR GROWTH, EFFICIENCY AND MEASURES OF FEEDING BEHAVIOR IN STEERS FED A FINISHER DIET IN TWO FEEDING PERIODS[4].

6.1 INTRODUCTION

Current research indicates that feed intake, growth and feed efficiency (**FE**) of steers are affected by various environmental factors such as diet, age and weather conditions (Crews et al., 2003; Mujibi et al. 2010; Durunna et al., 2011). Residual feed intake (**RFI**) is gaining popularity as the preferred measure of efficiency in cattle. It is calculated as the difference between the actual feed intake and predicted feed intake based on growth and BW (Arthur et al., 2001a,b) and any other measurable energy sink, such as body composition (Richardson et al., 2001; Basarab et al., 2003) and feeding activity (Chapter 5).

Previous studies have shown that RFI is moderately repeatable over two successive diet regimes (Crews 2003; Kelly et al., 2010; Durunna et al., 2011). Kelly et al. (2010) reported that RFI and feeding behaviors were repeatable in heifers during the yearling and finishing phases while Crews et al., (2003) and Durunna et al. (2011) reported that RFI is repeatable in steers fed backgrounding and finishing diets, successively in two feeding periods. There are limited reports in the literature regarding the variations in FE and feeding behaviors of steers fed the energy-dense finisher diet in different production phases. It is worthy of note

[4] A version of this chapter has been submitted for publication. Durunna et al. 2011c. E-2011-4277. J. Anim. Sci.

that under normal production timelines, these feeding periods are confounded by differences in age or maturity. Therefore, information on FE and feeding behavior from steers fed a finishing diet during these feeding phases will consolidate the existing knowledge from other studies about the consistency of these traits over different environmental and mature phases.

The objective of the present study was to examine the differences in the phenotypic and genetic estimates for DMI, ADG, MWT, G:F, RFI and feeding behavior traits in steers that were fed energy-dense finisher diets in two feeding periods.

6.2 MATERIALS AND METHODS

6.2.1 Animals and Management

The steers used in this study were born in the Spring of 2003 to 2008 from hybrid, Angus or Charolais sires (n = 114) mated to composite dams (n = 660). The details on the breed composition of the hybrid dam line were given by Goonewardene et al. (2003). The steers were castrated within 24 hr after calving and they grazed with their dams until weaned at approximately 184 ± 17days of age in October of each year. All steers had been vaccinated for infectious bovine rhinotracheitis, parainfluenza-3 virus, bovine viral diarrhea, bovine respiratory syncytial virus, *haemophilus somnus*, *pasteurella multocida* and clostridial diseases four weeks before entering the test facility. Upon arrival at the test facility, the steers were treated with a pour-on parasiticide that controls warble

larvae, mites, lice and horn fly. Subsequently, each steer was identified with a radio frequency transponder button (half duplex RFID, Alflex USA, Inc., Dallas/Ft. Worth Airport, TX 75261-2266) in the right or left ear. All animals were located at the University of Alberta research ranch at Kinsella, Alberta and were cared for according to the Canadian Council on Animal Care (CCAC, 1993) guidelines.

Each year, there were two feeding periods whereby the first feeding period (**FP1**) was during the Fall-Winter season, while the second feeding period (**FP2**) was during the Winter-Spring season. In FP1, feed intake and feeding behavior observations were collected on 80, 73, 78, and 88 steers in 2003, 2004, 2005 and 2007, respectively while observations from FP2 were collected on 61, 68, 73, 174, 84, and 72 steers in 2003, 2004, 2005, 2006, 2007 and 2008, respectively. Within each year, the steers tested in both periods came from the same calf-crop. However, the steers prior to being tested in FP2 were kept on a backgrounding diet that contained 20% grass hay, 74% oat grains and 6% feedlot supplement.

The diet composition and nutritive value of the finisher diets provided to the steers are shown in Table 6- 1. For all years, the steers were adjusted to their trial rations for at least 21 days before the commencement of feed intake data collection. This adjustment period enabled the animals to adapt to the automatic feeding units and test rations.

6.2.2 Data collection, Trait definitions and Statistical Analyses

The data on feed intake and feeding behaviors were collected over 71 to 93 days within periods (FP1 or FP2) as reported in Nkrumah et al. (2004) and Durunna et al. (2011). The live weights of all steers were measured once every 2 wk throughout the test periods. Ultrasound back-fat (**UBF**) thickness, ultrasound ribeye area (**UREA**) and ultrasound marbling (**UMB**) were measured at the beginning and at the end of the feeding period using an Aloka 500V real-time ultrasound with a 17.5 cm 3.5MHz probe (Overseas Monitor Corporation Ltd., Richmond, British Columbia, Canada). Feed intake of each steer was measured daily using the GrowSafe automatic feeding system (GrowSafe Systems Ltd., Airdrie, Alberta, Canada).

The measures of feeding behavior recorded by the GrowSafe System include feeding duration (**FD**), headdown time (**HDT**) and feeding frequency (**FF**), which were collected within feeding events. A feeding event is an uninterrupted detection of a steer's transponder (Basarab et al., 2003). Feeding interruptions arise when the time of non-detection of a steer's transponder is over 300 s or when another ear tag is detected at the same bunk. Each independent feeding event is one FF while the FD is the total time spent within feeding events. The FD can also be defined as the difference between the first and last electronic tag reads for any steer at a particular bunk as long as there is no feeding interruption. The FD can also be the length of time animals spent at the bunk for feeding related activities such as eating, chewing, licking, socializing etc (Nkrumah et al., 2007).

The HDT was calculated as the number of times the electronic tag of a particular steer was read by the system multiplied by the scanning time (1 s).

The linear regression procedure was used to compute the ADG, initial weight and mid-test body weight for each animal in SAS (Version 9.2, SAS Inst., Inc., Cary, NC). The mid-test body weight was converted to metabolic mid-weight (**MWT**) by $BW^{0.75}$. Each steer's average daily feed intake (as fed) was multiplied by the dry matter content of the feed to derive the DMI, which was standardized to 10 MJ ME/kg DM. The RFI was calculated within cohorts (Mujibi et al., 2010) as the difference between the actual standardized-DMI (sDMI) and the predicted DMI based on ADG, MWT and UBF using the GLM procedure of SAS.

$$RFI = sDMI - (\beta_0 + \beta_1 ADG + \beta_2 MWT + \beta_3 UBF)$$

where RFI is the residual feed intake, sDMI is the standardized DMI, β_0 is the regression intercept, β_1 is the ADG regression coefficient, β_2 is the MWT regression coefficient and β_3 is the UBF regression coefficient. The R-squares ranged from 50% to 76% with UBF accounting for about 2 to 5% of the variation in DMI. Other data integrity checks for the 2006 to 2008 were reported in Durunna et al. (2011). Each steer was assigned to an RFI-class based on 0.5 standard deviations above or below the mean. There were three classes namely 'Low' (RFI < 0.5 SD), 'Medium' (± 0.5 SD) and 'High' (> 0.5 SD). The G:F ratio was calculated for each steer as the ratio of ADG to average daily DMI.

Multiple comparison of least-squares means (**LSM**) for each trait calculated within each feeding period were tested with the GLM procedure of SAS using the PDIFF option with a Tukey adjustment. The model included RFI group (Low,

Medium and High), breed of sire and year-of-test as fixed effects with age on-test as the linear covariate. Genetic analyses were implemented in ASReml (Gilmour et al., 2008) using a bivariate animal model which included year-of-test and breed of sire as fixed effects while the age of steer was fitted as a linear covariate. The model equation is shown below

$$\begin{bmatrix} \boldsymbol{y}_1 \\ \boldsymbol{y}_2 \end{bmatrix} = \begin{bmatrix} \boldsymbol{X}_1 & 0 \\ 0 & \boldsymbol{X}_2 \end{bmatrix} \begin{bmatrix} \boldsymbol{b}_1 \\ \boldsymbol{b}_2 \end{bmatrix} + \begin{bmatrix} \boldsymbol{Z}_1 & 0 \\ 0 & \boldsymbol{Z}_2 \end{bmatrix} \begin{bmatrix} \boldsymbol{a}_1 \\ \boldsymbol{a}_2 \end{bmatrix} + \begin{bmatrix} \boldsymbol{e}_1 \\ \boldsymbol{e}_2 \end{bmatrix}$$

where $\mathbf{y}_1$ and $\mathbf{y}_2$ are the vectors of phenotypic measurements for traits measured in FP1 (length = $N_1 \times 1$) and FP2 (length = $N_2 \times 1$), respectively; $\mathbf{X}_1$ and $\mathbf{X}_2$ are incidence matrices relating the fixed effects to records in y_1 and y_2, respectively; $\mathbf{b}_1$ and $\mathbf{b}_2$ are vectors of fixed effects (year and sire-breed) in FP1 and FP2, respectively;. $\mathbf{Z}_1$ and $\mathbf{Z}_2$ are incidence matrices relating the phenotypic observations to the vectors of polygenic (a) effects for the FP1 and FP2, respectively. $\mathbf{e}_1$ and $\mathbf{e}_2$ are vectors of random residuals in the FP1 and FP2, respectively.

The expectations and variances were

$$E \begin{bmatrix} \boldsymbol{y}_1 \\ \boldsymbol{y}_2 \end{bmatrix} = \begin{bmatrix} \boldsymbol{X}_1 & 0 \\ 0 & \boldsymbol{X}_2 \end{bmatrix} \begin{bmatrix} \boldsymbol{b}_1 \\ \boldsymbol{b}_2 \end{bmatrix}$$

and

$$V \begin{bmatrix} a_1 \\ a_2 \\ e_1 \\ e_2 \end{bmatrix} = \begin{bmatrix} A\sigma_{a1}^2 & A\sigma_{a21} & 0 & 0 \\ A\sigma_{a21} & A\sigma_{a2}^2 & 0 & 0 \\ 0 & 0 & I\sigma_{e1}^2 & 0 \\ 0 & 0 & 0 & I\sigma_{e2}^2 \end{bmatrix}$$

a and e were assumed to be normally distributed with mean of zero and (co)variances $A\sigma^2_a$, $I\sigma^2_e$ for a and e, respectively. A is the additive relationship matrix, σ^2_a is the random polygenic effect variance, I_n is an identity matrix with order equal to the number of animals. The residual errors between the two environments were assumed independent. Heritability estimates were obtained from the bivariate analyses.

6.3 RESULTS AND DISCUSSION

This study investigated the possible differences in the phenotypic and genetic variances existing in steers that received the finisher diet in FP1 versus FP2, which correspond to feedlot production timelines. Any observed difference may be attributed to the influence of genes or genomic regions that are activated as a result of the feeding period or stage of maturity. It is important to note that these feeding periods were confounded by the age, body weight and ambient temperature. A limitation of this study was the inability of the experimental design to separate these confounding factors while maintaining a sufficient sample size for analysis although age effect was adjusted in the analysis model as a linear covariate.

6.3.1 Phenotypic differences

The LSM and their differences between the performances measured in FP1 and FP2 are shown in Table 6- 2. The initial weights on test were 342 kg and 364 kg, respectively for FP1 and FP2. Significant ($P < 0.0001$) differences were found

between the two feeding periods for ADG and MWT whereby the values in FP2 were greater ($P < 0.003$) than those in FP1, as expected but DMI was not different ($P = 0.13$). The LSMs of UMB was slightly greater ($P = 0.06$) in FP1 than that in FP2. Both the LSMs of UBF and UREA were significantly ($P < 0.004$) greater in FP1 than that of FP2. The FF was fewer ($P < 0.0001$) in FP2 than in FP1 while there was no difference ($P > 0.12$) between the two feeding periods for FD and HDT. In addition, (as expected) there was no difference ($P > 0.05$) in the LSM of RFI between the two feeding periods while the G:F was greater ($P = 0.004$) in FP2 than in FP1.

Limited studies have reported feedlot performances of young steers of about 200 days of age. Basarab et al. (2003) reported feed intake of about 6 to 8kg DM d^{-1} in composite steers which weighed on average 297 kg and were 238 days old at the beginning of the test. The steers in their study had a lower DMI despite receiving a ration similar to the diet in this study. The LSM of phenotypes for DMI, ADG and feeding behaviors for steers in FP2 were similar to that reported by Nkrumah et al. (2007). The greater LSM value of ADG in FP2 may be due to compensatory gain (Fluharty et al., 2000) because of the previous dietary regime. Hicks et al. (1990) reported an average DMI of 10.31 kg d^{-1} for yearling steers weighing 322 kg at the beginning of the test with an ADG of 1.6 kg d^{-1}, which were similar to the DMI and ADG in FP2. Arthur et al. (2001a) used Angus bulls of 268 ± 23 days of age for their study and reported a mean DMI of 9.65, which was similar to the DMI in FP1 but the ADG (1.26 kg d^{-1}) was lower compared to the ADG in FP1. Even though the average age of the bulls used in Arthur et al.

(2001a) was similar to those of FP1, the diet used in that study contained 2.5 Mcal/kg, which was lower than the ME content of this study. The DMI (10.4 kg d^{-1}) and ADG (1.61 kg d^{-1}) of Charolais bulls at 15 months (Arthur et al., 2001b) were similar to those of the steers in FP2.

The greater ultrasound carcass characteristics observed for the steers fed in FP1 agreed with the observations of Fluharty et al. (2000), who reported that feeding energy dense diet to early-weaned calves increased the rate of growth in those steers by accelerating the rate of adipogenesis. Schoonmaker et al. (2002) reported that calves that entered the feedlot at 111 days had greater back-fat and longissimus area at 202 days than those that entered the feedlot at 202 days but there was no difference between the two groups for back-fat thickness at harvest. However, the calves that entered the feedlot as yearlings had the greatest back-fat thickness at harvest. Such increase of back-fat thickness may be expected because the yearling calves were 534 days at harvest while those that entered the feedlot at 111 and 202, were 333 and 391 days, respectively at harvest. These reports suggest that high grain diets induce adipogenesis in young calves. The difference in the UREA observed in this study was contrary to the reports of Schoonmaker et al. (2002) who reported greater longissimus area at target fat level for calves placed in the feedlot at an older age but finished at a much older age.

There were differences ($P < 0.0001$) among the three RFI-classes within the two feeding periods for DMI, RFI, G:F and FD as shown in Table 6- 3. There were no differences ($P > 0.12$) among the RFI-classes within each feeding period for initial weight on test, ADG and MWT. For HDT in the FP1, there was no

difference (P = 0.15) between the high and medium classes while the low class was significantly different (P < 0.0001) from the high and medium classes (Table 6- 3). During FP2, the three RFI-classes were significantly different (P < 0.0001) for the headdown time. There was no difference (P = 0.13) between the low and medium RFI-classes for the FF in FP1 while the low RFI-class had fewer (P < 0.01) FF than either the medium or the high RFI-class in FP2.

For DMI, G:F and RFI, differences observed among the RFI-classes were in agreement with previous studies (Bingham et al., 2009; Meyer et al., 2008; Nkrumah et al., 2004; Nkrumah et al., 2007) irrespective of the feeding period. The less-efficient (positive RFI) steers had greater feed-intake, smaller G:F, longer FD, longer HDT and more FF, than the more-efficient (negative RFI) steers.

6.3.2 Genetic parameters

Table 6- 4 shows the phenotypic variances, and heritability estimates for both feeding periods as well as the genetic correlations between the traits in FP1 and FP2. The DMI had larger genetic variances (data not shown) in FP1 but there were larger phenotypic variances in FP2. The phenotypic variance of ADG was also greater in FP2 while the heritability estimates for ADG and DMI obtained in the FP1 were greater than the FP2 estimates. The FE traits (RFI and G:F) had greater phenotypic variances and heritability estimates in FP2 than in FP1. The heritability estimates for FD and HDT were greater in FP1 while that of FF was greater in FP2. The genetic correlations (Table 6- 4) between FP1 and FP2

indicate that similar set of genes may be influencing each of ADG and HDT in the two feeding periods. It may also indicate that ADG and HDT measured during these two feeding periods may be the same traits. On the other hand, DMI, RFI, G:F, FD and FF measured in FP1 may be different from those measured in FP2 despite the steers receiving similar diets in the two feeding periods. The results also indicate that apart from FF, all traits measured in FP1 were related to their subsequent measurement in FP2.

Genetic studies related to FE and feeding behavior using cattle of about 200 days of age or performances at the grower and finisher phases for feed intake and FE (Arthur et al., 2001b; Crews et al., 2003; Kelly et al., 2010; Durunna et al., 2011) or feeding behavior (Chapter 5) are few. Fan et al. (1995) carried out performance tests on Hereford and Angus bulls (under 200 days of age) using high and medium-energy diets. They reported that pooled heritability estimates for ADG (0.26), DMI (0.24) and RFI (0.14) in the two breeds were lower than the estimates from the estimates in FP1. The differences between their results and those reported here may be due to differences in physiology of the animals used in the two studies. The results here were similar to the heritability estimates from Robinson and Oddy (2004) for ADG (0.23) and RFI (0.18) but their estimate for FD (0.36) was greater than the reports here, while their estimate for feed conversion ratio (0.06) was lower.

Arthur et al. (2001b) reported greater phenotypic variances for feed intake, ADG and RFI in bulls at 19 months than at 15 months and that the heritability estimate was slightly greater at 19 months (0.43) than at 15 months (0.39) for RFI,

which is in agreement with the results in the present study. The trend for ADG in this study disagreed with the reports of Cucco et al. (2010) but agreed with Sarmiento and Garcia (2007), Prince et al. (2010) and Chen et al. (2010) in Romosinuano cattle, Avikalin sheep and Duroc pigs, respectively. Cucco et al. (2010) reported a slight increase in heritability for weight gain measured at 365 days (0.18) versus 450 days (0.21). Observing the results made at different stages of maturity in mice, Archer et al. (1998) reported a slightly greater heritability for RFI measured postweaning (0.27) than at maturity (0.24).

These authors (Sarmiento and Garcia (2007), Prince et al. (2010) and Chen et al. (2010)), observed the decline of additive genetic component for postweaning weight traits in different species as the animals advanced in age. This may imply that the genes controlling such traits had smaller effects on the expression of the traits as the animals mature or that the environmental influences were greater at older ages. In the Avikalin sheep, Prince et al. (2010) suggested that the environment plays a larger role for growth rate as the animal ages, especially after 6 months of age. The mechanism by which this occurs is unclear; however, Middelbos et al. (2009) investigated the influence of age on the gene expression profiles of dogs, and they reported that age influenced the mRNA abundance of the skeletal tissue where there was down regulation (with advancing age) of genes involved in cellular organization and development, signaling mechanisms, calcium and lipid transport. In chickens, a decline in heritability due to increasing environmental variance was observed for body and egg traits (Anang et al., 2000; Dana et al., 2010; Liljedahl et al., 1984) indicating that reduced heritability was

not only due to declining additive genetic variance but also due to increasing environmental variance.

The genetic correlations reported here were lower than the reports of Arthur et al. (2001b) for RFI (0.65 vs 0.75) and daily feed intake (0.61 vs 0.90) but were greater than their report for ADG (0.92 vs 0.46) and feed conversion ratio (0.60 vs 0.42). These results were in agreement with Durunna et al. (2011a) who reported high genetic correlations for ADG (0.80) in steers fed grower and finisher diets in successive feeding periods. While the authors reported a greater genetic correlation for G:F (0.78) and DMI (0.78), their report for RFI was lower (0.50). The high genetic correlation for ADG and HDT in this study may indicate the absence of genotype by environment interactions for these traits from one feeding period to another while the performance of steers on the other traits may be dependent on the age and feeding period.

6.4 CONCLUSIONS

This study investigated the possible effects of feeding period and age on production, feed efficiency and feeding behavior traits using crossbred steers that were fed similar diets in two different periods. There was no consistent trend for the heritability estimates in FP1 and FP2. While RFI, G:F and FF had greater heritability estimates during FP2, DMI, ADG, FD and HDT had greater heritability estimates during FP1. The decline was mostly due to reduced genetic variances, increasing environmental variance or both. These results support the argument that postweaning performance of DMI, RFI, G:F, FD and FF in cattle

may be affected by age and feeding period but ADG and HDT were similar traits in both environments.

The mechanisms that reduce or increase the influence of genes at older ages in cattle need to be explored. Based on the differences in the additive genetic variances with age, genomic studies may be required to investigate these differences using genetic marker panels or micro-arrays. There is also the need to identify the appropriate time to evaluate cattle for feed efficiency traits.

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Table 6- 1. The ingredients (as-fed) and composition of the grower and finisher diets

Feed Composition	2003[a]	2004[a]	2005[a]	2006	2007	2008
Dry-rolled corn	80.0	-	-	-	-	-
Alfalfa Pellets	13.5	9.0	9.0	10.0	10.0	10.0
Oats grains	-	20.0	20.0	28.3	28.3	28.3
Barley grains	-	64.5	64.5	56.7	56.7	56.7
Canola oil	1.5	1.5	1.5	0.0	0.0	0.0
Feedlot-32 Supplement [1]	5.0	5.0	5.0	5.0	5.0	5.0
ME content, MJ/kg	12.1	12.2	12.2	12.1	12.1	12.1
Chemical composition, % of DM						
DM, %	90.5	88.9	88.9	87.0	87.0	87.0
CP, %	12.5	14.0	14.0	13.5	13.5	13.5
Crude fat, %	5.32	-	-	3.3	3.3	3.3
ADF,%	5.61	9.5	9.5	10.3	10.3	10.3
NDF,%	18.3	21.49	21.49	29.5	29.5	29.5

[a]Obtained from digestibility trials as described by Nkrumah et al.,2004, 2006.
[b]Obtained from digestibility trials detailed by Durunna et al., 2011.
[1] Contained 440 mg/kg of Monensin, 1.6 mg/kg of Selenium, 5.0% Ca, 0.58% P, 0.76% K, 16 mg/kg I, 80 mg/kg Fe, 170 mg/kg Cu, 480 mg/kg Mn, 485 mg/kg Z, 4.3 mg/kg Co, 1.98% Na, 0.17% S, 0.38% Mg, 80500Iu/kg Vitamin A, 8000 Iu/kg Vitamin D, 1111 Iu/kg.

Table 6- 2. Least-squares means of traits measured in the two feeding periods.

Trait	First feeding period LSMean ± SE	Second feeding period LSMean ± SE	P-value[1]
Start of test weight, kg	342.17 ± 4.95	363.98 ± 3.29	0.004
Dry matter intake, kg d^{-1}	9.99 ± 0.15	10.34 ± 0.10	0.13
Average daily gain, kg d^{-1}	1.50 ± 0.04	1.68 ± 0.03	0.002
Metabolic mid-weight, kg	89.40 ± 0.91	94.62 ± 0.60	0.0002
Ultrasound back fat thickness, mm	9.28 ± 0.37	7.71 ± 0.24	0.005
Ultrasound rib eye area, cm^2	83.12 ± 1.16	75.26 ± 0.77	<0.0001
Ultrasound marbling	5.08 ± 0.10	4.79 ± 0.07	0.06
Gain to feed ratio	0.15 ± 0.003	0.16 ± 0.002	0.004
Residual feed intake, kg DM d^{-1}	-0.01 ± 0.06	0.00 ± 0.04	0.88
Feeding duration, min d^{-1}	73.84 ± 2.00	69.16 ± 1.33	0.13
Head-down time, min d^{-1}	39.08 ± 1.62	35.57 ± 1.08	0.16
Feeding frequency, events d^{-1}	31.90 ± 0.84	25.74 ± 0.56	< 0.0001

[1]The P-value of the differences between the LS means measured in the two feeding periods.

Table 6- 3. Least-squares means of the RFI-classes of steers in both feeding periods[1]

	First feeding period			P-value	Second feeding period			P-value
Trait	High	Medium	Low		High	Medium	Low	
Start of test weight	300.13 ± 3.01	292.52 ± 2.59	295.09 ± 2.93	0.150	393.51 ± 3.68	389.31 ± 3.04	391.99 ± 3.49	0.540
Average daily gain, kg d^{-1}	1.45 ± 0.03	1.44 ± 0.02	1.47 ± 0.02	0.686	1.62 ± 0.03	1.64 ± 0.02	1.64 ± 0.02	0.673
Metabolic mid-weight, kg	82.08 ± 0.65	80.66 ± 0.50	81.32 ± 0.57	0.170	98.74 ± 0.66	98.21 ± 0.54	98.63 ± 0.63	0.716
Dry matter intake, kg d^{-1}	10.28 ± 0.11^{a}	9.30 ± 0.09^{b}	8.80 ± 0.10^{c}	< 0.0001	11.47 ± 0.10^{a}	10.59 ± 0.08^{b}	9.67 ± 0.10^{c}	< 0.0001
Ultrasound back fat thickness, mm	8.87 ± 0.27^{a}	8.00 ± 0.23^{b}	8.72±0.26^{ab}	0.027	7.70 ± 0.23	8.18 ± 0.19	7.97 ± 0.22	0.155
Ultrasound rib eye area, cm^2	79.47 ± 0.76	78.48 ± 0.65	79.21 ± 0.74	0.571	77.99 ± 0.70	78.22 ± 0.58	78.84 ± 0.67	0.547
Ultrasound marbling	5.01 ± 0.07^{a}	4.77 ± 0.06^{b}	4.94 ± 0.07^{ab}	0.018	4.80 ± 0.06^{a}	4.96 ± 0.05^{b}	4.93 ± 0.06^{ab}	0.040
Residual feed intake, kg DM d^{-1}	0.78 ± 0.04^{a}	-0.02 ± 0.03^{b}	-0.72 ± 0.03^{c}	< 0.0001	1.01 ± 0.04^{a}	-0.01 ± 0.04^{b}	-1.08 ± 0.04^{c}	< 0.0001
Gain to feed ratio	0.14 ± 0.002^{a}	0.16 ± 0.001^{b}	0.17 ± 0.002^{c}	< 0.0001	0.14 ± 0.002^{a}	0.16 ± 0.002^{b}	0.17 ± 0.002^{c}	< 0.0001
Feeding Duration, min d^{-1}	85.13 ± 1.52^{a}	77.98 ± 1.31^{b}	70.34 ± 1.48^{c}	< 0.0001	69.99 ± 1.26^{a}	64.26 ± 1.04^{b}	56.12 ± 1.20^{c}	< 0.0001
Head-down time, min d^{-1}	47.90 ± 1.22^{a}	44.96 ± 1.05^{a}	37.76 ± 1.19^{b}	< 0.0001	39.09 ± 1.03^{a}	33.19 ± 0.85^{b}	25.33 ± 0.97^{c}	< 0.0001
Feeding frequency, events d^{-1}	38.01 ± 0.69^{a}	35.34 ± 0.60^{b}	33.63 ± 0.68^{b}	<0.0001	24.54 ± 0.48^{a}	23.39 ± 0.39^{a}	20.74 ± 0.45^{b}	< 0.0001

[1] [a-c]Within each period, different superscripts indicate differences among feed-efficiency classes at P < 0.05.

Table 6- 4. Phenotypic and genetic parameters of traits in both feeding periods

Trait	Genetic Correlation between both feeding periods	First feeding period		Second feeding period	
		σ^2_p	h^2	σ^2_p	h^2
Average daily gain, kg d^{-1}	0.92 ± 0.36	0.06 ± 0.005	0.38 ± 0.18	0.07 ± 0.005	0.28 ± 0.12
Dry matter intake, kg d^{-1}	0.61 ± 0.28	1.32 ± 0.11	0.52 ± 0.19	1.52 ± 0.10	0.42 ± 0.14
Residual feed intake, kg DM d^{-1}	0.65 ± 0.51	0.46 ± 0.04	0.16 ± 0.17	0.83 ± 0.05	0.27 ± 0.12
Gain to feed ratio	0.60 ± 0.51	0.0004 ± 0.00003	0.18 ± 0.16	0.0005 ± 0.00003	0.33 ± 0.13
Feeding duration, min d^{-1}	0.84 ± 0.53	237.7 ± 19.4	0.22 ± 0.14	187.9 ± 11.8	0.14 ± 0.10
Head-down time, min d^{-1}	0.97 ± 0.34	150.4 ± 12.6	0.35 ± 0.19	134.1 ± 8.5	0.18 ± 0.11
Feeding frequency, events d^{-1}	0.05 ± 0.44	46.13 ± 3.81	0.26 ± 0.17	25.11 ± 1.71	0.46 ± 0.16

CHAPTER 7

GENERAL DISCUSSION AND CONCLUSIONS

7.1 General discussion

Integrating nutrition and genetics into beef production would advance our knowledge on the biology behind feed efficiency (**FE**) and feeding behavior traits of beef cattle. This study has examined the presence of genotype-by-environment interaction for feed intake, growth, FE and feeding behavior traits in crossbred steers fed different diets in different feeding periods. The FE traits include residual feed intake (**RFI**), gain to feed ratio (**G:F**) and Kleiber ratio (**KR**) while the feeding behavior traits include feeding duration (**FD**), headdown time (**HDT**), feeding frequency (**FF**) and feeding rate (**FR**). These traits were measured in two successive feeding phases where the steers received either a grower diet or a finisher diet. The major objective of the study was to examine the consistency of beef cattle performance ranking from one feeding period to the other. One of the important traits examined in this study was RFI because of the possible benefits it may attract to the beef industry. These benefits may include reduced feed cost and less negative impact on the environment. The measures of feeding behaviors were also included because of their relationships with feed intake. In addition, the published information on feeding behavior traits conducted on different feeding regimes is limited such that this study will add new information to existing literature.

The first study in Chapter 3 examined if crossbred steers changed their FE (RFI, G:F, KR) rankings from one feeding period to another. Two groups of steers were successively fed either the grower (grower-fed group) or finisher (finisher-fed group) diet in the two feeding periods while another group (feed-swap group) was fed the grower diet in the first feeding period (**FP1**) followed by the finisher diet in the second period (**FP2**). We did not consider the option of a grower diet preceded by a finisher diet because it was unusual and impractical in the beef industry. The study also examined part-whole correlations between each periodic FE measure and the entire period (i.e. both periods combined). The results showed that majority of the steers changed their FE ranking and RFI-class regardless of the diet they received in the FP2. The phenotypic rank correlations between FP1 and FP2 ranged from low to moderate for RFI (0.33,0.44, 0.42), G:F (0.20,0.38, 0.29) and KR (0.31, 0.46, 0.22) for the feed-swap, grower-fed and finisher-fed groups, respectively in agreement with Christopher, J. and Marston, T (Unpublished, Kansas State University, Manhattan), Archer et al. (1998) and Arthur et al. (2001). The feed-swap group had the least correlation between the two feeding periods for the FE measures. For the grower-fed group and the feed-swap group, the phenotypic measurements from the FP2 had a greater rank correlation (0.59-0.87) with the entire feeding period than those from the FP1 in agreement with Goonewardene et al. (2004). The study also reported greater phenotypic correlation between the entire period and the FP1 (0.72-0.85) for the steers fed the finisher diet in both periods.

The low phenotypic correlations between the FE measured in the two feeding periods indicate that the two periodic FE measures may not be the same trait. The study concluded that such low correlations might have arisen due to effects of the diet, age or period of feeding. Diet was not the only factor influencing the reranking because the groups of steers that received the same diet in the two successive periods also reranked. The study observed that the correlation between the two periods was greater with RFI than the other measures of FE, which may strengthen RFI's utility as the FE measure of choice.

Chapter 4 was a logical follow-up to the results in Chapter 3. The study examined whether the observations made at the phenotypic level agreed with the genetic parameters. If reranking also occurred for the estimated breeding values, then the genetic correlations between the two feeding regimes for the FE traits would be different from unity. Using the 331 steers in the feed-swap group, the study examined the genetic parameters obtained within each feeding period for this group from bivariate analyses. The genetic correlation between the two periods would indicate the extent of genotype-by-environment interactions for the traits being studied (Falconer and Mackay, 1996).

The heritability estimates for DMI, ADG, RFI and G:F were greater in FP2 when the animals received the finisher diet. Previous reports were not consistent regarding the trend of genetic variances or heritability estimates obtained at different ages or nutritional environments. Kearney et al. (2004) and Cienfuegos-Rivas et al. (1999) reported greater genetic variances for cows in better nutritional environment while Arthur et al. (2001) reported greater additive genetic variances

for FE traits in older animals but their heritability estimates were greater in the younger bulls. Consistent with other reports (Crews et al., 2003; Archer et al., 2002; Arthur et al., 2001), the genetic correlations in this study were less than unity for RFI (0.50) and G:F (0.78) indicating the existence of genotype-by-environment interaction for RFI and G:F. There were more serious permanent environmental effects during the grower-fed period for ADG, RFI and G:F while DMI had a greater permanent environmental effect during the finisher-fed period. As these results suggest, the diet, age, period of feeding, or a combination of these factors influence genes controlling FE traits. Taking the study further, we would expect to observe differential presence of QTLs associated with these traits in either the finisher-fed steers or the grower-fed steers.

Using the feed-swap group, Chapter 5 examined the relationship between the measures of feeding behavior (FD, HDT, FF) with feed intake and RFI performances. The study also examined whether feeding behavior traits were consistent among different RFI-classes within each feeding period. A bivariate animal model was used to estimate genetic correlations among the traits measured in the two feeding periods. The FD, HDT, and FF were greater in FP1 than FP2. Possible reasons could be the inclusion of hay in the diet, which may have increased the particle size of the grower diet thereby increasing sorting, chewing and general energy expenditure (Greter et al., 2008; Lancaster et al., 2009; Zebeli et al., 2009). Other traits (FR, DMI and ADG) were greater during the FP2. Including measures of feeding behavior into the model containing MWT, ADG and UBF increased the R^2 by up to 14%. The results agreed with Lancaster et al.

(2009) that feeding behaviors can explain a good proportion of the variation in feed intake. In contrast to the report of Kelly et al. (2010), FD was correlated with RFI and DMI. However, available reports are inconsistent regarding the relationship between diet type and FF (Azizi et al., 2009; Friggens et al., 1998; Zebeli et al., 2009). The differences among RFI-classes were consistent across diets for most feeding behavior traits especially for FD and HDT. This supports the reports of Nkrumah et al. (2007) which reported that the feeding behaviors may be used as indicator traits for FE. On the other hand, due to the high genetic correlations between the observations in the grower-fed and finisher-fed regimes for FD (0.91), HDT (0.93) and FF (0.94), these traits were deemed identical traits in the two environments.

Finally, chapter 6 investigated the possible differences in phenotypic and genetic variances of feed intake, growth, FE (FD, HDT, FF) and feeding behavior traits when steers received the same diet in two consecutive periods. This chapter took an in-depth look at the possible contribution of the feeding regimes to the differences observed in Chapters 3 and 4. These feeding regimes, however, were confounded by age and age-related phenotypes (such as body weight) and weather conditions. Using a bivariate animal model, genetic parameters were derived using steers that received the finisher diet in any of the two periods. The phenotypes were concordant with the reports of Nkrumah et al. (2007). However, there was no consistent trend in the additive genetic effects or heritability estimates of the traits from one period to the other. Arthur et al. (2001) reported greater heritability estimates for growth traits at older ages while a decreasing

trend for the heritability estimates of weight gain traits was observed by Cucco et al. (2010), Prince et al. (2010), Sarmiento and Garcia (2007) and Chen et al. (2010). The heritability estimates for RFI in the FP1 was greater than the report of Fan et al. (1995) while Robinson and Oddy (2004) reported lower heritability estimates compared to those estimated during FP2. Interestingly, Middelbos et al. (2009) reported a decline in the gene expression profiles in skeletal tissues as dogs advanced in age. Their study supported our suggestion that the diet may have been the major influence for the increased heritability estimates observed in the feed-swap group in Chapter 4 for DMI and ADG during the FP2. They reported a down-regulation of genes involved in cellular organization and development, signaling mechanisms as well as calcium and lipid transport. The trend for heritability estimates in their study agreed with the results from Chapter 4 for RFI and G:F. We do not know the reasons behind these trends but would suggest further research on gene expression based on these observations.

7.2 General conclusions and recommendations

The results presented in this study suggest that diet, age, and season play important roles in defining the performance of crossbred steers. This study has presented evidence of reranking at the phenotypic level and genotype-by-environment interaction at the EBV level for RFI. Because of the high genetic correlations between FP1 and FP2, the feeding behaviors (FD, HDT, FF) were identical traits in the two feeding regimes. There may be serious implications for RFI. The presence of reranking indicates that most steers do not have a constant

RFI status but we have also reported that some steers (though few) maintained the low-RFI class across the two feeding periods. Although the appropriate time of evaluating steers for RFI is inconclusive, we recommend that steers be tested when they are older (> 260 days). More research may be required to investigate the use of high roughage diets to evaluate the RFI performance of steers.

7.3 Implications for the beef industry

The results from this study may have serious implications for the beef industry. However, the conclusions should be treated with caution given that they were derived from crossbred steers. Considering the longevity and body weight of cows as well as the cost associated with feeding them, the feed efficiency of cowherds deserves an urgent attention. The use of a modified model for calculating RFI for cowherds will reduce the cost of feeding cows without impacting their productivity. The major points from this study indicate that…

- The RFI and G:F performances measured on a grower diet may not give a good prediction of the steers' performances on a finisher diet and vice versa. This suggests that the performances of steers immediately after weaning in the cow-calf sector may not be a good indicator of their subsequent performances in the feedlot.
- Separate genetic evaluations may be required when observations are collected either in a forage- or grain-based diet. Therefore, in order to reduce the cost of feeding in cowherds as well as reduce the negative impact of methane emission into the environment, a separate RFI performance for cowherds is

recommended. Selecting efficient cows may translate to faster genetic improvement in feed efficiency across the beef industry.

- Evaluating RFI performance on a finisher-fed regime may give a greater indicator of the overall performance when observations are measured in young steers of about 200 days. This may be appropriate for well-framed calves that do not require any backgrounding.
- The FD, HDT and FF account for some proportion (up to 13%) of variation in DMI. Therefore, models for future RFI evaluations should consider adjusting for these factors in order to increase the accuracy of selecting feed efficient animals. In addition, the FD, HDT or FF measured in steers fed the grower diet had a strong genetic relationship with the same trait measured on a succeeding finisher-fed regime, which implies that these measures of feeding behavior may be consistent across the different diets in the beef industry.

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