Phenotypic relationships between residual feed intake, feeding behaviour and temperament in Western Canadian beef cattle

By
Lindsey Doris Lippens

A Thesis Submitted to
The Faculty of Graduate Studies of
The University of Manitoba

in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

Department of Animal Science
University of Manitoba
Winnipeg, Manitoba, Canada
R3T 2N2

ABSTRACT

Feed costs have led the cattle industry to examine the merit of selecting cattle for inputs (feed efficiency) rather than for outputs exclusively (growth). Residual feed intake (RFI) has become a preferred measure of biological efficiency. Feeding behaviour traits (feeding event duration, frequency, head-down time, length and eating rate) and temperament may provide insight into the variation in feed efficiency. Feeding behaviour, RFI ($n = 868$) and temperament ($n = 58$) were examined using five classes of beef cattle. Cattle were sorted into low, medium and high RFI groups. Feeding behaviour traits were moderately (-0.21 to 0.56; $P < 0.05$) related to RFI. Bulls fed a grain-based diet spent longer periods lying down than bulls fed a forage-based diet. No relationships ($P > 0.1$) were observed between RFI and bull temperament, indicating that temperament is not correlated with RFI and selecting for low RFI cattle will not negatively impact temperament.

ACKNOWLEDGMENTS

I would like to express my utmost gratitude and indebtedness to my advisor, Dr. Kim Ominski, who is one of the most committed and compassionate people I know. Your infinite patience, gentle (and yes, motherly!) advice, guidance and encouragement have contributed not only to completion of my degree, but also to my own personal growth. Throughout this journey, some of the most valuable lessons you have given me apply beyond the context of this thesis. You have made such a positive and profound impact on my life and you have many qualities that I aspire to. You never gave up on me. No words can express my gratitude.

I am sincerely thankful for the invaluable advice and expertise provided by my co-advisor, Dr. John Basarab. Your dedication toward research is inspiring, and I am grateful to you for providing data sets for this project. It has been a privilege to work with you.

An extra special thank you to my committee members, Dr. Gary Crow, Dr. Karen Schwartzkopf-Genswein and Dr. Francis Zvomuya. Gary: your gentle nature and meticulous attention to detail never wavered, and my thesis will reflect that. Many hours were spent at the computer both defining and calculating feeding behaviour traits on numerous large data sets, and you approached each session with as much dedication and thoughtfulness as the one preceding. Karen: your passion for cattle behaviour and your insightful comments on the complexity of cattle temperament have fueled my own passion. Francis: your statistical knowledge and kind disposition are most appreciated. Thank you to each of you for your contributions to this project!

My deepest gratitude is extended toward Dr. Loreen Onischuk. Loreen, you tirelessly endured my many, often repetitive statistical-related questions. There were many times when you simply understood me, without words ever needing to be said. You are a tremendous inspiration to me and someone I hold in highest regard. A very warm and sincere thank you to Dr. Laurie

Connor. Laurie, your compassion, encouragement, belief and confidence in me have strengthened my belief in myself. I hope to one day have the opportunity to influence someone else’s life to the extent in which you’ve bettered mine.

I extend my heartfelt appreciation to Janice Haines for sewing pouches (and on a Sunday) for accelerometer work, graduate students Carson Callum, Sean Thompson and Tawnya Cormier for your help in data collection, summer students Katrina Delaquis and Joel Ballard who had courage second to none taking on the bulls for the flight distance assessments, Lisa McKeown for your assistance in addressing questions throughout the duration of the Alberta data analyses, and to Deanne Fulawka and Dr. Emma McGeough for your understanding support and friendship as I balanced my work commitments with completing this thesis. A special thank you to Dr. Gordon Carstens and Dr. Luis Tedeschi for input in defining feeding behaviour traits.

And to my family: Mom, Dad, Terri. Throughout my challenges and my triumphs, each of you have been with me every single step of the way. Your unconditional love, encouragement and support have been a saving grace, and have carried me through the course of this program. You are the reason for my love of – and respect for - cattle. To my two sisters, who are also my two best friends: your sense of humour and love have been uplifting and inspirational.

I am extremely fortunate to have such a strong network of supporters. I owe my success and completion of my degree to each and every one of you, as I know I never would have completed this without you. Doors have opened up to me because of each of you. My success is your success, and I am forever indebted to each of you. <u>*WE*</u> did it!

I gratefully acknowledge the financial support from the following organizations which made this project possible: Alberta Agriculture and Rural Development, Alberta Beef Producers, Manitoba Agriculture, Manitoba Beef Producers, Manitoba Rural Adaptation Council and the Saskatchewan Cattlemen’s Association.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF ABBREVIATIONS

ADF = Acid detergent fibre

ADG = Average daily gain

AFD = Assigned feed disappearance

BCRC = Beef Cattle Research Council

BCS = Body condition score

CCAC = Canadian Council on Animal Care

CG1 = Contemporary group 1

CG2 = Contemporary group 2

CP = Crude protein

CS = Chute score

DAQ = Data acquisition

DM = Dry matter

DMI = Dry matter intake (kg DMI/day)

ER = Eating rate (kg DMI/minute)

ENS = Entry score

EV = Exit velocity

EXS = Exit score

FB = Feeding behaviour

FBF = Final backfat thickness

FD = Flight distance (m)

FED = Feeding event duration (minutes/day)

FEF = Feeding event frequency (bunk visits/day)

FEHD = Feeding event head-down time (minutes/day)

FEL = Feeding event length (minutes/visit)

LD = Lying duration (%/day)

LSM = Least squares means

MMW = Metabolic mid-weight

NDF = Neutral detergent fibre

NRC = National Research Council

RES = Restraint score

RFI = Residual feed intake

RFI$_{fat}$ = Residual feed intake adjusted for final backfat thickness

RFID = Radio frequency identification

SD = Standard deviation

SDFI = Standardized daily feed intake

TMR = Total mixed ration

FOREWORD

This thesis is written in manuscript style, with each manuscript having its own abstract, introduction, materials and methods, results, discussion and conclusions. There is also a general introduction, literature review, general discussion and direction of future research, followed by the literature cited. None of the manuscripts have been submitted for publication at the time of thesis completion.

1. GENERAL INTRODUCTION

Feed is a major expense for cattle producers, and improving feed efficiency can have a significant economic benefit. Substantial variation in feed efficiency exists among individual animals both within (Lancaster et al., 2009) and across breeds (Basarab et al., 2003), indicating room for improving efficiency in the cattle industry. A greater understanding of individual feeding behaviour (FB) patterns and their relationship to feed efficiency may offer further insight into the underlying biological factors that are associated with long-term feed intake regulation and performance variation in beef cattle (Yeates et al., 2001). Further, a greater understanding of FB patterns may improve overall bunk management in feedlots by providing optimum bunk space and bunk management strategies, as well as enhancing overall animal health (Schwartzkopf-Genswein et al., 2011).

Residual feed intake (RFI) or net feed efficiency is one strategy by which feed efficiency can be measured (Basarab et al., 2003). It is defined as the variation in feed intake that remains (a residual portion) once animal growth and maintenance requirements are met (Basarab et al., 2008). Efficient animals have a low or negative RFI and consume less feed, whereas inefficient animals have a positive or high RFI and consume more feed than expected (Basarab et al., 2003). Several major biological factors possibly contributing to this variation in efficiency including: digestibility of the feed, physical activity and heat expenditure, body composition and tissue turnover rates (Kelly et al., 2010; Herd, 2009; Herd et al., 2004). It has also been hypothesized that genotypic variation may be dependent on the individual's (i) temperament measured by susceptibility to stress, and (ii) by FB traits (Chen et al., 2014; Sebastian et al., 2011; Herd, 2009; Basarab et al., 2003). Therefore, a clearer understanding of the underlying biological mechanisms influencing variation in RFI is important not only to improve selection for feed efficient animals, but also to optimize overall cattle health, bunk management and feeding practices, and finally, to reduce feed costs.

Temperament has been defined as the animal’s overall behavioural style which influences how the animal perceives and reacts to environmental stimuli (Lyons, 1989). Behaviours indicative of an animal's temperament include: aggression, docility, avoidance, boldness, excitability, alertness, hesitation and fearfulness (Sebastian et al., 2011). Understanding the extent to which behavioral traits are heritable may lead to improved selection for desirable temperament, enhanced animal welfare and improved feed efficiency, achieved through the reduction of stress elicited by husbandry and production practices (Sebastian et al., 2011). Studies indicate that cattle less susceptible to stress are more efficient at feed utilization as measured by gain-to-feed ratio (G:F), and adaptation to a given stressor (Sebastian et al., 2011; Herd, 2009).

To date, the majority of the literature examining FB traits and temperament focuses primarily on growing feeder cattle (Chen et al., 2014; Nkrumah et al., 2007; Robinson and Oddy, 2004). To the author’s knowledge, there are no studies that present FB data in relation to RFI on other beef cattle classes including cows and replacement heifers. Automated feeding systems (e.g., GrowSafe Systems Ltd., Calan Broadbent Feeding System, Insentec, C-Lock Inc.) in the cattle industry have the capacity to provide individual feed for all animals on test, thereby facilitating the use of RFI as a selection tool. Further, these systems have allowed researchers to examine the relationship between RFI and individual cattle FB variables (Schwartzkopf-Genswein et al., 2011; Basarab et al., 2011; Nkrumah et al., 2007).

The purpose of this thesis is to: 1) evaluate the phenotypic relationships of RFI, residual feed intake adjusted for backfat thickness ($\mathrm{RFI}_{\mathrm{fat)}}$ and dry matter intake (DMI) with FB traits; 2) determine if daily feeding behaviours differ between low, medium and high RFI and $\mathrm{RFI}_{\mathrm{fat}}$ groups; and 3) determine if low RFI and $\mathrm{RFI}_{\mathrm{fat}}$ yearling bulls already acclimated to their surroundings are less susceptible to stress elicited during routine handling.

2. LITERATURE REVIEW

In western Canadian beef cattle production systems, feed costs contribute toward 55% to 80% of the total calf-to-slaughter production system costs (Lamb and Maddock, 2009; Arthur et al., 2004; Basarab et al., 2002); of this, approximately 66% of the total dietary energy consumed is used to meet maintenance energy requirements (Basarab et al., 2013; Kelly et al., 2010; Montano-Bermudez et al., 1990). Cattle with poor feed efficiency have a greater cost of production (Crews, 2005) and a larger impact on the environment due to increased nutrient excretion (Nkrumah et al., 2006). There is considerable animal-to-animal variation in maintenance requirements independent of body size and growth (Basarab et al., 2013, 2003; Crowley et al., 2010; Nkrumah et al., 2006). Therefore, increasing feed efficiency without increasing maintenance energy costs through genetic selection reduces feed costs for the producer while simultaneously reducing nutrient excretion to the environment (Basarab et al., 2013; Kelly et al., 2010); both desirable goals for the beef industry.

2.1 Modern measures of feed efficiency

The concept of assessing quantitative traits to identify and select for livestock with superior performance is common practice within the livestock industries. Since assessing performance traits quantitatively has great economic benefits for the industry, research into reducing feed costs by selecting for the most feed efficient cattle has been of primary importance. Historically, efficiency has been defined as the ratio of outputs to inputs, but a universal method of accurately selecting for feed efficient cattle has been lacking. This may be partly due to the limited understanding of the biological processes that contribute to phenotypic variation and, likewise, feed efficiency between animals (Herd et al., 2004). Advancements in feed intake monitoring systems have facilitated accurate individual feed intake, as well as a greater understanding of the biological processes that contribute largely to the genetic variation in feed efficiency. As a consequence, efforts have shifted focus exclusively from measuring animal output, toward measuring output in relation to input (Herd et al., 2004; Richardson et al., 1996). Common methods used in feed efficiency evaluation are summarized in Table 1:

Table 1. Definition of and strategies to calculate feed efficiency traits.

Feed Efficiency Trait	Definition	Calculation
Feed conversion ratio (FCR)	Actual dry matter intake (DMI) required per one unit of weight gain	DMI / ADG
Partial efficiency of growth (PEG)	Ratio of average daily gain (ADG) per unit of DMI after DMI has been adjusted for maintenance requirements, to determine growth	ADG / (Actual DMI - $\mathrm{DMI_m}^{a}$)
Residual feed intake (RFI)	Difference between standardized (actual) daily DMI (SDFI) and expected DMI (EFI) for maintenance of body weight and gain, ie: based on actual mid-test weight (MMW) and ADG on a contemporary group	SDFI – EFI[b]

Adapted from Hennessy and Arthur (2004), and Arthur et al. (2001b).

[a] $\mathrm{DMI_m}$ = expected DMI required for maintenance, when maintenance is calculated as 0.077 x BW $^{0.75}$ / $\mathrm{NE_m}$ concentration of the diet ($\mathrm{NE_m}$ obtained from NRC, 2000).

[b] Where EFI is obtained by regressing SDFI on mid-test metabolic body weight (MMW $^{0.75}$) and ADG.

Historically, feed conversion ratio (FCR) has been widely used as a measure of feed efficiency in the beef industry, as it is both moderately heritable, and has the potential to improve most growth traits (Arthur et al., 2001b). However, FCR has its own limitation, as it fails to account for variation in maintenance energy requirements (Herd and Bishop, 2000; Arthur et al., 1996) and is therefore not an accurate tool to estimate feed efficiency (Arthur et al., 1996). Furthermore, several studies have reported a negative correlation between ADG and FCR

(Nkrumah et al., 2004; Arthur et al., 2001a). Therefore, selection for low FCR cattle inadvertently leads to an increase in mature size, and as a result, increased feed requirements and associated feed costs (Herd and Bishop, 2000).

2.2 Residual feed intake (RFI)

It is well known that individual cattle of equal body weight (BW) require different amounts of feed for the same level of production (Herd et al., 2003). Koch et al. (1963) was the first to propose that differences in growth and maintenance in growing beef cattle affect feed requirements. He suggested that feed intake could be adjusted for BW and weight gain (or any production/energy expenditure such as milk production; fat deposition), thus partitioning feed intake into two distinct components: 1) expected level of feed intake at a given stage in production, and 2) a residual, or remaining portion. This residual portion can be used as an index to identify the degree to which an individual deviates from its expected feed intake level (Basarab et al., 2003; Herd et al., 2003). Essentially, it is this residual portion that provides a true depiction of the metabolic variation between cattle (Crews, 2005). The ability to calculate a residual portion from the expected level of feed intake provides an estimate of efficiency that is phenotypically independent of any production traits used in the regression model (Herd, 2009; Basarab et al., 2008). Efficient cattle have a negative or low RFI and consume less feed than expected; inefficient animals have a positive or high RFI and consume more than expected (Basarab et al., 2007, 2003; Herd et al., 2003). Further, RFI has been shown to be moderately heritable ($h^2 = 0.29$-0.46), providing for opportunity to select for feed efficient cattle without compromising growth performance or carcass quality (Bishop, 1992).

2.2.1 Measuring RFI

Residual feed intake is typically measured in young cattle between 7 to 10 months of age with a maximum age difference of 60 d (Basarab et al., 2013, 2011, 2003). Basarab et al. (2013) and Wang et al. (2006) reported a required 76 d test period for the determination of accurate feed intake and growth measurements, where feed intake is recorded daily and animal BW recorded at 14- to 28-d intervals in addition to the two consecutive weigh days at the start and end of the test period. Durunna et al. (2011) used a 63-d test period with weekly weights. More recently, duration of feed intake measurements has been reduced to 40-55 d by uncoupling the complete feed intake period (e.g., 40 d) from the growth measurement period (e.g., 80 d; Manafiazar et al., 2015) or by automated daily monitoring of body weight (Culbertson et al., 2015).

Cattle may be tested for RFI on-farm if facilities for individual animal intake exist, or at centralized test facilities (Basarab et al., 2013, 2011; Herd et al., 2003). Two limitations associated with both regimens include expense associated with accurately measuring feed intake in cattle, as well as the effects of pre-test environment on performance during the RFI ranking of the animal (Herd et al., 2003). Basarab et al. (2013) and Archer et al. (1999a) proposed a biological approach which may alleviate these effects. This pre-test adjustment period of 21- to 28-d is crucial to adapt the test cattle to the test diet and pen mates, and to reduce differences between animals due to previous housing and management environments that may otherwise impact an animal's ability to perform in comparison to the other animals on test (Basarab et al., 2013, 2011; Archer et al., 1999a). Thus, establishing a valid CG (same gender, diet, pen, animal type, physiological stage) is vital to feed efficiency evaluations, especially at a genetic level (Archer et al., 1999a).

Basic requirements for accurate measurement of RFI consist of: i) *ad libitum* feed available to all test animals to allow for differences in intake to be expressed; and ii) accuracy of measure of feed intake, live weight and weight gain (Herd, 2009).

Advancements in individual feed monitoring systems have made it possible to measure individual intake on a large scale, which has previously been a limitation for using RFI to estimate cattle feed efficiency. Feed intake for each animal is measured on a feeding event (many feeding events during each day) and summed daily using equipment such as the GrowSafe automated feed monitoring system. As described by Schwartzkopf-Genswein et al. (2002), the system uses radio frequency technology to document feeding patterns of individuals within large groups of cattle in a commercial setting. Each test animal is ear tagged with a half-duplex radio frequency identification (RFID) transponder encased in a plastic button, allowing for easy identification of individual animals by the feed system. An antenna embedded in the lip of each feed bunk emits a 130 kHz electromagnetic field and detects the RFID transponder when within 50 cm of the feed bunk that is suspended on two load cells (Schwartzkopf-Genswein et al. 2002). A data-logging reader panel connected to the antenna logs the presence of each transponder every second and transmits these data to a desktop computer to which data are uploaded and analyzed (Schwartzkopf-Genswein et al., 2011; Gibb et al., 1998). With advancements made in individual feed monitoring equipment, including the GrowSafe automated feed monitoring system, coupled with the expanding knowledge in animal energetics, RFI has become a frequently used method of determining feed efficiency of livestock.

2.2.2 Calculating RFI

Residual feed intake is computed as the difference between standardized daily feed intake (SDFI) and expected feed intake (EFI):

$$RFI = SDFI - EFI$$

where SDFI is obtained by multiplying the daily DMI by the metabolizable energy content of the diet and dividing this value by 10 to standardize intake to an energy density of 10 MJ ME/kg DM (NRC, 2000). Expected feed intake is predicted by regressing metabolic mid-test weight (MMW) and ADG on SDFI, using the following general model (Basarab et al., 2007):

$$Y_i = \beta_0 + \beta_1 ADG_i + \beta_2 MMW^{0.75}{}_i + e_i$$

where Y_i = SDFI calculated for animal i, β_O = regression intercept, β_1 = partial regression coefficient of SDFI on ADG, β_2 = partial regression coefficient of SDFI on MMW, and e_i = the residual error of SDFI for the i'th animal (Basarab et al., 2007). Further, RFI measurements may be adjusted by adding phenotypic traits into the generalized model. For example, RFI may be adjusted for ultrasound backfat (RFI_{fat}) with MMW, ADG and final ultrasound backfat regressed on SDFI (Chen et al., 2014; Basarab et al., 2007).

2.2.3 Biological basis for variation in RFI

While the phenotypic variation in RFI can be easily measured through feed intake, body weight, and growth rate via individual feed monitoring systems like GrowSafe, understanding the underlying genetic variation in RFI due to differences in biological efficiency between animals requires further investigation. Accurate measurement of RFI is essential to allow for genetic improvement and an improved understanding of the biology of this variation (Kelly et al., 2010; Herd, 2009). Data obtained by Herd et al. (2004) have supported a correlation between variation in RFI and maintenance energy requirements at a biological level. Although the biological basis of this variation in RFI is not fully comprehended, researchers have attributed 73% of this variation to these major underpinning biological processes: (i) digestibility of feed;

(ii) body composition and tissue turnover rates (catabolism and anabolism); and (iii) physical activity and heat loss (Kelly et al., 2010; Herd, 2009; Herd et al., 2004). It is hypothesized that variation in feed intake, digestibility of feed, and physical activity and heat loss accounted for one third of this biological variation in RFI, while the other two thirds are accounted for by protein turnover, ion transport and variation in other processes (Herd et al., 2004).

2.2.3.1 Digestibility

An increase in feed intake relative to maintenance tends toward a decrease in DM digestibility (Herd, 2009). This is in part due to the increased energy expended to digest the feed by the digestive organs (Young and Dekkers, 2012; Herd, 2009). Richardson et al. (1996) determined that digestibility was 1% higher for low versus high RFI calves fed a pelleted roughage-based diet. A subsequent study reported a 14% difference in intake between the low and high RFI groups, with the magnitude (r = -0.44) and direction of the correlation suggesting that more efficient cattle had increased digestibility (Richardson and Herd, 2004). Measuring subtle differences in ruminant digestibility is challenging, and as a result should not be used as the major process to explain variation in RFI (Herd, 2009).

2.2.3.2 Body composition and tissue turnover rates

Increased feed intake is associated with greater energy costs to digest the feed. Expended tissue energy also increases as unit weight of the ruminant increases. This is defined as the heat increment of feeding (HIF) (Herd, 2009; Webster et al., 1975). In cattle, it has been estimated that HIF contributes to approximately 9% of metabolizable energy intake (Herd, 2009; Standing Committee on Agriculture, 2000). Webster et al. (1975) reported that 40% of the total HIF in sheep was due to the amount of energy expended in the gut after ingestion of the feed. The remaining 60% is predicted to be due to increased metabolism in peripheral tissues. Selection for RFI in cattle is highly associated with differences in feed intake; thus, low-RFI cattle which eat less at the same level of performance are expected to expend less energy as HIF (Kelly et al., 2010; Herd, 2009).

Body composition can also influence energy costs and nutrient utilization due to differences in organ growth and lean and fat gain between animals. Efficiency is influenced by differences in protein and fat deposition (Ferrell and Jenkins, 1998). While fat has a higher energy density than protein, protein deposition is more variable between beef cattle of the same age, weight and fed the same diet due to protein turnover and the energy costs expended for protein metabolism within the muscle (Herd, 2009; Oddy et al, 1998; 1995; Ferrell and Jenkins, 1998). Herd (2009) reported a 20% variation between energy expenditure per unit mass of muscle in cattle and sheep that were grouped into high and low growth rate categories. Richardson and Herd (2004) reported low RFI cattle having lower levels of aspartate amino transferase, a marker used to measure liver function to indicate protein catabolism levels, and therefore greater synthesis of lean tissues compared with high RFI cattle. This validates the results reported by Arthur et al. (2001b) in which RFI was positively and genetically correlated with subcutaneous fat depth over the 12th and 13th ribs (0.17) and rump (0.06) of weaned bull and heifer calves. These results suggest that low RFI cattle had less intramuscular fat and were leaner than high RFI cattle.

2.2.3.3 Physical activity and heat loss

Variation in energy costs associated with level of physical activity contributes to the variation in heat production and available energy for maintenance and growth (Herd, 2009; Mousel, 1998). Mousel (1998) studied a line of mice selected for heat loss, reporting that high maintenance mice (greater heat loss) were twice as active and consumed on average 11.8 g/kg$^{0.75}$/d more feed, and had lower fat percentages than low maintenance mice. Overall, differences between the two lines were 36% and 11.5% for feed intake and heat loss due to activity, respectively (Mousel, 1998). This phenomenon has also been demonstrated in swine (Henken et al., 1991), where selection for low heat loss resulted in an unintentional selection for decreased activity and increased fat percentages.

Richardson et al. (1999) examined the impact of activity level on RFI in beef cattle based upon locomotion, rumination and work expended during feeding activities, and found that 9% of the variation in RFI was attributable to level of activity. Further to this, Herd et al. (2004) reported the energy cost of the aforementioned activities accounting for up to 5% of the increased feed energy intake seen in low efficiency cattle. Richardson et al. (2004) proposed that cattle that are more excitable or susceptible to environmental stressors naturally expend more energy on increased physical activity, with plasma cortisol levels of 21.1 (high RFI steers) versus 19.4 ug/dL (low RFI steers) providing evidence that the less efficient cattle are more susceptible to stress compared to more efficient cattle.

The degree of activity expended during feeding events is closely related to the individual’s FB traits, including daily FED (min/d), FEHD (min/d), FEF (visits to the feed bunk/d), FEL (min/feed event) and ER (g of DMI/min), as defined by Bailey et al. (2011), Mendes et al. (2010) and Basarab et al. (2003).

2.3 Feeding behaviour

Feed intake patterns in beef cattle are influenced by many variables, including weather conditions (Hahn, 1995), available bunk spacing and management strategies (Schwartzkopf-Genswein et al., 2011), animal health, and temperament of the animal (Nkrumah et al., 2007). Differences in individual FB patterns may contribute to the variation in energetic efficiency between animals (Kelly et al., 2010). Assuming that cattle have *ad libitum* access to feed, the extent to which feed efficiency is influenced by FB is not fully understood (Chen et al., 2014), and has become an area of significant research interest. Understanding the FB of individual cattle in a feedlot setting is necessary to understanding variation in individual growth performance otherwise not evident in group-averaged data obtained from pens of cattle (Lancaster et al., 2009), and may provide biological insight regarding diet preferences, health status of the beef animal, and long-term feed intake regulation (Forbes, 1985). Bovine FB patterns tend to be highly repeatable (Streeter et al., 1999) and research regarding relationships between FB variables and feed efficiency suggests that FB has potential to act as a predictor of cattle performance (Lancaster et al., 2009). This, coupled with an understanding of individual growth performance variation, will allow for development of enhanced bunk management programs in feedlot and cow-calf operations through controlled feed and bunk space availability (Schwartzkopf-Genswein et al., 2011).

2.3.1 Defining feeding behaviour traits

Multiple feed intake monitoring systems are available to collect feed bunk frequency and duration data to study FB in cattle. As described above, the GrowSafe System has become increasingly popular world-wide as it has the capacity to measure individual animal intake. In addition, it has the capacity to monitor and store individual feeding patterns within large groups while simultaneously recording individual feeding event frequency (FEF) and duration (FED).

Feeding behaviour has been characterized by a series of traits as described in Table 2.

Table 2. Description of feeding behaviour traits using data captured by the GrowSafe feeding system.

Trait Name	Units	Definition
Feed Events		
Feed event criterion		Attendance at a **single** node with intervals shorter than 300 seconds and uninterrupted by other animals constitute the same feed event **as long as intake is > 0 grams**. Begins when the RFID is first detected; ends when time between last 2 RFID readings is greater than 300 seconds, the same RFID is detected at another node, or a different RFID is encountered
Feed event duration (FED)	min/d	Daily sum of the difference between end and start time of a feeding event as described above
Feed event frequency (FEF)	events/d	Number of independent feed event bunk visits per day
Feed event head-down time (FEHD)	min/d	Sum of transponder detections of an animal during a feeding event multiplied by the scanning time (1.0-6.3 seconds), depending on the system configuration
Feed event length (FEL)	min/event	Average duration of a feed event
Eating rate (ER)	kg DMI/min	Average DMI consumed per minute

[1] Table modified from Bailey et al. (2011), Mendes et al. (2010) and Basarab et al. (2003).

2.3.2 Phenotypic correlations of feeding behaviour with RFI

Correlation coefficients of RFI and RFI_{fat} in Charolais and Angus steers (Chen et al., 2014), growing Angus bulls (Lancaster et al., 2009) and composite cattle (Nkrumah et al., 2007; Robinson and Oddy, 2004) with FB traits range from: 0.16 to 0.49 for FED, 0.38 to 0.50 for FEHD, 0.15 to 0.26 for FEF, and 0.08 to 0.44 for ER. To summarize, ER was weakly correlated with RFI across the reported studies, suggesting there is a limited association between ER and RFI (Chen et al., 2014). In comparison to the other aforementioned FB traits, FED and FEHD had a weak to moderate positive phenotypic correlation across studies, suggesting that FED and FEHD may be the strongest FB indicators in assessing variation in RFI. Therefore, selecting for low RFI cattle could favorably lead to correlated FED and FEHD responses, with efficient cattle spending shorter durations at the feed bunk (Chen et al., 2014). Interestingly, growing yearling Angus bulls had moderately positive phenotypic correlation of FED with RFI (0.26; Lancaster et al., 2009); however, only weak positive phenotypic correlations of FEF with RFI (0.15 - 0.18) in composite cattle (Nkrumah et al., 2007; Robinson and Oddy, 2004). This discrepancy between studies suggests several possibilities such as biological variation in FB may exist between breeds, diets, environments and management.

In addition to the above studies, Kelly et al. (2010) found no significant differences in daily FED ($P = 0.84$) between growing beef heifers categorized into high, medium and low RFI classes, and no correlation between FED and RFI, but found a significant ($P < 0.001$) positive correlation (0.26) between RFI and ER. However, a time-on-trial effect was detected for ER, such that there were no differences in ER between RFI classes during the last 20 d of the experimental period.

These findings collectively suggest that high RFI cattle invest more energy engaging in feeding related activities, with an increased energetic cost required to meet their activity level. Kelly et al. (2010) and Lancaster et al. (2009) reported that daily feeding events account for 20% and 35%, respectively, of the variation in RFI not explained by DMI or ADG. Therefore, analyzing the correlations between FB traits and RFI may enhance the understanding of the underlying genetic variation in RFI due to biological efficiency differences between cattle, and may provide the opportunity to implement FB traits into beef cattle genetic programs to subsequently enhance feed utilization, health of the animal, and reduce associated feed and health costs (Chen et al., 2014; Lancaster et al., 2009; Nkrumah et al., 2007).

In conclusion, high efficiency (low RFI) cattle have demonstrated a decrease in FED and FEF, with faster ER (Chen et al., 2014; Lancaster et al., 2009; Nkrumah et al., 2007; Robinson and Oddy, 2004). Further research is required to clearly identify the relationships between FB and performance traits under a variety of conditions defined by feeding management, diet, season, breed, sex, and stress levels. Large data sets are necessary due to variation among individual cattle (Chen et al., 2014; Schwartzkopf-Genswein et al., 2011).

2.3.3 Phenotypic correlations among feeding behaviour traits

Strong positive phenotypic correlations between daily FED and FEHD have been observed in independent research studies led by Chen et al. (2014), Durunna et al. (2011) and Nkrumah et al. (2007) in finishing steer populations, with phenotypic correlation ranges of 0.64 to 0.83. Strong and positive correlations between these traits are expected since cattle who occupy feed bunks for a longer period likely spend more time with their head lowered at the feeder (Chen et al., 2014).

Greater inconsistencies have been reported across studies for phenotypic correlations of FED and FEHD with FEF in finishing steers of Angus, Charolais and mixed breeds (Chen et al., 2014; Durunna et al., 2011; Nkrumah et al., 2007; Robinson and Oddy, 2004). These authors reported correlations of FED with FEF ranging from 0.07 to 0.33 and correlations of FEHD with FEF ranging from -0.10 to 0.44. In addition, Chen et al. (2014) reported a negative correlation of ER with FED in purebred Angus and Charolais steer populations, ranging from -0.78 to -0.79. They reported a negative correlation of meal ER with FEHD in the same Angus and Charolais steer populations, ranging from -0.78 to -0.83. Negative and weak to moderate phenotypic correlations of FEF with ER (ranging from -0.10 to -0.28) suggest cattle that spend longer at the feed bunk, visit the feed bunk more frequently and eat at a slower rate (Chen et al., 2014). Observed differences in FB correlations across studies may be attributed to: test diet, feedlot environment including feed bunk density (competition at feed bunks), differences in test cattle breed, population size of test cattle, age of test cattle, ambient and seasonal temperatures, as well as the statistical model used (Chen et al., 2014).

2.3.3.1 Forage-based vs. concentrate-based diets

Cattle have the capability to adjust their short-term FB to suit the nature of their diet (Allen, 2000). Diet characteristics influence the degree of stomach distension and trigger metabolic receptors in the liver as well as chemical and osmotic receptors in the digestive tract wall (Allen, 2000; Forbes, 1985). These in turn have a direct effect on the brain’s satiety center which regulates intake of feed (Allen, 2000), and similarly, FB traits.

Schwartzkopf-Genswein et al. (2011) and Basarab et al. (2000) demonstrated decreased feeding frequencies and length of consumption associated with concentrate-based diets as opposed to forage-based (high fibre) diets**.** Animals consume more energy with concentrate diets, which may in turn decrease the feeding frequency.

Eating rates increase with high concentrate diets as opposed to high-fibre diets (149 vs. 98 g/min, respectively), largely due to the decreased time required for mastication and rumination (Schwartzkopf-Genswein et al., 2011). Therefore, concentrate-based diets can be consumed more quickly (Schwartzkopf-Genswein et al., 2011; Golden et al., 2008), resulting in shorter non-feeding intervals and FEL, as smaller particle sizes decrease the need for mastication and rumination.

2.3.3.2 Feedlot environment and ambient temperatures

Feeding activity within confinement is influenced by bunk design and available bunk space in relation to pen stocking density, the time(s) of feed delivery events, and the amount of feed available to the animals (Streeter et al., 1999). Smaller calves have been observed to spend twice as long at the feed bunk per day (79.3 vs. 33.6 ± 1.9 min/d) due to height restraints in relation to bunk size, compared with calves of larger size (Gibb et al., 1998). Keys et al. (1978) reported a decreased overall FED of 288 min/d down to 213 min/d with an increased pen stocking density. As a consequence of limited bunk access and increased bunk competition, ER increased.

Additionally, seasonal conditions and ambient temperatures also influence acute and long-term FB patterns. When exposed to temperatures that exceed their upper critical limit, cattle become stressed, and both feed intake and production performance decline as energy requirements are partitioned toward heat dissipation (West, 2003). If temperatures drop below the animal's lower critical limit, maintenance energy requirements and feed intake increase in response to increased metabolism necessary to maintain body temperature (NRC, 2000; Young, 1981).

2.3.3.3 Cattle breed, sex and feedlot environment

Schutt et al. (2009) observed breed differences in FB as Angus-sired test cattle spent an additional 15.4 min/d at the feed bunk compared to Charolais-cross cattle. Similarly, Chen et al (2014) observed significant differences ($P < 0.01$) in FB between breeds, with Charolais steers spending less time at the feed bunks per bunk visit per day, even though both breeds were mixed together in groups in each trial pen. Studies comparing and contrasting breeds in same test environment on same diets remain sparse, but it is reasonable to conclude that breed impacts FB traits, possibly due to biological differences across breeds (Chen et al., 2014).

Although no literature has been published to date that contrasts the varying test facility feedlot set-ups, including animal density per bunks and pen layout, it should be noted that feedlot test-site set-up is a contributing factor to variation in FB traits. Schwartzkopf-Genswein et al. (2002) examined the impact of sex and feeding regime on FB traits in 6 cross-bred heifers and 6 cross-bred steers, penned individually. Heifers had significantly ($P < 0.0001$) higher FEF than did steers (17.68 visits/d vs. 15.38 visits/d, respectively), and heifers had significantly ($P < 0.0001$) higher FED compared with steers (124.9 min/d vs. 101.9 min/d, respectively). Caution should be considered when interpreting or comparing these results to other studies, as the sample size of this test animal population was small ($n = 12$; 6 heifers and 6 steers) and animals were penned individually, eliminating competition at the feed bunks.

Schwartzkopf-Genswein et al. (2002) also observed that *ad-libitum* versus restricted feeding has an impact, as both genders exhibited significantly longer FED (131.1 min/d vs. 95.2

min/d; *P* < 0.0001, respectively) and significantly greater FEF (17.1 visits/d vs. 15.9 visits/d; *P* < 0.0001, respectively), when feed was available *ad libitum*. Restricted feed access may impact an animal's true expression of FB as a consequence of decreased incentive to visit or remain at a feed bunk if there is no feed present (Schwartzkopf-Genswein et al., 2002).

2.3.4 Additional challenges when comparing feeding behaviour across studies

In addition to the differences described above, other parameters that may influence FB outcomes include system configuration settings, as well as differences in definitions and criterion (Bailey et al., 2012; Tolkamp et al., 2000). Bunk visits frequencies and FED across 6 studies ranged between 8-68 events/d and 48-170 min/d, respectively (Kelly et al., 2010; Basarab et al., 2007; Nkrumah et al., 2007, 2006; Shabi et al., 2005; Robinson and Oddy, 2004). Differences in cattle temperament may contribute to the observed variation in FB (Nkrumah e al., 2007).

2.4 Temperament

2.4.1 Defining temperament

Temperament is a complex series of traits that influence an individual animal's reaction to novel or challenging situations, and is the result of the animal's inherent disposition in combination with its prior experiences and environmental stimuli (Schwartzkopf-Genswein et al., 2012). More precisely, temperament reflects an animal's level of excitatory or inhibitory reactions, degree of locomotion, persistent habits and perceptivity in response to unfamiliar or stressful events (Schwartzkopf-Genswein et al., 2012; Sebastian et al., 2011; Hurnik et al., 1995). A beef animal encounters varying stress-eliciting procedures in a production setting, including but not limited to castration, dehorning, branding, tagging, vaccinating, weaning, transportation and social re-grouping (Vann et al., 2009). Acclimation to human handling and training may decrease an animal's reactivity response to a particular situation or method of handling, but may not necessarily overcome the animal's innate disposition in unfamiliar situations (Cooke et al., 2012; Francisco et al., 2012).

2.4.2 Methods of measuring temperament – the temperament index

Temperament has economic importance and therefore, use of simple labor- and cost-efficient, repeatable and reliable methods to predict and assess temperament in a beef production setting during standard animal handling procedures to identify and cull highly reactive animals has merit (Le Neindre et al., 1995; Grandin, 1993; Fordyce et al., 1985).

The goal of assessing temperament within a herd is to develop a robust method that can be carried through in a timely and consistent manner during routine on-farm and feedlot cattle handling and processing practices (Cooke et al., 2011). Temperament is an attribute of individual cattle that can be evaluated through a temperament index that may be useful in predicting and managing an animal's handling, welfare and performance in both feedlot and cow-calf production settings (Cafe et al., 2011; Sebastian et al., 2011). Tables 3 and 4 describe the subjective and objective temperament scoring assessment tests that are emerging as the most robust methods to measure cattle temperament, based on natural escape and avoidance behaviours in response to stressful events such as human handling.

Table 3. Chute score system (scale 3-10) used to assess temperament in cattle.

Entry Score (ENS)	1	Enters head gate calmly
	2	Coaxed in, enters head gate with moderate force
	3	Running entry, enters head gate with excessive force
Restraint Score (RES)	1	Little to no movement
	2	Restless, low amplitude movement
	3	Nervous, obvious forward and backward movement
	4	Nervous, continuous violent movements
Exit Score (EXS)	1	Calm exit
	2	Slow trot exit
	3	Running/jumping exit

Table modified from Grandin (1993).

Table 4. Description of assessment techniques and equipment required to assess cattle reactivity during handling.

Assessment Technique	Description	Equipment required
Exit velocity (EV; meters/second)	A measure that obtains a quantifiable value of the speed of an individual travelling a set distance (meters/second) when released from the confined area of the chute and head gate. Upon release from the chute, the animal proceeds down an alley at its own pace with no intervention to leave the chute or ability to see other animals.	Two sets of laser beam generators, reflectors on a stand raised to head level of the animal, and a timer. Positioning of equipment depends on facility design. The timer starts when the animal breaks the first laser beam and stops when it breaks the second.
Flight distance (FD; meters)	The flight zone of an animal, determined by its flight distance, is defined as the surrounding space that elicits an escape response if invaded by a perceived threat, and can be used to gauge the level of excitatory response (Grandin, 1993). A measurement is obtained by marking the point of shoulder at the time when the animal attempts to move away from the human advancing at a slow, steady pace. This indicates their reactivity to a human on a scoring scale of 1 (calm, docile and approachable) to 5 (aggressive, volatile and highly reactive) (Schwartzkopf-Genswein et al., 2012; Vann et al., 2009).	Laser pointer is used to mark distance from the human to the point of the animal's shoulder.

Table modified from Schwartzkopf-Genswein et al. (2012) and Sebastian et al. (2011).

2.4.3 Comparison and reliability of subjective and objective temperament index measures

2.4.3.1 Comparison between chute score and exit velocity

Schwartzkopf-Genswein et al. (2012), Kilgour et al. (2006), Grandin (2003) and Petherick et al. (2002) reported a decrease in exit velocity (EV) in response to repeated exposure to handling. Furthermore, these studies reported consistent recordings of chute score (CS) points (entry score (ENS), restraint score (RES) and exit score (EXS)) by the observer after the scores were standardized to remove the effect of difference in CS scale. Several studies (Schwartzkopf-Genswein et al. 2012; Kilgour et al. 2006; Muller and von Keyserlingk 2006; and Petherick et al. 2002) reported that faster EV from the chute was correlated with greater struggling during restraint (higher RES), and lower CS and slower EV were consistent of more docile cattle. Schwartzkopf-Genswein et al. (2012) and Grandin (2003) reported a significant negative correlation between EV and EXS, which suggested that the faster the animal left the chute, the less time it took to cover the designated EV distance. Exit velocity was significantly correlated with ENS (r = -0.32) and RES (r = -0.15), suggesting that higher CS on entry and restraint in the head gate equated to a faster EV. On the contrary, Kilgour et al. (2006) reported a phenotypic correlation of r = 0.44 between EXS and RES for Angus calves, but no correlation between EV and ENS and RES, suggesting that CS should be used with caution as a temperament measurement tool.

2.4.3.2 Comparison between chute score and flight distance

Flight distance is defined as the area surrounding an animal that, when invaded, elicits an avoidance response (Schwartzkopf-Genswein et al., 2012). Several studies (Schwartzkopf-Genswein et al. 2012; Kilgour et al. 2006; Burrow et al. 1988) have demonstrated that FD was correlated with EXS (*r* = 0.41), suggesting that the least approachable animals exhibited a faster EXS. Schwartzkopf-Genswein et al. (2012) suggested that the relationship between temperament and flight distance (FD) may actually be indicative of previous handling experience rather than the temperament of the animal, and so alone, it is not a reliable temperament assessment.

2.4.4 Natural pen lying behaviour

The indication of temperament is not solely limited to an animal's response to human interaction during handling and restraint, but also extends to its overall capacity to cope with social and environmental influences within its surroundings (Lyons, 1989). The use of activity monitors such as the HOBO Pendant G Acceleration Data Logger, Onset Computer Corporation, or IceTags (IceRobotics Ltd., South Queensferry, Edinburgh, Scotland), provide an alternate way to measure temperament via degree of activity (lying behaviour) of animals continuously over a set period of time in their home pen without human interaction. These data obtained have the potential to indicate an individual's capacity to endure its environmental and social influences, as well as cattle comfort (Ito et al., 2009; O'Driscoll et al., 2008; Haley et al., 2000; Lyons, 1989) and whether behaviour in the home pen is reflective of behaviour during objective and subjective temperament testing (MacKay et al., 2013). These authors were the first to report that cattle behaviour in the home pen (measured via IceTags fitted to each animal to log activity) is related to short-term temperament tests that included four measures for each of the following parameters: EV (higher EV were associated with more activity in the home pen, with *r* = 0.35, *P* = 0.004), CS (no correlations were observed), aggression at the feeder (no correlations were observed), and ability to dominate access to the feeder (dominant steers had shorter lying bout durations, with *r* = 0.26, *P* = 0.036), using 67 *Bos taurus* beef steers.

2.4.5 Benefits of selecting for desirable temperament

Chronic stress may negatively impact cattle performance by reducing growth, reproductive function and immune function (Vann et al., 2009; Fordyce et al., 1988). Early detection of cattle more prone to stress, in combination with minimizing stressful incidents, have received increased research interest, both from an economical and an animal welfare point of view. As temperament is a moderately heritable trait, improvements in overall herd temperament can be made relatively quickly through breeding and culling decisions (Vann et al., 2009; Grandin, 2003). This has potential to improve animal welfare by reducing levels of stress that both management practices (Burrow, 1997) and housing (Schmutz et al., 2001) may elicit. For this reason, Grandin (2003) suggested that the elimination of highly reactive cattle should become a widely practiced genetic selection strategy.

Including temperament as a selection criterion in breeding and culling decisions has the potential to improve: 1) cattle welfare during handling and transportation; 2) cattle health and resistance to heat stress; 3) feed efficiency (production performance); and 4) management of weaned calves abruptly transitioned from a pasture environment into a feedlot.

2.4.6 The effects of acclimation to handling

Acclimating weanling cattle to human interaction and handling procedures can improve cattle temperament, decrease cortisol blood concentrations elicited by handling stress, increase ADG and enhance heifer reproductive development, in turn improving production performance of feeder cattle and replacement heifers (Cooke et al., 2012; Francisco et al., 2012).

In a two-year study, Cooke et al. (2012) assigned 88 Angus x Hereford heifers to either an acclimation or a control treatment group based upon body weight and an average temperament score computed from a CS and EV at time of weaning. Those assigned to the acclimation treatment were pre-conditioned to human handling for a four week period, three times per week, and again on d 40 and 200, while those assigned to the control treatment were left undisturbed on pasture. Following the 4-week pre-conditioning period, heifers subjected to the acclimation treatment had reduced plasma cortisol concentrations on d 40 ($P = 0.01$), and reduced EV on d 200 ($P = 0.02$) compared with the control treatment. A treatment x day interaction was observed for EV ($P < 0.01$) on d 200, with a reduced EV for the acclimated heifers compared with the control treatment. The acclimated heifers reached puberty sooner compared to the control heifers ($P = 0.01$), although heifer body weight and growth rate also had a large influence on age of puberty (Cooke et al., 2012). These results suggested that those cattle with excitable temperaments may have delayed reproductive performance, and those that are pre-conditioned to human handling following weaning may have a reproductive advantage, coupled with lower concentrations of stress related hormones such as plasma cortisol (Cooke et al., 2012).

Francisco et al. (2012) examined the impact of temperament at weaning in a rangeland-based cow-calf operation on overall productivity. This study also partitioned a group of 60 Hereford x Angus steers into an acclimation treatment ($n = 30$) and a control treatment ($n = 30$), using the same temperament assessment criteria described above, as well as body weight at time of weaning. Acclimation took place over a 4-week period, two times per week. Following the 4-week period, all trial animals were assigned a temperament score, and those in the acclimation treatment displayed a decreased EV ($P = 0.05$), a decreased CS ($P < 0.01$), a decreased overall temperament score that averaged both measures ($P = 0.02$), and reduced plasma cortisol ($P =$

0.02) in comparison with the control treatment. These findings agree with Cooke et al. (2012) in that acclimatizing cattle to routine human handling procedures can improve cattle temperament.

2.4.7 When to assess temperament

To increase the accuracy of employing the temperament index before making any culling decisions, it is crucial to either evaluate temperament during multiple handling sessions at more than one point in time (less practical), or at multiple points during one session (ENS, RES and EXS; Grandin, 1993). Curley et al. (2006) reported a decreased or leveling response in cattle with repeated human handling, and proposed that this may be the best point in time to accurately assess temperament due to uniform previous acclimation among test animals. Alternatively, EV may correspond with the animal's response to previous experience(s) when restrained, as unpleasant experiences may impact results.

Cafe et al. (2011) observed a decline in the mean and variation in CS and an increase in the mean and variation in EV seen after the first three assessments. It was concluded that the variation between animals stabilized after a small number of consistent handling events through the same facilities due to habituation to the handling (Cafe et al., 2011). These results were consistent with results obtained from repeated temperament assessments by Curley et al. (2006) and Kilgour et al. (2006) and are not unexpected, as behavioural response is a combination of genetic and environmental influences (Cafe et al., 2011). Furthermore, Cafe et al. (2011) acknowledged that average measures provided a more reliable assessment of cattle temperament than did any single measure.

Similarly, it has been suggested that EV can be assessed in cattle of all ages from three weeks onward (Burdick et al., 2009). However, from a production standpoint, these authors suggested an EV test should be conducted closer to weaning time so producers can objectively rank their cattle based on “flightiest” and cull those with the most reactive temperament before incurring further costs raising animals which may subsequently be culled. In addition, by ranking cattle at weaning, the option to assign them to different management groups better suited to their production potential (feeder or replacement breeding stock) based on their EV assessment is possible (Burdick et al., 2011, 2009; Vann et al., 2009). Cooke et al. (2012) measured response of replacement heifers after weaning and mature cows during a 4-week acclimation period to human handling and reported that the replacement heifers had improved temperament, reduced cortisol and became pregnant sooner than non-acclimated replacement heifers. There was no benefit for the mature cows, suggesting that acclimation to human handling early in their productive lifetime may be an alternative to improving temperament.

2.5 Relationships between RFI, feeding behaviour and temperament

In the last decade, there has been growing interest in the relationship between temperament, FB and RFI. Sebastian et al. (2011) reported that highly efficient (low RFI) cattle are less susceptible to stress than those assigned a high RFI ranking, as assessed by EV. It is presumed that cattle that are less susceptible to stress are more efficient at metabolizing feed energy on the basis of weight gain alone. In addition, these animals may be more effective at coping with and/or adapting to any given stressor(s) in comparison to individuals that are highly susceptible to stress (Sebastian et al., 2011; Herd, 2009; Nkrumah et al., 2007).

Reports on non-ruminant species such as poultry (Luiting et al., 1991) and swine (de Haer et al., 1993) suggested that a substantial proportion of the variation in RFI is due to the degree of physical activity. Physical activity is partially dependent upon the animal’s temperament, where flightier animals are more active. Research with cattle in Canada (Nkrumah et al., 2007, 2006) and the United States (Golden et al., 2008; Lancaster et al., 2005) concur with these findings, reporting that the more energetically efficient cattle engaged in 22% fewer daily feeding events, suggesting that less energy was expended acquiring feed.

Genetic variability among FB traits in cattle does exist. The degree to which variation in feeding duration and frequency exist is likely regulated by an underlying genetic factor that may be associated with biological signals controlling short-term hunger and satiety (Allen, 2010; Nkrumah et al., 2007). Short-term biological signals, combined with the animal's overall energy balance or body composition, trigger both time and duration of the next feeding event (Allen, 2010). However, factors determining FB have a far broader scope that encompasses the animal's surrounding environment and temperament.

An in-depth examination of FB has only been possible in the recent past through innovations in feed delivery systems. Research efforts must continue advancing toward a more in-depth understanding of system efficiency in order to improve profitability and reduce the cost of production in the cattle industry. Knowledge of feed efficiency, FB and temperament, and the phenotypic correlations between these traits are an important element of efforts to develop successful and cost-effective cattle selection strategies in western Canadian beef cattle production systems.

3. RESEARCH HYPOTHESES AND OBJECTIVES

3.1 HYPOTHESES

Presently, seed stock producers in Canada and throughout the world are increasing their capacity to test potential breeding stock for residual feed intake (RFI) in a feedlot setting, as this is a moderately heritable measure of feed efficiency. The goal of a beef feedlot is to attain consistent and repeatable feed intake, which ensures consistent and repeatable performance and profit. Using FB traits and/or temperament assessment measures will provide a reliable method of assessing and predicting feed efficiency in all classes of beef cattle, and will provide the potential for indirectly selecting for RFI based upon selecting for FB and temperament traits. Examining individual cattle FB traits in relation to RFI and residual feed intake adjusted for final backfat (RFI_{fat}) will demonstrate the potential of identifying the more feed efficient individuals. It is anticipated that cattle grouped into RFI and RFI_{fat} groups (low, medium, high) differ in FB within RFI ranking, with more efficient (low RFI) cattle having decreased feeding frequencies and durations and increased ER regardless of diet type (forage-based vs. grain-based) and cattle class (replacement heifers, feeder heifers and steers, mature cows and yearling bulls). Previously acclimated yearling beef bulls within different RFI and RFI_{fat} classes will differ in temperament, as measured by CS, EV, FD and pen lying duration (LD), with the more feed efficient cattle possessing lower CS, slower EV, decreased FD and longer LD indicative of a less reactive temperament.

3.2 OBJECTIVES

The overall objectives of this thesis are to evaluate the relationship between FB traits and RFI group within different beef cattle classes, and the relationship between FB traits, RFI group and temperament in yearling Angus beef bulls. Specific objectives include: **(i)** an evaluation of the effects of CG, year, diet, RFI and RFI_{fat} on FB traits as measured by the GrowSafe feed monitoring system (GrowSafe Systems Ltd., Airdrie, Alberta, Canada) using cattle of various ages (260-1773 d of age), breeds (purebred Angus, Aberdeen Angus Hereford cross, Red Angus Charolais cross, Charolais-Maine Anjou cross, Charolais and Hereford) and classes: commercial stock (producer-owned breeding bulls, replacement heifers and mature cows) and feeders (heifers and steers) from three locations in western Canada; **(ii)** an examination of the phenotypic correlations between RFI, RFI_{fat} and the following FB traits calculated by the GrowSafe feeding system: FED (min/d), FEF (events/d), FEHD (min/d), FEL (min/event) and ER (kg DMI/min); **(iii)** an examination of the effect of diet (forage-based vs. grain-based) on FB traits; **(iv)** an exploration of the phenotypic relationship between RFI and RFI_{fat} group (low, medium, high) within diet (forage and grain) on temperament as measured by objective (EV, FD) and subjective (CS) methods, in addition to LD in the home pen without human interaction via an activity monitor (HOBO Pendant G Accelerometer, Onset Computer Corporation, Bourne MA) on producer-owned yearling Angus bulls already acclimated to the same handling facility six months prior to temperament assessment; and **(v)** an assessment of the phenotypic correlations between temperament and FB traits in yearling Angus beef bulls.

4. MANUSCRIPT I

Relationships between residual feed intake, dry matter intake and feeding behaviour in five classes of beef cattle

L. Lippens, K.H. Ominski, G. Crow, K. Schwartzkopf-Genswein, F. Zvomuya, J.A. Basarab

Department of Animal Science, Faculty of Agricultural and Food Sciences, University of Manitoba, Winnipeg, Manitoba, Canada, R3T 2N2

4.1 ABSTRACT

The objective of this study was to quantify the relationships between feeding behaviour (FB) traits as measured by the GrowSafe feeding system (GrowSafe Systems Ltd., Airdrie, Alberta, Canada) and feed efficiency (residual feed intake) in *Bos taurus* beef cattle. The study was conducted using five animal classes (breeding bulls, replacement heifers, mature cows and feeder heifers and steers) of commercial beef cattle (n = 868) of various breeds and ages (260-1773 d), fed different diets from three locations in western Canada. Phenotypic relationships between residual feed intake (RFI), RFI adjusted for final backfat thickness (RFI_{fat}), dry matter intake (DMI) and FB traits were examined. Cattle were grouped into low, medium and high classes based upon ± 0.5 RFI standard deviation and evaluated for the following FB traits: daily feeding event duration (FED; min/d), daily feeding event frequency (FEF; events/d), daily feeding event head-down time (FEHD; min/d), feeding event length (FEL; min/event) and eating rate (ER; kg DMI/min).

With the exception of the replacement heifers, significant differences ($P < 0.05$) in FB traits - most pre-dominantly FED, FEF and FEHD - between RFI and RFI_{fat} groups, contemporary groups (CG) or year were observed for all cattle classes. Bulls fed the forage-based diet had 15.9% longer FED ($P < 0.0001$), 15.4% slower ER and consumed 16% less DMI compared with bulls fed the grain-based diet. Significant ($P < 0.05$) phenotypic correlations were observed for RFI, RFI_{fat}, DMI and FB traits including FED, FEF, FEHD, FEL and ER among all cattle classes.

Abbreviations used in Manuscript I: ADG, average daily gain; **AFD**, assigned feed disappearance; **CG1**, contemporary group one; **CG2**, contemporary group two; **DM**, dry matter; **DMI**, dry matter intake (kg DMI/day); **ER**, eating rate (kg DMI/minute); **FBF**, final backfat thickness (mm); **FED**, feeding event duration (minutes/day); **FEF**, feeding event frequency; **FEHD**, feeding event head-down time (minutes/day); **FEL**, feeding event length (minutes/event); **MMW**, metabolic mid-weight; **NDF**, neutral detergent fibre; **RFI**, residual feed intake; **RFI_{fat}**, residual feed intake adjusted for final backfat thickness; **RFID**, radio frequency identification; **SDFI**, standardized daily feed intake; **TMR**, total mixed ration

Keywords: cattle, feeding behaviour, feeding event, GrowSafe Systems Ltd., residual feed intake

4.2 INTRODUCTION

Cost of feed, bedding and pasture is the largest economic obstacle in the beef industry, accounting for 55-80% of the total costs of beef production (Larson et al., 2010). The cost of feeding one cow is estimated to be $354.71/year (MAFRD, 2017). In the last decade, feed costs associated with beef production have greatly increased; as a result, breeding and selection strategies have shifted emphasis from traditionally selecting for output traits (average daily gain (ADG), maternal weaning weight, hot carcass weight), to selecting for input/output-based traits such as feed efficiency, as a way to reduce feed costs (Lamb and Maddock, 2009).

Feedlot studies have demonstrated that a 10% improvement in ADG can increase profitability by 18% (Basarab et al., 2002; Arthur et al., 2001a), but a 10% improvement in feed efficiency may increase profits by 43% (Lamb and Maddock, 2009; Fox et al., 2001). The economic benefits of selecting for feed efficient beef cattle has become recognized world-wide as a means of improving the economic sustainability of the industry in both the cow/calf and feedlot sectors. Historically, feed efficiency has been measured via feed conversion ratio (FCR) which inadvertently led to the indirect selection for larger animals with increased feed intake and feed costs, thereby mitigating any potential benefit (Basarab et al., 2002). Recognizing that individual cattle of the same body weight and level of production can have feed requirements that differ by as much as 35% (Byerly, 1941), Koch et al. (1963) were the first to develop the concept of residual feed intake (RFI), a strategy to predict feed efficiency based upon the magnitude of the residual portion of feed that remains after an animal’s actual intake and expected intake have been determined. Cattle with a low or negative residual portion are deemed as more efficient since their actual feed intake is less than predicted, so maintenance requirements are lower than expected. Since RFI is phenotypically independent of growth, body weight, ADG or backfat thickness, it has the capacity to precisely identify cattle with lower maintenance and feed consumption without compromising other performance parameters such as growth rate, body size or carcass characteristics (Elzo et al., 2009; Nkrumah et al., 2007; Basarab et al., 2003; Herd et al., 2003).

Residual feed intake is a moderately heritable trait, and is therefore a useful tool to improve the efficiency of the cattle herd through breeding programs. To date, cost, time required to complete the test and the need for expensive infrastructure has limited widespread industry adoption of RFI as a selection tool. However, industry is adapting to this barrier by reducing intake testing costs. In order to develop more cost-effective strategies at assessing feed efficiency, a more in-depth understanding of the underlying biological and metabolic factors that influence feed efficiency is warranted. Assessing cattle FB may provide further insight into biological and metabolic differences that contribute to the variation in feed efficiency. Further, FB arguably has the potential to be a cost-effective strategy to predict feed efficiency, more specifically RFI.

Feeding behaviour activities provide a biological understanding of long-term feed intake patterns. Feeding events are not random, for as the length of time increases since the last meal, the probability of the next meal commencing increases (Tolkamp et al., 1998). The mutual goal of feedlots and cow/calf production systems is to attain consistent and repeatable intake, which ensures consistent and repeatable performance (Nkrumah et al., 2007). Intake is influenced by FB variables, and a greater understanding of individual FB traits will improve overall feeding management (Schwartzkopf-Genswein et al., 2002), not only in feedlots, but also on commercial cow/calf operations.

The relationship between RFI and FB variables including FED, FEF, FEHD, FEL and ER have been explored in feedlot cattle and, to a lesser extent, breeding stock (Fitzsimons et al., 2014; McGee et al., 2014; Lancaster et al., 2009; Basarab et al., 2003, 2002; Schwartzkopf-Genswein et al., 2002). High efficiency (low RFI) cattle have a decrease in feeding-associated activities: faster ER (kg DMI/min), shorter eating durations (min/d) and fewer feeding frequencies (Chen et al., 2014; Lancaster et al., 2009; Nkrumah et al., 2007; Robinson and Oddy, 2004). Further research is required to clearly identify the relationships between FB and feed efficiency traits in different situations defined by cattle class, diet, gender, breed and ambient temperature (Schwartzkopf-Genswein et al., 2011). Large data sets replicated across multiple cattle classes are necessary to rigorously assess the relationship between FB and RFI due to variation among individual cattle (Chen et al., 2014; Schwartzkopf-Genswein et al., 2011). Furthermore, FB may also be related to temperament of the animal, where the more excitable animals invest more energy in locomotion and acquiring feed, compared to the calmer animals that may spend more time in other activities such as rumination (Gaspers et al., 2014) or lying down.

4.3 MATERIALS AND METHODS

4.3.1 Data sets used

This study was conducted using five classes of beef cattle of various breeds (Angus, Charolais, Charolais-Maine Anjoux, Hereford, crossbreeds), contemporary groups (CG1 and CG2; Table 1), ages and number of head (Table 2). A CG was defined as a group of test cattle of same classification status (replacement heifer, feeder, mature cow, yearling bull) housed within the same pen, receiving the same diet, during the same period of time. Two CGs of replacement heifers (*n* = 85 and 80; mean age 315 ± 20 d and 311 ± 31 d, respectively) and mature cows (*n* = 39 and 42; mean age 1675 ± 373 d and 1773 ± 377 d, respectively) were located at the Lacombe Research and Development Centre, Alberta, Canada. Two CGs of feeder heifers (*n* = 149 and 91; mean age 260 ± 16 d and 420 ± 20 d, respectively) and feeder steers (*n* = 141 and 123; mean age 263 ± 20 d and 342 ± 17 d, respectively) were located at Namaka Farms Inc., Strathmore, Alberta, Canada. Two years (two CGs per year) of growing yearling bulls (*n* = 60 and 58; mean age 383 ± 27 d and 355 ± 23 d, respectively) completed the data sets used to examine the phenotypic relationships between RFI, RFI_{fat}, daily DMI and FB variables.

Table 1. Overview of data sets included in our study.

Cattle class	Trial start	Contemporary group total	Location	Breed
Repl Heifers	February, 2012	2	Lacombe Research and Development Centre, AB	Aberdeen Angus x Hereford cross, Red Angus x Charolais cross
Repl Heifers	February, 2013			
Mature Cows	November, 2011	2	Lacombe Research and Development Centre, AB	Aberdeen Angus x Hereford cross, Charolais x Maine Anjou cross
Mature Cows	November, 2012			
Feeder Heifers	January, 2011	2	Namaka Farms Inc, AB	Crossbred
Feeder Heifers	July, 2011			
Feeder Steers	January, 2011	2	Namaka Farms Inc, AB	Crossbred
Feeder Steers	April, 2011			
Yearling Bulls (Forage, Grain)	March, 2012	2	Glenlea Research Station, MB	Purebred Angus
Yearling Bulls (Forage, Grain)	March, 2013	2		

4.3.2 Animal management

Cattle at all sites were cared for in compliance with the Canadian Council on Animal Care (CCAC). Upon arrival at the test sites, each CG of feeder steers and heifers at Namaka Farms Inc., and replacement heifers and mature cows at Lacombe Research Station were weighed, body condition scored (BCS) to assess their fat reserves covering their body frame, and then moved into a single pen. In both years, the yearling bulls at the Glenlea Research Station were vaccinated, weighed, body condition scored and randomly assigned to four feedlot pens.

Two pens received the forage-based diet (*n* = 30; 29) and two pens received the grain-based diet (*n* = 30; 29) in Years 1 and 2, respectively. The GrowSafe feeding system (GrowSafe Systems Ltd., Airdrie, Alberta, Canada), an electronic feed bunk monitoring system requiring radio frequency technology, recorded individual daily feed intake and bunk attendance data by using the GrowSafe Data Acquisition (DAQ) software. Feeding stations at all sites were sheltered from harsh weather elements and precipitation by an open-front wooden shed with an overhang that allows animal access to the feed bunks. As explained extensively by Schwartzkopf-Genswein et al. (2002), one GrowSafe node consists of a feed tub unit suspended on two load bars, with an antenna embedded in the tub lip that enables RFID identification within a 50 cm range of the feed tub. A PC computer and GrowSafe data acquisition and analysis software are required to collect and store the data (Basarab et al., 2003). Cattle at the Lacombe site (replacement heifers and mature cows) had unlimited access to sixteen nodes total within the test pen, while the feeder heifers and steers at Namaka Farms Ltd had access to fourteen nodes per CG, and the yearling bulls at Glenlea Research Station had access to four nodes per CG.

Adaptation period varied according to treatment group: 29-35 d (replacement heifers and mature cows), 21 d (yearling bulls) and 40 d (feeder heifers and steers). Ingredient and nutrient composition of all diets are described in Tables 3 and 4. Replacement heifers and the feeder cattle were fed twice daily to ensure *ad libitum* access to feed. The first CG of mature cows were fed a cubed forage diet (70% hay, 30% straw) *ad libitum* from d 0-30; however, cows were consuming 30% more forage cubes than needed to meet their maintenance and lactation requirements, thereby exceeding the targeted BCS range of 2.5-3.0. Therefore, animals were fed on a restricted basis from d 31-70 in an attempt to return to and maintain a BCS of 2.5-3.0. The second CG of mature cows was selected to ensure consistent body weight, thereby partially reducing feed bunk competition. The mature cows, replacement heifers and feeder cattle were offered free choice salt and a mineral plus a vitamin premix (Feed-Rite Rite-Mins Beef Cow Calving Plus Mineral, Feed Rite, A Division of Ridley Inc., 34 Terracon Place, Winnipeg, MB, Canada R2J 4G7). The yearling bulls were fed four to five times daily to ensure *ad libitum* access to feed, two diets in each of two years: one a forage-based silage diet and the other a grain-based silage diet. All cattle had free choice access to fresh water via heated watering bowls, and were bedded with non-palatable by-products to discourage consumption and minimize impact on feed intake; the Lacombe Research Centre and Namaka Farms Ltd. sites used wood chips, and the Glenlea Research Station used flax shives.

Each of the two CGs of replacement heifers (Lacombe, Alberta), feeder heifers and feeder steers (Strathmore, Alberta) were vaccinated with Bovishield Gold FP5 VL5 (Pfizer Animal Health, Pfizer Canada Inc., Kirkland, Quebec, Canada), Ultrabac 7/Somnubac (Pfizer Animal Health) and One Shot Ultra (Pfizer Animal Health) at two months of age, and administered a booster along with an Ivomec parasiticide (Merial, Baie d'Urfe, Canada) six weeks prior to weaning. The yearling bulls (Glenlea, Manitoba) were vaccinated in both years upon arrival at the Glenlea Research Station test facility, with Vista® Once SQ (Merck Animal Health) and Vision® 8 Somnus with Spur® (Intervet/Merck Animal Health), and administered a prophylactic subcutaneous injection of Draxxin (Zoetis). A booster of the Vision® 8 Somnus with Spur® vaccine was injected three weeks following the initial injection, and a vitamin A and D injection administered every three months in both years.

Cattle in all test locations were weighed on two consecutive days at the start and at the end of each feeding period. The replacement heifers, mature cows, feeder heifers and feeder steers were weighed at 21-28 d intervals throughout the test period. The yearling bulls were weighed biweekly during Year 1 to coincide with the 78 d feeding period, and were weighed weekly in Year 2 to accommodate a 63 d RFI period (Wang et al., 2006). Backfat (mm), intramuscular fat (mm), rump fat (mm) and ribeye area (mm) were measured at the end of each feeding trial, by a trained technician using an Aloka 500V diagnostic real-time ultrasound with a 17-cm 3.5-MHz linear array transducer (Overseas Monitor Corporation Ltd., Richmond, BC).

4.3.3 Validation of feed intake data

Table 2 provides an overview of the valid GrowSafe System days for all data sets and includes only those animals with valid data. Any animals that were culled from the study due to health reasons (ex: pneumonia, lameness, peritonitis, sudden death) were excluded from the data sets. Further, assigned feed disappearance (AFD) is a daily value (%) generated by the GrowSafe system for each node, to ensure that all feed that disappears is accounted for. It is a measure of confidence in the intake data and is important to ensure the accuracy of the RFI ranking. A valid feed intake day must meet the following two criteria: 1) all nodes within the pen must have an AFD of ≥ 90%, and 2) the average pen AFD must be ≥ 95%. There was a high degree of data integrity, as all mean AFD values exceeded 99% (Table 2). Reasons that feed intake days were excluded from the data sets included: a) excessive winds interfered with the load bars; b) an animal lost its RFID transponder tag; c) the time change affected the intake calculations at all sites on one occasion; d) feed delivery events that allowed animals to access feed without having to insert their heads into the feed bunk; e) a dislocated vertical restriction bar that resulted in more than one animal accessing a feed bunk at the same time; f) equipment malfunction; and g) power failure.

Small year-to-year differences were noted in the CG as depicted in Table 2. The replacement heifers in CG1 were on average 5 d older compared to CG2. The mature cows in CG2 were on average 98 d older compared to CG1. Feeder heifers were on average 160 d older in CG2 compared to CG1. Feeder steers in CG2 were on average 79 d older compared to CG1. Yearling bulls were on average 28 d older at the start of the test period in Year 2 compared to Year 1.

Table 2. Summary and validation of GrowSafe feed intake data for all classes of cattle.

	Replacement Heifers		Mature Cows		Yearling Bulls		Feeder Heifers		Feeder Steers	
Parameters	CG 1	CG 2	CG 1	CG 2	Year 1	Year 2	CG 1	CG 2	CG 1	CG 2
Number of animals	85	80	39	42	60	58	140	91	141	123
Mean age at start of feeding period	315 ± 20	311 ± 13	1675 ± 373	1773 ± 377	383 ± 27	355 ± 23	260 ± 16	420 ± 20	263 ± 20	342 ± 17
Number of test pens	1	1	1	1	4	4	1	1	1	1
Number of nodes	16	16	16	16	16 (4 per pen)	16 (4 per pen)	14	14	14	14
Number of head per node	5.31	5	2.44	2.63	3.75	3.63	10.64	6.5	10.07	8.79
Number of valid days	68	74	70	76	78	67	73	65	73	73
Number of days excluded	6	2	9	3	7	6	2	1	2	2
Mean daily assigned feed disappearance (AFD), %	99.5	99.7	99.2	99.4	99.3	99.1	99.3	99.5	99.1	99.4
Total feed station days (FSD)[1]	1088	1184	1120	1216	1248	1072	1022	910	1022	1022

[1] Feed station days (FSD) is calculated by multiplying days on test by number of nodes.

4.3.4 Feed sample collection

A representative grab sample of the total mixed ration (TMR) was taken at time of feeding, once per week, and composited monthly. Monthly composited samples were dried in a forced air oven at 60° C (yearling bulls) or at 100° C (other cattle classes) to a constant weight, ground in a Tecator and analyzed for nutrient composition (Tables 3 and 4). The average dry matter (DM) percent of all composited monthly samples was calculated over the entire test period, and this was the DM value used for the overall DMI calculation. Acid detergent fibre (ADF) and neutral detergent fibre (NDF) were calculated using an ANKOM 200 fibre analyzer (Fairport, NY). Gross energy was derived by combusting a pelleted feed sample in a Par 6300 Automatic Isoperibol Calorimeter (Moline, IL). Crude protein (CP) was analyzed via the LECO NS 2000 analyzer (LECO Corporation, St. Joseph, MI) and calculated as 6.25 x N (AOAC 1996, Official Method 973.03). A 1 g ground portion of the feed sample was ashed in a furnace and further analyzed for calcium, phosphorus, potassium and magnesium using inductively-coupled plasma emission spectroscopy (Vista MPX ICP, Varian Canada Inc., Mississauga, ON; AOAC 2005, method no. 985.01).

Table 3. Replacement heifer, mature cow, feeder heifer and feeder steer diet composition.

	Replacement Heifers		Mature Cows		Feeder Heifers		Feeder Steers	
Item	CG1	CG2	CG1	CG2	CG1	CG2	CG1	CG2
Ingredient composition, %, as-fed basis	-	-	-	-	-	-	-	-
Barley silage	90	90	-	-	7.41	7.41	7.41	7.41
Steam rolled barley	10	10	-	-	-	-	-	-
Hay	-	-	70	70	-	-	-	-
Straw	-	-	30	30	-	-	-	-
Barley grain	-	-	.	.	90.25	90.25	90.25	90.25
32-20 feedlot supplement	-	-	.	.	2.35	2.35	2.35	2.35
Nutrient composition, DM basis								
Dry matter, %	39.03	47.06	89.44	86.69	93.57	93.57	93.57	93.57
Acid detergent fiber, %	35.10	32.68	42.60	43.40	12.16	12.16	12.16	12.16
Total digestible nutrients, %	62.90	64.61	57.70	57.10	75.93	75.93	75.93	75.93
Metabolizable energy, MJ/kg	9.50	9.76	8.73	8.67	11.53	11.53	11.53	11.53
Crude protein, %	10.37	10.35	8.50	8.80	11.02	11.02	11.02	11.02
Calcium, %	0.35	0.48	2.49	2.30	0.95	0.95	0.95	0.95
Phosphorus, %	0.31	0.32	0.12	0.14	0.36	0.36	0.36	0.36
Magnesium, %	-	-	-	-	0.15	0.15	0.15	0.15
Potassium, %	-	-	-	-	0.56	0.56	0.56	0.56

Table 4. Yearling bull forage- and grain-based diet composition (Years 1 and 2).

	Year 1		Year 2	
Item	Forage	Grain	Forage	Grain
Ingredient composition, %, as-fed basis				
Alfalfa hay	26.40	-	17.90	-
Corn silage	73.40	38.50	81.70	39.00
Alfalfa silage	-	38.60	-	33.10
Corn grain	-	22.20	-	27.50
Limestone	-	-	0.30	-
Mineral	0.10	0.10	0.10	0.10
Salt	0.10	0.10	0.10	0.10
Nutrient composition, DM basis				
Dry matter, %	50.90	49.70	50.70	52.70
Acid detergent fiber, %	30.93	23.49	21.78	15.63
Total digestible nutrients, %	64.05	70.71	73.51	79.87
Metabolizable energy, MJ/kg	9.67	10.67	11.10	12.06
Crude protein, %	11.90	10.30	13.10	12.30
Calcium, %	0.68	0.72	0.89	0.77
Phosphorus, %	0.32	0.26	0.45	0.42
Magnesium, %	0.32	0.26	0.42	0.34
Potassium, %	0.98	1.22	2.16	1.65

4.3.5 Feeding behaviour and DMI

Methodology to determine FB traits has previously been defined by Bailey et al. (2011), Nkrumah et al. (2007) and Basarab et al. (2003). Individual animal FB traits (duration, frequency, head-down time) and feed intake (as-fed) were recorded 24 hr/d by the GrowSafe System based on continuous recordings for the entire trial duration for all cattle classes. From duration, frequency and feed intake (converted to DMI), feeding length and ER were calculated. Feeding event variables are defined in Table 5. Feeding event criterion was based on only those bunk visits recorded by the GrowSafe system where feed (> 0 g) was consumed. Any feed event data where 0 g was consumed were excluded from the FB analyses. Research by Carstens et al. (2006) found that 95% + of the time, feed is consumed during bunk visit events, so the difference in methodology likely does not produce data that is significantly different, but it is still necessary to note. After quality control to eliminate excluded data (non-valid days and culled test animals) and to remove any feed events where 0 g of feed was consumed, the feeding event variables were summed to obtain total feeding duration (sum of min), frequency (sum of bunk visits), head-down time (sum of min) and total feed intake (overall kg consumed, as-fed). Feed intake was then converted to DMI and the sums of feeding duration, frequency, head-down time and feed intake were then divided by total days on trial at each test location to derive an average daily FED, frequency (FEF; bunk visits/d) and head-down time (FEHD; min/d) for each animal. Feeding event length was computed as FED (sum of min) divided by FEF (sum of bunk visits), to determine average min/feed event. Eating rate was calculated as the sum of DMI (kg) divided by the FED (sum of min), to derive kg DMI/minute consumption for each animal. Feeding event length (FEL min/event) and ER were not converted into daily averages, but instead represented the average for each animal over the entire test period.

Table 5. Description of feeding behaviour traits using data captured by the GrowSafe feeding system.

Trait Name	Units	Definition
Feed Events		
Feed event criterion		Attendance at a **single** node with intervals shorter than 300 seconds and uninterrupted by other animals constitute the same feed event **as long as intake is > 0 grams**. Begins when the RFID is first detected; ends when time between last 2 RFID readings is greater than 300 seconds, the same RFID is detected at another node, or a different RFID is encountered
Feed event duration (FED)	min/d	Sum of difference between daily feed event end and start times
Feed event frequency (FEF)	events/d	Number of independent feed event bunk visits per day
Feed event head-down time (FEHD)	min/d	Sum of transponder detections of an animal during a feeding event multiplied by the system's scanning time (1.0-6.3 seconds), depending on the feeding system's configuration
Feed event length (FEL)	min/event	Average duration of a feed event
Eating rate (ER)	kg DMI/min	Average DMI consumed per minute

Modified from Bailey et al. (2011), Mendes et al. (2010) and Basarab et al. (2003).

A feeding event commenced when the animal's half-duplex RFID transponder was detected by the antenna, and ended when the elapsed time between the last two readings exceeded 300 s (Basarab et al., 2003), provided that the animal consumed > 0 g of feed. Head-down time refers to the frequency of RFID transponder detections for an animal multiplied by the system's scanning time of 5.7 s. Feeding event duration is the sum of feeding event end times and start times as long as the time between the last two successive RFID detections does not exceed 300 s. Therefore, FED may also include time an animal invests on non-feed related activities such as backing away from the feed bunk, socializing, licking or rubbing against the feed bunk or removing the head from the scanner range. By comparison, FEHD includes only the time period(s) when the animal has its head within scanner range (50 cm), excluding those intervals the animal may have backed away from the bunk to engage in other activities (Nkrumah et al., 2007). While FEHD may be more accurate than FED in terms of depicting time spent actively consuming feed, it is not a fool-proof assessment of active ingestion of feed. The animal may have its head low enough to be detected by the scanner but may not necessarily be eating during that time frame.

4.3.6 Calculations and statistical analyses

4.3.6.1 Residual feed intake

As described by Basarab et al. (2007), a linear regression of weight against time was used to model the growth of each animal, with the majority of growth curves having a coefficient of determination greater than 0.95 to conclude that cattle were free of nutritional deficiencies and health issues. Start of test weight, metabolic mid-weight (MMW) and ADG were derived from each animal's growth curve. Total DMI was calculated by obtaining daily feed intake from the GrowSafe feeding system and multiplying by dry matter content of the diet and then by the total days on test (Table 2) for each animal. Total standardized feed intake was then calculated by multiplying each animal's total DMI by the metabolizable energy content of the diet, and then dividing the total metabolizable energy intake by 10 MJ ME/kg DM (Tables 3 and 4), and then by the total days on test to standardize intake to a uniform energy density (SDFI; kg DM/d).

Residual feed intake, as well as RFI adjusted for final backfat thickness (FBF) measured at end of test (equations 1 and 2, respectively) for each animal were calculated as follows, as described by Basarab et al. (2003):

$$(1)\ SDFI_i = \beta_O + \beta_1 ADG_i + \beta_2 MMW_i + +e_i$$

$$(2)\ SDFI_i = \beta_O + \beta_1 ADG_i + \beta_2 MMW_i + \beta_3 FBF_i + e_i$$

where i = SDFI for the i'th animal, β_O = regression intercept, β_1 = partial regression coefficient of SDFI on ADG, β_2 = partial regression coefficient of SDFI on MMW, β_3 = partial regression coefficient of SDFI on FBF in the case of RFI_{fat}, and e_i = the residual deviation (random error term) of SDFI for the i'th animal. Cattle were sorted into either a low (RFI < -0.5), medium (RFI ± 0.5) or high (RFI > 0.5) RFI or RFI_{fat} group (Basarab et al., 2003).Average RFI and RFI_{fat} values are displayed in Table 6 for the five cattle classes.

4.3.6.2 Mixed models

Each class of cattle was analyzed separately in a randomized complete block design. Contemporary group was considered a block for the replacement heifers, mature cows, feeder heifers and feeder steers (two CG per cattle class), while year was considered a block (two CG per year with two diet treatments per year and two pens nested within diet by trial year) for the yearling bulls. Differences in DMI and FB traits among classes of RFI and RFI_{fat} were analyzed using a mixed model procedure (SAS Institute Inc., Cary, NC). Fixed effects in all models included CG (1, 2; all classes except for bulls), trial year (1, 2; bulls only), RFI and RFI_{fat} group (low, medium, high). Contemporary group was considered a fixed effect so we could evaluate interactions of CG or year with RFI and RFI_{fat}. Diet treatment (forage-based, grain-based) was included as an additional fixed effect in the bull model. Age on test was initially included in all models as a linear covariate to test for significance ($P < 0.05$), and was removed from the model if no significance was found. Individual cow effects were included in the mature cow model as random effects to account for eleven cows that were repeated in both CGs. In this case, there was also a within-cow error term included in the model. The FB traits (FED, FEF, FEHD, FEL, ER) and DMI were the dependent variables. The following models were run separately for each of the six dependent variables, and run twice for each variable: once with RFI (1), and again with $\mathrm{RFI}_{\mathrm{fat}}$ (2):

Replacement heifer, mature cow and feeder models

$$(1)\ y_{ijk} = \mu + \mathrm{RFIgroup}_{i} + \mathrm{CG}_{j} + b{*}\mathrm{age}^{1} + \mathrm{RFID}^{2} + \mathrm{RFIgroup}{*}\mathrm{CG}_{ij} + e_{ijk}$$

$$(2)\ y_{ijk} = \mu + \mathrm{RFI}_{\mathrm{fat}}\mathrm{group}_{i} + \mathrm{CG}_{j} + b{*}\mathrm{age}^{1} + \mathrm{RFID}^{2} + \mathrm{RFI}_{\mathrm{fat}}\mathrm{group}{*}\mathrm{CG}_{ij} + e_{ijk}$$

[1] Age was significant ($P < 0.05$) and therefore included in the mature cow model for FED ($P = 0.04$), FEF ($P = 0.004$), FEL ($P=0.004$), DMI ($P = 0.02$); and included in the replacement heifer model for FEF ($P = 0.05$) and FEHD ($P = 0.04$).

[2] RFID was only included in the mature cow model to account for eleven cows that were included in both CGs (random effect).

where y_{ijk} is the dependent variable (FED, FEF, FEHD, FEL, ER, DMI) on the k'th animal (k = replacement heifer, mature cow, feeder heifer, feeder steer) with the i'th RFI or $\mathrm{RFI}_{\mathrm{fat}}$ classification located in the j'th CG (j = 1, 2); μ is the population mean; $\mathrm{RFIgroup}_{i}$ is the effect of the i'th RFI or $\mathrm{RFI}_{\mathrm{fat}}$ group (i = -1, 0, 1, representing low, medium and high RFI classes, respectively; fixed effect); CG_{j} is the effect of the j'th CG (j = 1, 2; fixed effect); $\mathrm{RFIgroup}{*}\mathrm{CG}_{ij}$ is the interaction of RFI or $\mathrm{RFI}_{\mathrm{fat}}$ group (low, medium, high; fixed effect) and CG (1, 2; fixed effect); b*age is the linear covariate of age on y_{ijk}, and e_{ijk} is the error (residual deviation) of the k'th animal.

Yearling bull models

(1) $y_{ijklm} = \mu + \text{RFIgroup}_i + \text{year}_j + \text{diet}_k + \text{pen(year*diet)}_{jkl} + \text{RFIgroup*diet}_{ik} + \text{year*diet}_{jk}{}^1 + e_{ijklm}$

(2) $y_{ijklm} = \mu + \text{RFI}_{fat}\text{group}_i + \text{year}_j + \text{diet}_k + \text{pen(year*diet)}_{jkl} + \text{RFI}_{fat}\text{group*diet}_{ik} + \text{year*diet}_{jk}{}^1 + e_{ijklm}$

[1] Year*diet$_{jk}$ is considered a CG.

where y_{ijkl} is the dependent variable (FED, FEF, FEHD, FEL, ER, DMI) on the m'th bull with the i'th RFI and RFI$_{fat}$ classification located in the j'th year (j = 1,2) on the k'th diet (k = forage-based, grain-based) in the l'th pen (l = 1, 2, 3, 4) nested within the k'th diet treatment (k = forage-based, grain-based) and j'th year (j = 1, 2); μ is the population mean; RFIgroup$_i$ is the effect of the i'th RFI or RFI$_{fat}$ group (i = -1, 0, 1, representing low, medium and high RFI values, respectively; fixed effect); year$_j$ is the effect of the j'th year (j = 1, 2; fixed effect); diet$_k$ is the effect of the k'th diet treatment (k = forage-based, grain-based; fixed effect); pen(year*diet)$_{jkl}$ is the effect of the l'th pen (l = 1, 2, 3, 4; random effect) nested within the k'th diet (k = forage-based, grain-based; fixed effect) in the j'th year (j = 1, 2; fixed effect); RFIgroup*diet$_{jk}$ is the interaction of RFI or RFI$_{fat}$ group (low, medium, high; fixed effect) and diet (forage-based, grain-based; fixed effect); and e_{ijklm} is the error (residual deviation) of the m'th bull. Pen is considered a random effect. Bull age was initially tested in the model as a covariate, but was found to be non-significant ($P > 0.05$), so it was excluded from the represented model.

For all classes of cattle, mean separation among CG, year, diet, RFI and RFI$_{fat}$ groups was analyzed by least squares (LSM) using SAS. Significance of the fixed effects was determined by F-values (Tables 7, 10, 13, 16, 19) using Type 3 tests of fixed effects (CG, year, diet, RFI and RFI$_{fat}$ group). Tukey's range test (*t*-tests) was performed to compare LSMs between CG, year, diet, RFI and RFI_{fat} groups for the dependent variables FED, FEF, FEHD, FEL, ER, DMI (Tables 8, 11, 14, 17, 20).

4.3.6.3 Pearson partial phenotypic correlations

The models as described above were used to generate residuals. The PROC CORR procedure of SAS was then used to determine partial pearson correlation coefficients for RFI, RFI_{fat}, DMI and FB variables (FED, FEF, FEHD, FEL, ER) for the replacement heifers, mature cows, yearling bulls, feeder heifers and feeder steers. Statistical significance was reported when $P < 0.05$. Trends were reported when $P < 0.1$.

4.4 RESULTS AND DISCUSSION

4.4.1 Performance and feeding behaviour data

Descriptive statistics for performance and FB traits for the ten trial groups (five classes of cattle; two trial groups per class) are presented in Table 6.

Table 6. Descriptive statistics (± SD) for performance and feeding behaviour traits in replacement heifers, mature cows, yearling bulls, and feeder heifers and steers.

	Replacement Heifers		Mature Cows		Yearling Bulls		Feeder Heifers		Feeder Steers	
	CG1	CG2	CG1	CG2	Year 1	Year 2	CG1	CG2	CG1	CG2
Performance										
ADG, kg/d	0.90 (0.20)	0.96 (0.17)	0.71 (0.28)	0.63 (0.29)	1.63 (0.31)	1.83 (0.32)	1.24 (0.20)	1.08 (0.29)	1.28 (0.23)	1.96 (0.31)
Metabolic mid-weight, kg	80.13 (7.08)	83.78 (5.23)	137.59 (10.40)	135.70 (8.02)	103.24 (9.11)	113.24 (7.34)	85.91 (7.72)	107.28 (8.66)	90.96 (7.98)	102.56 (7.04)
RFI, kg DMI/d	0.00 (0.38)	0.00 (0.36)	0.00 (1.13)	0.00 (1.48)	0.00 (0.61)	0.00 (0.90)	0.00 (0.40)	0.00 (0.43)	0.00 (0.48)	0.00 (0.48)
RFI_{fat}, kg DMI/d	0.00 (0.38)	0.00 (0.36)	0.00 (1.07)	0.00 (1.32)	0.00 (0.58)	0.00 (0.86)	0.00 (0.40)	0.00 (0.43)	0.00 (0.47)	0.00 (0.46)
Intake (DMI), kg DMI/d	6.59 (0.84)	8.16 (0.70)	12.62 (1.84)	11.97 (2.33)	10.23 (1.59)	12.96 (1.45)	6.88 (0.78)	9.43 (1.05)	7.24 (0.77)	10.25 (0.96)
Feeding Behaviour *Feeding Events*										
Feeding event duration (FED), min/d	157.90 (21.24)	151.84 (20.35)	146.67 (48.48)	80.16 (36.39)	172.81 (28.82)	152.49 (25.40)	69.56 (15.01)	66.44 (12.61)	71.05 (13.92)	77.28 (12.94)
Feeding event frequency (FEF), events/d	115.58 (22.98)	106.77 (20.84)	96.87 (22.19)	84.26 (26.60)	80.85 (17.64)	46.26 (12.50)	47.74 (11.91)	38.07 (9.10)	46.85 (11.56)	37.68 (9.58)
Feeding event head-down time (FEHD), min/d	85.42 (20.80)	87.14 (21.39)	86.86 (36.33)	48.92 (23.88)	84.36 (24.10)	82.26 (28.19)	50.16 (13.54)	46.01 (12.30)	53.89 (12.59)	49.33 (14.06)
Feeding event length (FEL), min/event	1.43 (0.39)	1.49 (0.40)	1.59 (0.68)	1.03 (0.58)	2.23 (0.62)	3.44 (0.75)	1.51 (0.38)	1.81 (0.38)	1.57 (0.34)	2.14 (0.48)
Eating rate (ER), kg DMI/min	0.04 (0.01)	0.05 (0.01)	0.09 (0.02)	0.17 (0.05)	0.06 (0.01)	0.07 (0.01)	0.10 (0.02)	0.15 (0.03)	0.10 (0.02)	0.14 (0.02)

4.4.2 Intake and feeding behaviour of replacement heifers

Contemporary group was significant ($P < 0.0001$) for DMI and ER, but did not differ ($P > 0.1$) for the other measured feeding event traits (Table 7). Eating rate was faster by an average of 0.01 kg DMI/min in CG2 compared to CG1. Dry matter intake was greater for CG2 (8.21 kg DMI/d) compared to CG1 (6.63 kg DMI/d) as indicated in Table 8. This 21.3% increase in DMI in CG2 compared to CG1 cannot be attributed to wind-chill corrected ambient temperature that fell below -20°C (49% and 46% of trail days in CG1 and CG2, respectively), diet, DMI as a percent of body weight (1.9% and 2% for CG1 and CG2, respectively), difference in body weight at start of test (314.10 kg and 325 kg in CG1 and CG2, respectively), number of head per feed bunk, group size and breed comprising both CGs, as all were comparable between groups. However, while no data were collected to support this theory, a possible explanation for difference may be that a greater proportion of heifers in CG2 attained puberty during the course of the feeding trail. Replacement heifers must reach sexual maturity within twelve to fourteen months of age so that they conceive by fifteen months of age and calve by two years old. This often results in feed efficiency trials being conducted on growing animals during the time period when they may be entering puberty (Bellows and Short, 1994). While moderately heritable and influenced to an extent by both environment and genetics (Snelling et al., 2012; Patterson et al., 2002), puberty cannot be fully controlled for, as it is unique to each animal and poses difficult to measure (Brinks, 1995); therefore, heifers will reach puberty at various times during feed test periods. Due to the associated increase in energy demands resulting from sexual development and activity, sexually mature cattle will often consume more feed compared to the pre-pubescent cattle who do not yet have the increased energy demands associated with reproduction (Basarab et al., 2011; Richardson et al., 1999). It is speculated that the 21.3% increase in DMI in CG2 compared to CG1 suggests that a greater proportion of heifers in CG2 may have attained puberty during the course of the feeding trial. Basarab et al. (2011) evaluated effect of puberty on feed efficiency and FB (n = 109) on mixed-breed beef heifers, and found that post-pubertal heifers consumed 4.7% more feed compared to pre-pubertal heifers (7.50 vs. 7.85 kg DMI/d), respectively.

Dry matter intake was 5.1% less in low RFI heifers compared to high RFI heifers ($P <$ 0.05; Table 8). Basarab et al. (2011) reported a 7.1% decrease in DMI in the low RFI heifers compared with the high RFI group. The significant difference seen in DMI between RFI groups is expected, given that RFI is determined as a deviation about the mean of zero, where the adjusted mean represents predicted consumption and any animals that are below the mean consume less than expected, whereas animals that are above the mean consume more than expected. There were no differences between RFI groups of any of the FB traits. Similarly, Kelly et al. (2010) found no significant differences in daily FED (P = 0.84) between growing beef heifers categorized into low (116.9 ± 4.52 min/d), medium (114.2 ± 4.74 min/d) and high (116.2 ± 4.94 min/d) RFI classes. Basarab et al. (2003) reported no significant differences for FED or FEF between RFI group (P > 0.1) in growing cattle on a backgrounding diet.

When RFI was adjusted for final backfat, low RFI heifers consumed 8.1% less DM compared to the high RFI heifers. Similarly, Basarab et al. (2011) saw a 6.1% decrease in DMI between low and high RFI_{fat} groups.

As depicted in Table 7, there were no significant two-way interactions observed for CG x RFI or CG x RFI_{fat} with DMI or any of the FB variables (P > 0.1).

Table 7. Significance of contemporary, RFI and RFI_{fat} groups and their interactions on DMI and feeding behaviour in replacement heifers.

Cattle Class	Parameter	Contemporary Group (CG)	RFI Group (G)	RFI_{fat} Group (FG)	CG*G	CG*FG
Replacement Heifers						
	Intake (DMI), kg DMI/d	<0.0001	0.0019	<0.0001	0.7882	0.0904
	Duration (FED), min/d	0.7307	0.7287	0.0634	0.1493	0.3905
	Frequency (FEF), events/d	0.1115	0.9148	0.6072	0.9963	0.9757
	Head-down (FEHD), min/d	0.6291	0.5473	0.3403	0.6363	0.4427
	Length (FEL), min/event	0.1912	0.9549	0.1385	0.3824	0.6822
	Eating rate (ER), kg DMI/min	<0.0001	0.2239	0.2128	0.2626	0.8004

Table 8. Dry matter intake and feeding behaviour traits in replacement heifers categorized by contemporary, RFI and RFI_{fat} groups.

		Contemporary Group			RFI Group				RFI_{fat} Group			
Cattle Class	Parameter	1	2	SE	Low	Medium	High	SE	Low	Medium	High	SE
Replacement Heifers												
	Intake (DMI), kg DMI/d	6.63^b	8.21^a	0.11	7.06^b	7.38^a	7.82^a	0.13	7.07^b	7.37^a	7.67^a	0.09
	Duration (FED), min/d	154.13	152.42	3.32	151.27	154.15	154.40	3.83	152.20	151.60	160.58	2.78
	Frequency (FEF), events/d	114.89	106.45	3.53	110.60	111.87	109.55	4.07	109.58	113.44	110.33	2.93
	Head-down (FEHD), min/d	86.11	88.50	3.31	84.10	86.03	91.77	3.81	84.57	84.75	89.68	2.74
	Length (FEL), min/event	1.38	1.50	0.06	1.42	1.44	1.46	0.07	1.44	1.39	1.54	0.05
	Eating rate (ER), kg DMI/min	0.04^b	0.05^a	0.0009	0.05	0.05	0.05	0.001	0.05	0.05	0.05	0.0008

Least squares means with different superscripts within rows differ significantly ($P < 0.05$).
SEM varied very slightly from mean to mean, so simple averages are presented in this table.

Pearson partial phenotypic correlation coefficients between RFI, RFI_{fat}, DMI and FB traits are displayed in Table 9. Residual feed intake and RFI_{fat} were positively correlated with DMI ($r_p = 0.36$, $P < 0.0001$; $r_p = 0.34$, $P < 0.0001$), FED ($r_p = 0.26$, $P < 0.01$; $r_p = 0.23$, $P < 0.01$) and FEHD ($r_p = 0.24$, $P < 0.01$; $r_p = 0.25$, $P < 0.01$), respectively. These results are similar to those reported by Kelly et al. (2010), Nkrumah et al. (2007), Basarab et al. (2003) and Richardson et al. (2001), who found moderate to high positive correlations ($r_p = 0.60 – 0.72$) between RFI and DMI in growing beef heifers. Residual feed intake was positively correlated ($r_p = 0.18$, $P < 0.05$) with FEL, and RFI_{fat} tended to be correlated with FEL ($r_p = 0.13$, $P = 0.09$). Residual feed intake and RFI_{fat} were not correlated with FEF or ER ($P > 0.1$). In contrast, weak positive phenotypic correlations of FEF with RFI ($r_p = 0.15 – 0.18$) have been reported in composite cattle in other literature (Nkrumah et al. 2007; Robinson and Oddy, 2004); given these discrepancies, further research should be done to determine the extent to which breed and gender influence the relationship of FB with RFI and RFI_{fat}.

Dry matter intake in our study was positively correlated ($P < 0.0001$) with ER ($r_p = 0.64$), FEHD (rp = 0.36) and FED ($r_p = 0.29$, $P < 0.01$), and negatively correlated with FEF ($r_p = -0.20$, $P < 0.05$). Feeding event duration was positively correlated ($P < 0.0001$) with FEHD ($r_p = 0.64$) and FEL ($r_p = 0.62$), and negatively correlated with ER ($r_p = -0.54$). Feeding event frequency was positively correlated with FEHD ($r_p = 0.19$, $P < 0.05$), and was negatively correlated with FEL ($r_p = -0.81$, $P < 0.0001$). Feeding event head-down time was positively correlated with FEL ($r_p = 0.17$, $P < 0.05$) and negatively correlated with ER ($r_p = -0.19$, $P < 0.05$).

Table 9. Pearson partial phenotypic correlations between RFI, RFI_{fat}, DMI and feeding behaviour traits for replacement heifers.

Traits	RFI, kg DMI/d	RFI_{fat}, kg DMI/d	Intake (DMI), kg DMI/d	FE duration, min/d	FE frequency, events/d	FE head-down, min/d	FE length, min/event	Eating rate, kg DMI/min
RFI, kg DMI/d	1.00	0.98 ***	0.36 ***	0.26 **	-0.02	0.24 **	0.18 *	0.09
RFI_{fat}, kg DMI/d		1.00	0.34 ***	0.23 **	0.03	0.25 **	0.13	0.11
Intake (DMI), kg DMI/d			1.00	0.29 **	-0.20 *	0.36 ***	0.32 ***	0.64 ***
FE duration, min/d				1.00	-0.13	0.64 ***	0.62 ***	-0.54 ***
FE frequency, events/d					1.00	0.19 *	-0.81 ***	-0.07
FE head-down, min/d						1.00	0.17 *	-0.19 *
FE length, min/event							1.00	-0.21 *
Eating rate, kg DMI/min								1.00

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.0001$.

4.4.3 Intake and feeding behaviour of mature cows

The significance of CG, RFI and RFI_{fat} group, as well as their interactions on DMI, FED, FEF, FEHD, FEL and ER for mature beef cows is presented in Table 10. Least squares means for RFI and RFI_{fat} group (low, medium, high) are portrayed in Table 11. Dry matter intake did not differ between CGs. However, CG was significant for ER and FED ($P < 0.0001$), FEHD and FEL ($P < 0.01$), and tended to be significant for FEF ($P = 0.07$). Feeding event duration, FEL and FEHD were longer in CG1 compared to CG2; however, ER was greater in CG2 compared to

CG1. The difference in ER could strongly impact the relationship between DMI and FB variables (Schwartzkopf-Genswein et al., 2002), where those animals who spent shorter periods of time at the bunk are not necessarily ingesting less feed, if they are eating quickly. Indeed, their DMI may be comparable to those animals that spend longer durations at the feed bunks.

Feeding event frequency tended to be greater for CG1 compared to CG2 ($P = 0.07$). Therefore, on average, the cows comprising CG1 visited the bunks 9.9% more frequently each day and spent 53.6% longer at the bunks per day, resulting in a 42.2% increase in FEL.

The increased ER observed in CG2 compared to CG1 is not surprising, given that feed was restricted throughout the feeding period to maintain an ideal BCS of 2.5-3.0, whereas in CG1, cows were fed *ad libitum* for the first 30 d of the feed trial (40% of the trial duration), before they were restricted to prevent over-conditioned (high BCS) cows at time of calving. According to Schwartzkopf-Genswein et al. (2002), animals fed *ad libitum* spend a longer time per day at the feed bunks, visit the feed bunks more frequently, and consume more DMI per day ($P < 0.0001$) than the restricted-fed animals. These authors also found that ER was faster in restricted cattle compared to those fed *ad libitum*. Cattle fed on restricted basis are likely to express more eagerness at feed delivery times, thereby increasing the rate with which they consume the feed, compared to cattle who have feed in front of them at all times (Schwartzkopf-Genswein et al., 2002). In addition, animals that are restricted-fed may experience greater competition at the feed bunks around feed delivery times, compared to those with unrestricted access to feed. Bunk competition may alter FB as animals compete for bunk access; the more subordinate animals will be displaced at the feed bunks and therefore may not be able to fully express their natural FB and this may impact DMI. Conversely, the more dominant cattle may adjust their FB to correspond with feed delivery times to access the feed first, thereby altering FED, FEF, FEL and ER.

Residual feed intake impacted DMI, as low RFI cows consumed an average of 2.83 kg less feed per day than the high RFI cows ($P < 0.01$). Further, the effect of RFI ranking was significant for FED ($P < 0.05$), FEF ($P < 0.01$), FEHD ($P < 0.05$) and ER ($P < 0.05$) in that low RFI cows had significantly shorter FED, fewer FEF, decreased FEHD and faster ER compared to the high RFI cows. However, FEL was non-significantly ($P > 0.1$) different between RFI groups. Therefore, on average, low RFI cows had 37.7% shorter FED, 34.6% fewer FEF, 49.9% shorter FEHD, 30.8% slower ER and consumed 22.9% less DMI per day compared to the high RFI cows. The effect of RFI_{fat} ranking was significant for DMI ($P < 0.05$) and FEF ($P < 0.01$), as low RFI_{fat} cows consumed 13.8% less DMI and had 29.9% fewer FEF per day than high RFI_{fat} cows. There were no observed significant two-way interactions of CG and RFI or RFI_{fat} group on DMI or any of the assessed FB traits ($P < 0.1$).

Most published literature on FB includes feedlot cattle fed concentrate-based diets, not mature cows that are five years of age and older and fed low-quality forage diets (Fitzsimons et al., 2014). These authors examined pregnant beef cows on a grass silage diet and results agreed with this study: low RFI cows had 25% lower DMI and shorter daily FED ($P < 0.001$) compared to high RFI cows.

Table 10. Significance of contemporary, RFI and RFI_{fat} groups and their interactions on DMI and feeding behaviour in mature cows.

Cattle Class	Parameter	Contemporary Group (CG)	RFI Group (G)	RFI_{fat} Group (FG)	CG*G	CG*FG
Mature Cows						
	Intake (DMI), kg DMI/d	0.2681	0.0045	0.0298	0.6012	0.5238
	Duration (FED), min/d	<0.0001	0.0140	0.1579	0.7949	0.2428
	Frequency (FEF), events/d	0.0709	0.0060	0.0074	0.7875	0.4824
	Head-down (FEHD), min/d	0.0006	0.0102	0.1200	0.6142	0.1018
	Length (FEL), min/event	0.0033	0.6271	0.8526	0.4506	0.7393
	Eating rate (ER), kg DMI/min	<0.0001	0.0328	0.1453	0.2103	0.4033

Table 11. Dry matter intake and feeding behaviour traits in mature cows categorized by contemporary, RFI and RFI$_{fat}$ groups.

		Contemporary Group			RFI Group				RFI$_{fat}$ Group			
Cattle Class	Parameter	1	2	SE	Low	Medium	High	SE	Low	Medium	High	SE
Mature Cows												
	Intake (DMI), kg DMI/d	12.46	12.07	0.27	10.95^{b}	12.08^{b}	13.78^{a}	0.34	11.72^{b}	11.80^{b}	13.46^{a}	0.35
	Duration (FED), min/d	144.43^{a}	83.39^{b}	5.60	94.56^{c}	108.62^{b}	138.54^{a}	7.00	106.17	107.62	127.97	7.08
	Frequency (FEF), events/d	95.36	86.34	3.20	76.00^{b}	88.73^{b}	107.81^{a}	4.04	80.16^{b}	87.07^{b}	108.31^{a}	3.91
	Head-down (FEHD), min/d	83.91^{a}	52.70^{b}	4.09	52.82^{b}	64.13^{b}	87.96^{a}	5.17	63.29	62.44	79.16	5.08
	Length (FEL), min/event	1.58^{a}	1.03^{b}	0.09	1.21	1.31	1.39	0.11	1.31	1.33	1.25	0.11
	Eating rate (ER), kg DMI/min	0.09^{b}	0.17^{a}	0.01	0.15^{a}	0.13^{ab}	0.11^{b}	0.01	0.14	0.13	0.12	0.01

Least squares means with different superscripts within rows differ significantly ($P < 0.05$).
SEM varied very slightly from mean to mean, so simple averages are presented in this table.

Pearson partial phenotypic correlation coefficients between RFI, RFI_{fat}, DMI and FB traits are displayed in Table 12. Residual feed intake and RFI_{fat} were positively correlated ($P < 0.0001$) with DMI ($r_p = 0.62$; $r_p = 0.57$) and FEF ($r_p = 0.56$; $r_p = 0.47$), FED ($r_p = 0.41$, $P < 0.0001$; $r_p = 0.38$, $P < 0.01$) and FEHD ($r_p = 0.45$, $P < 0.0001$; $r_p = 0.40$, $P < 0.01$), respectively. Eating rate was negatively correlated with RFI and RFI_{fat} ($r_p = -0.25$, $P < 0.05$). Neither RFI nor RFI_{fat} were correlated with FEL ($P > 0.1$).

Dry matter intake was positively correlated ($P < 0.0001$) with FED ($r_p = 0.70$), FEHD ($r_p = 0.69$), FEL ($r_p = 0.49$) and FEF (0.40, $P < 0.01$), and negatively correlated with ER ($r_p = -0.50$, $P < 0.0001$). Feeding event duration was positively correlated ($P < 0.0001$) with FEHD ($r_p = 0.93$), FEL ($r_p = 0.79$) and FEF ($r_p = 0.32$, $P < 0.01$), and negatively correlated with ER ($r_p = -0.86$, $P < 0.0001$). Feeding event frequency was positively correlated with FEHD ($r_p = 0.36$, $P < 0.01$), and negatively correlated with FEL ($r_p = -0.28$, $P < 0.05$) and ER ($r_p = -0.29$, $P < 0.01$). Feeding event head-down time was strongly and positively correlated with FEL ($r_p = 0.69$, $P < 0.0001$), and negatively correlated with ER ($r_p = -0.79$, $P < 0.0001$).

Table 12. Pearson partial phenotypic correlations between RFI, RFI_{fat}, DMI and feeding behaviour traits for mature cows.

Traits	RFI, kg DMI/d	RFI_{fat}, kg DMI/d	Intake (DMI), kg DMI/d	FE duration, min/d	FE frequency, events/d	FE head-down, min/d	FE length, min/event	Eating rate, kg DMI/min
RFI, kg DMI/d	1.00	0.92 ***	0.62 ***	0.41 **	0.56 ***	0.45 ***	0.07	-0.25 *
RFI_{fat}, kg DMI/d		1.00	0.57 ***	0.38 **	0.47 ***	0.40 **	0.10	-0.25 *
Intake (DMI), kg DMI/d			1.00	0.70 ***	0.40 **	0.69 ***	0.49 ***	-0.50 ***
FE duration, min/d				1.00	0.32 **	0.93 ***	0.79 ***	-0.86 ***
FE frequency, events/d					1.00	0.36 **	-0.28 *	-0.29 **
FE head-down, min/d						1.00	0.69 ***	-0.79 ***
FE length, min/event							1.00	-0.69 ***
Eating rate, kg DMI/min								1.00

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.0001$.

Dry matter intake and all FB traits in this study were correlated with RFI and RFI_{fat}. As RFI or RFI_{fat} value increased, so did daily DMI, FED, FEF, FEHD. However, ER decreased as RFI increased. Basarab et al. (2007) evaluated the phenotypic relationship between cow RFI and FB, and concluded similar findings; RFI had a strong positive correlation to DMI ($r_p = 0.83$, $P < 0.001$), as well as to FED and FEHD ($r_p = 0.36$ to 0.62, $P < 0.001$).

Increased DMI resulted from greater FED. Similarly, Schwartzkopf-Genswein et al. (2002) found a significant phenotypic correlation between DMI and FED ($r_p = 0.38$, $P < 0.0001$) in cross-bred heifers and steers, affirming that longer FED results in increased DMI. However, these same authors found no phenotypic correlation between DMI and FEF ($r_p = 0.09$, $P > 0.1$), suggesting that FED may be the better indicator of DMI compared to FEF. However, their trial had a substantially smaller number of animals ($n = 12$), penned individually which removes bunk competition and may also reduce FEF as cattle are not displaced at the feeder by herd mates and subsequently returning.

Dry matter intake and ER were significantly and negatively correlated. This was not observed for any of the other cattle classes in our study that had *ad libitum* access to feed. Therefore, it can be speculated that, under restricted feed conditions, the dominant cattle who gain first access to the feed bunks may ingest more DMI and are not driven to consume the feed rapidly; however, the lesser dominant cows who later gain access to the feed bunks may adjust their ER to consume the limited feed quickly, but have lower DMI as they are last to eat and feed access is restricted. Thus, while their ER increases due to competition at the bunks for limited access to feed, their DMI may be hindered given the restricted access to feed. Similarly, group penned pigs ingested feed more quickly compared to pigs penned individually, supporting the argument that feed competition present in group pens influences ER (de Haer and Merks, 1992).

Eating rate decreased as FEHD, FED and FEF increased. It can be speculated that, given the negative correlation between FEHD (RFID within 50 cm scanning range of the bunk) and ER, slower ER may have resulted from slower ingestion and mastication of feed as opposed to engagement in non-feed related activities such as rubbing or licking feed bunks when the RFID may momentarily exceed the 50 cm scanning range.

4.4.4 Intake and feeding behaviour of feeder heifers and steers

4.4.4.1 Feeder heifers

The significance of CG, RFI and RFI_{fat} group, as well as their interactions for DMI, FED, FEF, FEHD, FEL and ER for feeder heifers are presented in Table 13. Least squares means values for RFI and RFI_{fat} group are summarized in Table 14. The effect of CG was significant for DMI ($P < 0.0001$) and for ER ($P < 0.05$). There were no other significant differences observed between CG and FB traits ($P > 0.1$). Dry matter intake and ER were 25% less in CG1 compared to CG2. Intake may have been depressed as a consequence of the following: 1) the CG2 heifers were on average 160 d older than those in CG1 at the start of the feeding period, increasing the likelihood that the majority of heifers in CG2 were post-pubertal. As previously discussed, research by Basarab et al. (2011), Donoghue et al. (2011) and Shaffer et al. (2011) concur that DMI increases in sexually mature cattle compared to pre-pubescent cattle given the greater energy demands associated with fully developmental reproductive organs and expression of sexual behaviour; 2) the heifers in CG2 were 137 kg heavier than those in CG1 and therefore had increased DMI as a consequence of the greater energy demands that increase proportionally with body weight and frame size; and 3) CG2 had a ratio of 6.5 head to every one feed bunk, whereas CG1 had a ratio of 10.07 head per feed bunk (Table 2). To the author's knowledge, there is no GrowSafe literature that reports a maximum head to feed bunk ratio, so it is only speculated that the feeder heifers in CG1 may have experienced competition at the bunk, potentially altering DMI and FB. As previously stated, DMI is likely to be suppressed if any degree of bunk competition is present, even if *ad libitum* access to feed is provided (Schwartzkopf-Genswein et al., 2002; de Haer and Merks, 1992).

Interestingly, although CG1 had a greater stocking density at the feed bunks, ERs were slower by 25% compared with CG2. This is contrary to FB observed in individual versus group penned pigs where group-housed pigs ate faster (de Haer and Mercks, 1992), and in transitioning dairy cows fed a lactation ration where bunk competition increased ER especially in the lesser dominant cows (Proudfoot et al., 2009). Slower ER seen in CG2 may be attributed to summer heat; given the differing seasons (Table 1), FB may have been impacted by increased ambient temperatures. In hot ambient temperatures that exceed an animal's upper critical temperature (UCT), the heat stressed animal will begin to display behavioural coping mechanisms such as modifying feed intake patterns toward cooler times of the day or night, and even decreasing DMI by 10-12 % and, in turn, potentially compromising rumen functionality (West, 2003; Young, 1981). Ambient temperatures exceeding 25°C, combined with humid conditions, reduce the bovine's ability to dissipate heat (McKinnon, 2015). When experiencing ambient temperatures that exceed their thermo-neutral zone, cattle will adjust their physiological and behavioural responses to cope with the stressors (Young, 1981) by seeking shade, increasing water intake and decreasing feed intake (McKinnon, 2015). In CG2, ambient temperatures that exceeded 25°C occurred in 29.9% of the days in the feeding period. Given that DMI did not decrease in CG2, presumably the heifers may have temporarily adjusted their FB patterns to feed during the cooler periods of the day (West, 2003), thereby increasing their ER when they had opportunity to feed during more optimal ambient temperatures.

Effects of RFI group were significant for DMI, FED, FEHD ($P < 0.0001$), FEF and ER ($P < 0.01$), but not FEL ($P > 0.1$). Least squares means values for each RFI class are displayed in Table 14. Low RFI feeder heifers had 30% shorter daily FED, 17.7% fewer FEF, 34.9% shorter FEHD, 17% faster ER and consumed 13.6% less DMI compared to high RFI group heifers, respectively.

Effects of $\mathrm{RFI}_{\mathrm{fat}}$ group were similar for FB traits, although the difference observed between low and high $\mathrm{RFI}_{\mathrm{fat}}$ groups was less pronounced than it was for low and high RFI groups. The effect of $\mathrm{RFI}_{\mathrm{fat}}$ group was significant for FED, FEF, FEHD and DMI ($P < 0.0001$) and ER ($P < 0.01$). Low $\mathrm{RFI}_{\mathrm{fat}}$ heifers had 20% shorter daily FED, 17.2% fewer FEF, 26.2% shorter FEHD, 8% faster ER and consumed 11.4% less DMI compared with high $\mathrm{RFI}_{\mathrm{fat}}$ heifers, respectively. Therefore, results suggest that the low RFI and $\mathrm{RFI}_{\mathrm{fat}}$ feeder heifers ate less, ate faster, and invested less time at the feed bunks, as reflected by lower DMI, faster ER, and decreased feeding durations, head-down times and frequencies, compared to the lesser efficient, high RFI and $\mathrm{RFI}_{\mathrm{fat}}$ heifers.

Table 13. Significance of contemporary, RFI and RFI_{fat} groups and their interactions on DMI and feeding behaviour in feeder heifers.

Cattle Class	Parameter	Contemporary Group (CG)	RFI Group (G)	RFI_{fat} Group (FG)	CG*G	CG*FG
Feeder Heifers						
	Intake (DMI), kg DMI/event	0.0001	<0.0001	<0.0001	0.5713	0.2589
	Duration (FED), min/d	0.6309	<0.0001	<0.0001	0.2719	0.0212
	Frequency (FEF), events/d	0.6054	0.0042	<0.0001	0.5363	0.9888
	Head-down (FEHD), min/d	0.6434	<0.0001	<0.0001	0.1262	0.0771
	Length, min/event	0.7240	0.1388	0.1148	0.1264	0.0202
	Eating rate (ER), kg DMI/min	0.0285	0.0014	0.0033	0.9604	0.1111

Table 14. Dry matter intake and feeding behaviour traits in feeder heifers categorized by contemporary, RFI and RFI_{fat} groups.

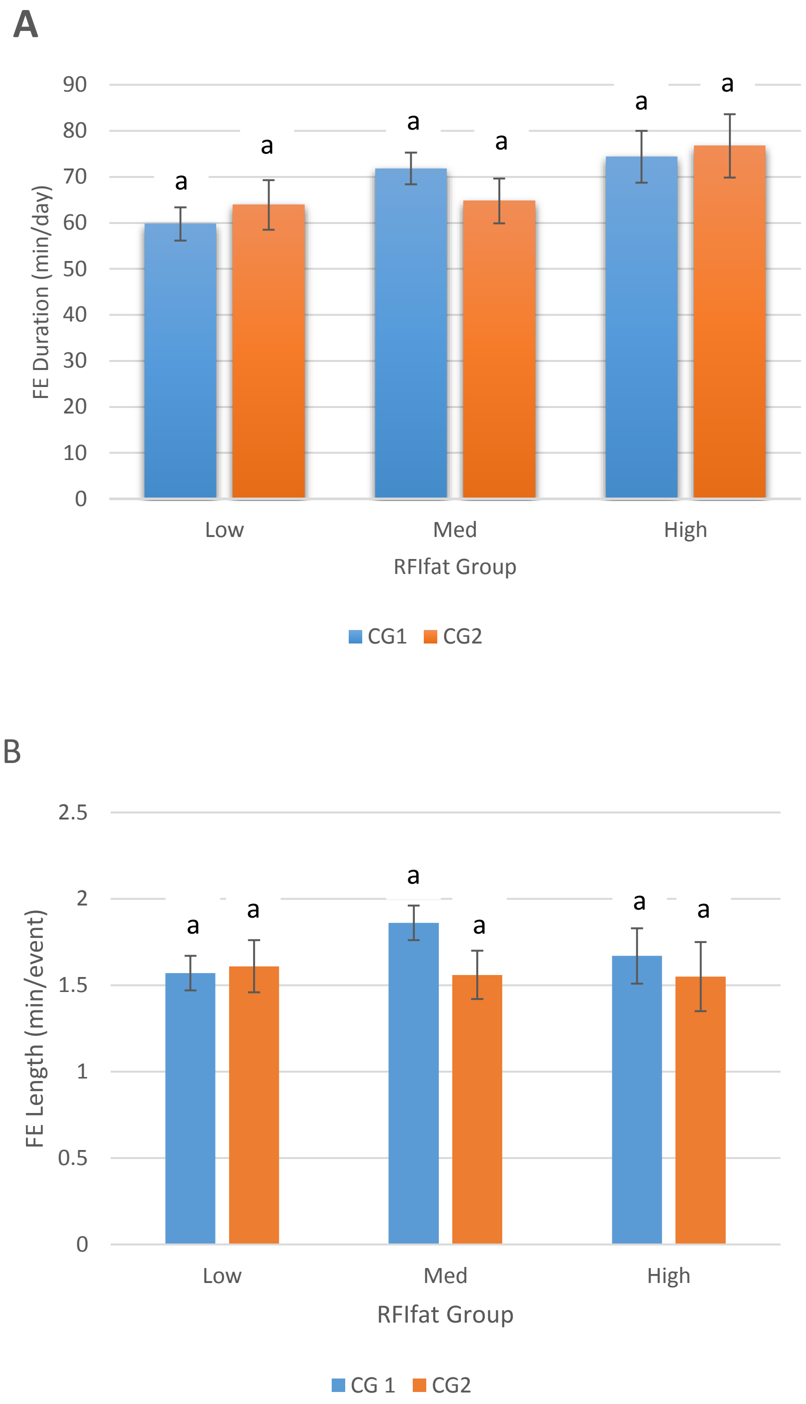
		Contemporary Group			RFI Group				RFI_{fat} Group			
Cattle Class	Parameter	1	2	SE	Low	Medium	High	SE	Low	Medium	High	SE
Feeder Heifers												
	Intake (DMI), kg DMI/d	7.23^{b}	9.32^{a}	0.28	7.70^{b}	8.31^{a}	8.82^{a}	0.14	7.70^{c}	8.11^{b}	8.63^{a}	0.11
	Duration (FED), min/d	73.78	69.85	4.30	61.26^{c}	70.67^{b}	83.53^{a}	2.22	61.83^{c}	68.30^{b}	75.56^{a}	1.71
	Frequency (FEF), events/d	43.35	46.64	3.35	40.99^{b}	45.06^{a}	48.93^{a}	1.73	41.14^{b}	42.07^{b}	48.86^{a}	1.28
	Head-down (FEHD), min/d	49.94	53.47	4.01	42.67^{c}	51.75^{b}	60.70^{a}	2.08	42.69^{c}	49.73^{b}	55.54^{a}	1.59
	Length (FEL), min/event	1.71	1.63	0.12	1.58	1.65	1.78	0.06	1.59	1.71	1.61	0.05
	Eating rate (ER), kg DMI/min	0.10^{b}	0.14^{a}	0.01	0.13^{a}	0.12^{b}	0.11^{b}	0.004	0.13^{a}	0.12^{ab}	0.12^{b}	0.003

Least squares means with different superscripts within rows differ significantly ($P < 0.05$).
SEM varied very slightly from mean to mean, so simple averages are presented in this table.

Significant two-way interactions for feeder heifers are illustrated in Figures 1A and 1B. Figure 1A demonstrates the interaction ($P < 0.05$) between CG and RFI_{fat} group for FED, where low RFI_{fat} heifers had shorter FED in both CG1 and CG2, compared to medium- and high RFI_{fat} heifers. The low RFI_{fat} heifers in CG1 spent 37.41 min/d feeding, which was 12.4% less than the low RFI_{fat} heifers in CG2. The high RFI_{fat} heifers in CG1 spent 52.08 min/d feeding, which was 12.5% less than the high RFI_{fat} heifers in CG2 by comparison. The opposite effect between CG was observed for the medium RFI_{fat} heifers, where CG1 spent 3% longer feeding compared to the medium RFI_{fat} heifers in CG2.

Figure 1B demonstrates the interaction ($P < 0.05$) between CG and RFI_{fat} group for FEL, with low RFI_{fat} heifers in CG1 and CG2 having comparable FEL means (1.57 min/event and 1.61 min/event), respectively. There was, however, a notable 17% increase in FEL seen in the medium RFI_{fat} group in CG1 compared to the low RFI_{fat} group in CG1. The medium RFI_{fat} group in CG1 also spent on average 10.8% longer at the bunk per feed event compared to the high RFI_{fat} group in CG1. Feed event length was not as variable across RFI_{fat} groups for CG2 as it was for CG1, where there was only a 0.06 min/event difference observed between the low RFI_{fat} and the high RFI_{fat} groups for CG2.

Figure 1. Effect of **(A)** CG x RFI_{fat} group interaction on FED; and **(B)** CG x RFI_{fat} group interaction on FEL for feeder heifers.



Pearson partial phenotypic correlation coefficients between RFI, RFI_{fat}, DMI and FB traits are presented in Table 15. Residual feed intake and RFI_{fat} were positively correlated ($P <$ 0.0001) with FED ($r_p = 0.48$; $r_p = 0.46$), FEF ($r_p = 0.31$ for both), FEHD ($r_p = 0.46$; $r_p = 0.45$) and DMI ($r_p = 0.27$ for both), respectively. A negative phenotypic correlation between RFI and RFI_{fat} was observed ($P < 0.01$) for ER ($r_p = -0.21$; $r_p = -0.19$), respectively. Residual feed intake nor RFI_{fat} were correlated with FEL ($P > 0.1$).

Dry matter intake was positively correlated ($P < 0.0001$) with FEL ($r_p = 0.38$), ER ($r_p =$ 0.56) and FED ($r_p = 0.16$, $P < 0.05$), and negatively correlated with FEF ($r_p = -0.24$, $P < 0.01$). Feeding event duration was positively correlated ($P < 0.0001$) with FEF ($r_p = 0.54$), FEHD ($r_p =$ 0.87) and FEL ($r_p = 0.20$, $P < 0.01$), and negatively correlated with ER ($r_p = -0.68$, $P < 0.0001$). Feeding event frequency was positively correlated ($P < 0.0001$) with FEHD ($r_p = 0.49$), and negatively correlated with FEL ($r_p = -0.65$) and ER ($r_p = -0.63$). Feeding event head-down time was positively correlated with FEL ($r_p = 0.18$, $P < 0.01$) and negatively correlated with ER ($r_p =$ -0.65, $P < 0.0001$). Feeding event length was positively correlated with ER ($r_p = 0.18$, $P < 0.01$). Therefore, the feeder heifers in this study demonstrated a moderate to high degree of phenotypic correlation among FB traits, and between DMI, RFI, RFI_{fat} and FB. Dry matter intake and all FB variables were correlated with one another, most with a significance of $P < 0.01$. As RFI or RFI_{fat} value increased, so did FED, FEF, FEHD and DMI. Further, ER decreased as RFI increased.

Table 15. Pearson partial phenotypic correlations between RFI, RFI_{fat}, DMI and feeding behaviour traits for feeder heifers.

Traits	RFI, kg DMI/d	RFI_{fat}, kg DMI/d	Intake (DMI), kg DMI/d	FE duration, min/d	FE frequency, events/d	FE head-down, min/d	FE length, min/event	Eating rate, kg DMI/min
RFI, kg DMI/d	1.00	0.99 ***	0.27 ***	0.48 ***	0.31 ***	0.46 ***	0.05	-0.21 **
RFI_{fat}, kg DMI/d		1.00	0.27 ***	0.46 ***	0.31 ***	0.45 ***	0.05	-0.19 **
Intake (DMI), kg DMI/d			1.00	0.16 *	-0.24 **	0.06	0.38 ***	0.56 ***
FE duration, min/d				1.00	0.54 ***	0.87 ***	0.20 **	-0.68 ***
FE frequency, events/d					1.00	0.49 ***	-0.65 ***	-0.63 ***
FE head-down, min/d						1.00	0.18 **	-0.65 ***
FE length, min/event							1.00	0.18 **
Eating rate, kg DMI/min								1.00

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.0001$.

Our results indicate that increased daily FEF resulted in longer overall daily FED, but decreased FEL. As FED and FEF increased, FEHD also increased. Longer FED and FEL resulted in increased DMI; however, DMI was negatively correlated with FEF, where heifers who visited the bunks more frequently consumed less DMI. There is no apparent reason why this happened, but it may be possible that those heifers who visited the bunks more frequently were pushed away from the bunk by other heifers trying to gain access. Bunk competition may have resulted in greater FEF in CG1 in particular (an additional 4.14 head/bunk compared to CG2; Table 2), displacing cattle at the feeders and thereby resulting in increased FEF relative to DMI.

As ER increased, DMI also increased, indicating that quicker ingestion of feed increases total daily intake.

4.4.4.2 Feeder Steers

The significance of CG, RFI and $\mathrm{RFI}_{\mathrm{fat}}$ group, as well as their interactions for DMI, FED, FEF, FEHD, FEL and ER for feeder steers are presented in Table 16. Least squares means values for RFI and $\mathrm{RFI}_{\mathrm{fat}}$ group are summarized in Table 17. The effect of CG was significant ($P < 0.0001$) for DMI and FED, as well as FEF and FEL ($P < 0.05$). Dry matter intake was 28.2% less in CG1. FED was 23.6% shorter, FEF was 15.5% lower and FEL was 15.8% shorter for CG1 compared to CG2.As discussed for the feeder heifers, these differences may be attributed to age as the feeder steers in CG2 were on average 99 d older and 79 kg heavier at start of test; and 2) competition at the bunk as there were 18 fewer steers in CG2 compared to CG1.

Effects of RFI group were significant for DMI and FED ($P < 0.0001$), FEF and FEHD ($P < 0.01$). Least squares means for each RFI class are displayed in Table 17. Low RFI steers consumed 16.2% less DMI, had 18.4% shorter daily FED, 18.1% fewer FEF and 20.7% shorter FEHD compared to high RFI steers, respectively. There was no observed significance between RFI group for FEL or ER ($P > 0.1$). Similarly, Nkrumah et al. (2007) found low RFI steers had 24% shorter FED, 14% fewer FEF and 29% shorter FEHD compared with high RFI grouped steers.

Effects of $\mathrm{RFI}_{\mathrm{fat}}$ group were similar for FB traits, although the difference between low and high $\mathrm{RFI}_{\mathrm{fat}}$ groups was less pronounced than it was for low and high RFI groups. The effect of $\mathrm{RFI}_{\mathrm{fat}}$ group was significant for DMI ($P < 0.0001$), FED, FEF ($P < 0.01$) and FEHD ($P < 0.05$). The low $\mathrm{RFI}_{\mathrm{fat}}$ steers consumed 11.8% less DMI, had 7.6% shorter daily FED, 13.2%

fewer FEF and 9.7% shorter FEHD compared to the high RFI_{fat} steers. Therefore, low RFI and RFI_{fat} steers had lower intakes, visited the feed bunks less frequently and spent less time at the feed bunks compared to the lesser efficient high RFI and RFI_{fat} steers who had greater DMI, longer FED and FEHD, and greater FEF.

Table 16. Significance of contemporary, RFI and RFI_{fat} groups and their interactions on DMI and feeding behaviour in feeder steers.

Cattle Class	Parameter	Contemporary Group (CG)	RFI Group (G)	RFI_{fat} Group (FG)	CG*G	CG*FG
Feeder Steers						
	Intake (DMI), kg DMI/event	<0.0001	<0.0001	<0.0001	0.7665	0.9712
	Duration (FED), min/d	<0.0001	<0.0001	0.0049	0.1190	0.0851
	Frequency (FEF), events/d	0.0316	0.0078	0.0004	0.2675	0.2209
	Head-down (FEHD), min/d	0.0707	0.0016	0.0305	0.0142	0.0126
	Length, min/event	0.0255	0.8069	0.3459	0.2938	0.4300
	Eating rate (ER), kg DMI/min	0.6519	0.1038	0.0620	0.2331	0.1991

Table 17. Dry matter intake and feeding behaviour traits in feeder steers categorized by contemporary, RFI and RFI_{fat} groups.

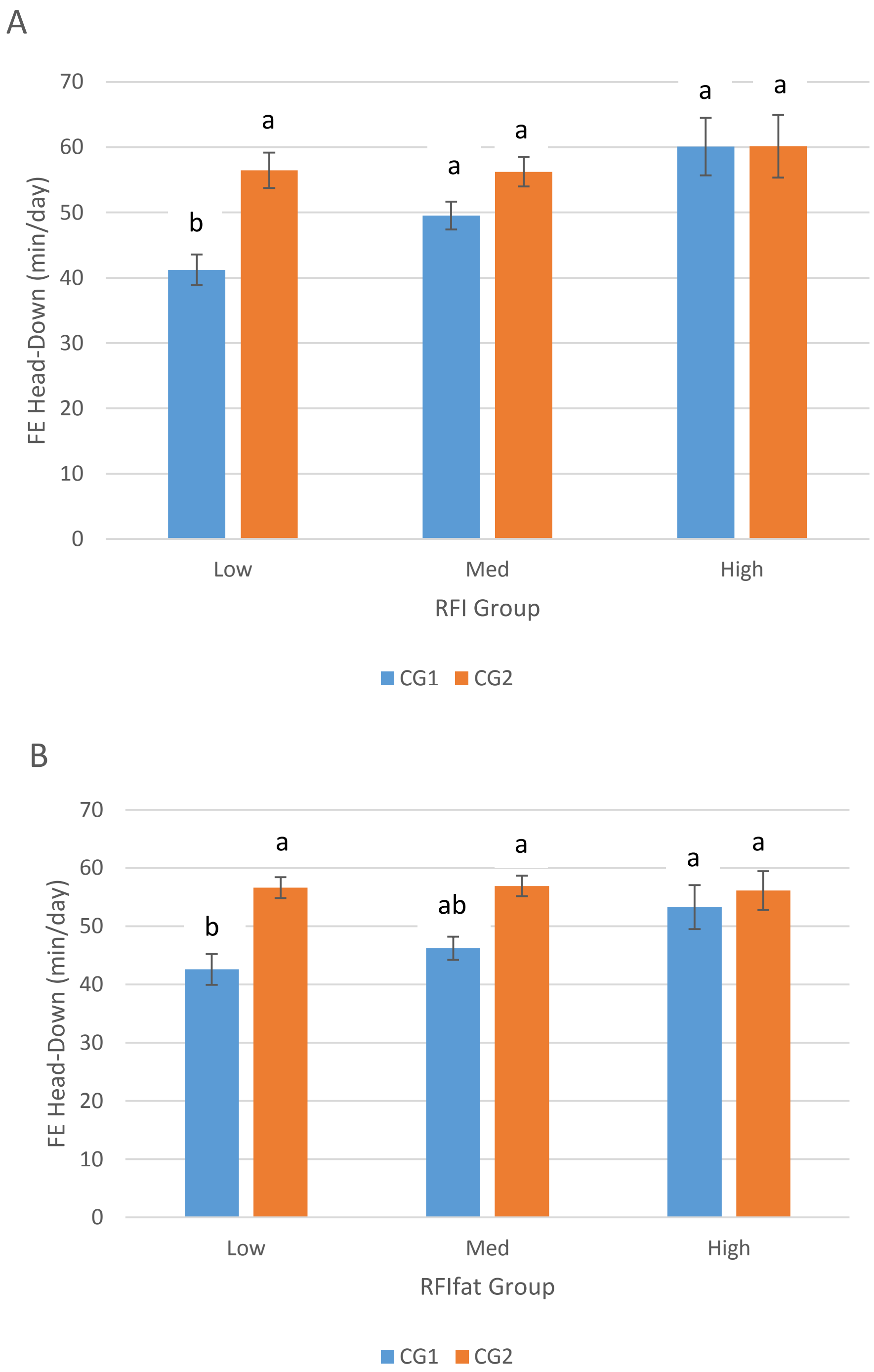
		Contemporary Group			RFI Group				RFI_{fat} Group			
Cattle Class	Parameter	1	2	SE	Low	Medium	High	SE	Low	Medium	High	SE
Feeder Steers												
	Intake (DMI), kg DMI/d	7.63^{b}	10.13^{a}	0.14	8.12^{c}	8.97^{b}	9.55^{a}	0.11	8.21^{c}	8.76^{b}	9.24^{a}	0.08
	Duration (FED), min/d	68.16^{b}	86.36^{a}	2.35	71.04^{c}	75.29^{b}	85.45^{a}	1.82	72.54^{b}	72.92^{b}	78.28^{a}	1.39
	Frequency (FEF), events/d	40.80^{b}	47.66^{a}	1.83	40.88^{b}	42.76^{b}	49.04^{a}	1.41	40.07^{b}	41.52^{b}	45.75^{a}	1.05
	Head-down (FEHD), min/d	50.28	57.62	2.33	48.84^{b}	52.88^{a}	60.12^{a}	1.80	49.63^{b}	51.57^{ab}	54.71^{a}	1.37
	Length (FEL), min/event	1.69^{b}	1.98^{a}	0.15	1.84	1.86	1.81	0.06	1.89	1.87	1.81	0.04
	Eating rate (ER), kg DMI/min	0.12	0.12	0.004	0.12	0.12	0.11	0.002	0.12	0.12	0.12	0.002

Least squares means with different superscripts within rows differ significantly ($P < 0.05$).
SEM varied very slightly from mean to mean, so simple averages are presented in this table.

The significant two-way interactions for feeder steers are illustrated in Figures 2A and 2B. Figure 2A demonstrates the interaction (*P* < 0.05) between CG and RFI group for FEHD, where low RFI steers had shorter FEHD in both CG1 and CG2, compared to medium- and high RFI steers in CG1 and CG2, respectively. The low RFI steers in CG1 had an average FEHD that was 12.4% shorter and an average FEHD that was 31.2% shorter than the high RFI steers in CG2. The medium RFI steers in CG1 had 12.7% shorter FEHD compared to the medium RFI steers in CG2, and the medium RFI steers in both CGs had 6.7 - 19.3% shorter FEHD compared to the high RFI steers in both CGs. The high RFI steers in CG1 and CG2 were comparable.

Figure 2B illustrates the interaction (*P* < 0.05) between CG and $\mathrm{RFI}_{\mathrm{fat}}$ group for FEHD, with similarity observed among low, medium and high $\mathrm{RFI}_{\mathrm{fat}}$ groups in CG2. In CG1, the low $\mathrm{RFI}_{\mathrm{fat}}$ steers had the shortest FEHD, the high $\mathrm{RFI}_{\mathrm{fat}}$ steers had the longest FEHD and the medium $\mathrm{RFI}_{\mathrm{fat}}$ steers were intermediate at 46.22 min/d.

Figure 2. Effect of **(A)** CG x RFI group interaction on FEHD; and **(B)** CG x RFI$_{fat}$ group interaction on FEHD for feeder steers.



Pearson partial phenotypic correlation coefficients between RFI, RFI_{fat}, DMI and FB traits are presented in Table 18. Residual feed intake and RFI_{fat} were positively correlated ($P <$ 0.0001) with DMI ($r_p = 0.28$; $r_p = 0.27$), FED ($r_p = 0.31$; $r_p = 0.26$), FEF ($r_p = 0.25$; $r_p = 0.27$) and FEHD ($r_p = 0.28$; $r_p = 0.25$), respectively. Residual feed intake nor RFI_{fat} were correlated with FEL or ER ($P > 0.1$).

Dry matter intake was positively correlated ($P < 0.0001$) with FED ($r_p = 0.32$), FEL ($r_p =$ 0.60) and ER ($r_p = 0.61$), and negatively correlated with FEF ($r_p = -0.36$). Feeding event duration was positively correlated ($P < 0.0001$), with FEF ($r_p = 0.36$), FEHD ($r_p = 0.77$) and FEL ($r_p =$ 0.32) and negatively correlated with ER ($r_p = -0.53$). Feeding event frequency was positively correlated ($P < 0.0001$), with FEHD ($r_p = 0.41$), and negatively correlated with FEL ($r_p = -0.71$) and ER ($r_p = -0.61$). Feeding event head-down time was negatively correlated with ER ($r_p = -$0.66, $P < 0.0001$). Feeding event length was positively correlated with ER ($r_p = 0.26$, $P < 0.01$).

Table 18. Pearson partial phenotypic correlations between RFI, RFI_{fat}, DMI and feeding behaviour traits for feeder steers.

Traits	RFI, kg DMI/d	RFI_{fat}, kg DMI/d	Intake (DMI), kg DMI/d	FE duration, min/d	FE frequency, events/d	FE head-down, min/d	FE length, min/event	Eating rate, kg DMI/min
RFI, kg DMI/d	1.00	0.96 ***	0.28 ***	0.31 ***	0.25 ***	0.28 ***	-0.04	0.01
RFI_{fat}, kg DMI/d		1.00	0.27 ***	0.26 ***	0.27 ***	0.25 ***	-0.09	0.04
Intake (DMI), kg DMI/d			1.00	0.32 ***	-0.36 ***	-0.06	0.60 ***	0.61 ***
FE duration, min/d				1.00	0.36 ***	0.77 ***	0.32 ***	-0.53 ***
FE frequency, events/d					1.00	0.41 ***	-0.71 ***	-0.61 ***
FE head-down, min/d						1.00	0.11	-0.66 ***
FE length, min/event							1.00	0.26 ***
Eating rate, kg DMI/min								1.00

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.0001$.

As with the feeder heifers, increased daily FEF resulted in longer overall daily FED, but decreased FEL. Longer FED and FEL resulted in increased DMI; however, DMI was negatively correlated with FEF, indicating that steers with a greater number of feed bunk visits consumed less DMI. As ER increased, DMI also increased, indicating that a quicker consumption rate increases total daily intake. The steers that were consuming feed more quickly did not require as long a FED or FEHD to consume the feed, thereby shortening the FED and FEHD, and reducing FEF.

4.4.4.3 Feeding behaviour comparisons in feeder cattle

The majority of FB studies have been conducted in growing feeder cattle, most predominantly steers fed backgrounding or finishing diets (Chen et al., 2014; Durunna et al., 2011; Nkrumah et al., 2007; Robinson and Oddy, 2004; Basarab et al., 2003, 2002). Comparisons of our RFI and FB data with the aforementioned research studies have revealed consistencies, as well as some discrepancies, suggesting that some FB traits may be more reliable predictors of improved feed efficiency in feedlot cattle on energy dense diets in a dry lot environment, compared to other FB traits.

Significant effects of RFI group on FED, FEF and FEHD observed in our study were also reported by Nkrumah et al. (2007). Basarab et al. (2003), however, found no significance of the effect of RFI group for either FED or FEF ($P > 0.05$). Strong negative correlations between FEF and ER ($P < 0.0001$) of -0.63 (heifers) and -0.61 (steers) was also observed by Chen et al. (2014) with values ranging from -0.10 to -0.28 in feedlot steers. Positive phenotypic correlations ($P < 0.0001$) of 0.54 for feeder heifers and 0.36 for feeder steers are comparable to those reported by Chen et al. (2014), Durunna et al. (2011), Nkrumah et al. (2007) and Robinson and Oddy (2004), which ranged from 0.07 to 0.33. Feeding event frequency and FEHD were positively correlated for heifers ($r_p = 0.49$) and steers ($r_p = 0.41$). Chen et al. (2014), Durunna et al. (2011), Nkrumah et al. (2007) and Robinson and Oddy (2004) found weak to moderate correlations between FEF and FEHD ranging from -0.10 to 0.44. Thus, the variation tends to suggest that FEF may not be the most reliable predictor variable of feed efficiency.

Dry matter intake and FED were moderately correlated for steers ($r_p = 0.32$, $P < 0.0001$), and weakly correlated for heifers ($r_p = 0.16$, $P < 0.05$). Similarly, low to moderate positive phenotypic correlations were reported by Nkrumah et al. (2007; 0.27), Robinson and Oddy (2004; 0.18) and Schwartzkopf-Genswein et al. (2002; 0.38). Contrary to the weaker correlations reported in these studies, Basarab et al. (2002) reported a strong positive phenotypic correlation of 0.69 between DMI and FED in feedlot cattle of mixed breed. Additionally, Basarab et al. (2002) found a moderate to strong positive correlation between DMI and FEHD ($r_p = 0.59$), whereas Nkrumah et al. (2007) reported a lower positive correlation of 0.33. Our study found no significance between DMI and FEHD ($P > 0.05$), but a weak correlation was observed ($r_p = 0.06$) for feeder heifers, and ($r_p = -0.06$) for feeder steers. Furthermore, varied results for DMI and FEF have been reported in the published literature. Negative phenotypic correlations for heifers ($r_p = -0.24$, $P < 0.01$) and steers ($r_p = -0.36$, $P < 0.0001$) observed in our study are comparable to Basarab et al. (2002) and Nkrumah et al. (2007), who reported phenotypic correlations of -0.21 and 0.31, respectively. However, Schwartzkopf-Genswein et al. (2002) found no significance ($P > 0.1$) and only a very weak positive correlation ($r_p = 0.09$). Non-significant correlations between DMI, FED and FEF observed by Schwartzkopf-Genswein et al. (2002) could be due to the small sample size of the test herd (6 heifers and 6 steers), and the fact that each animal was penned individually, whereas the other studies collected individual FB data on animals penned in groups with larger sample numbers.

Sex differences could be adding to the variation in feeding behavior results when comparing feeders to other literature. Schwartzkopf-Genswein et al. (2002) found that heifers had higher DMI ($P < 0.0001$) than steers (9.8 vs. 9.3 kg DMI/d). Elzo et al. (2009) reported that heifers consumed 1.24 ± 0.36 kg DM/d more feed ($P < 0.0006$) compared with steers. Our study concluded the opposite, as feeder heifers had lower DMI than steers (8.16 ± 0.92 kg DMI/d vs. 8.75 ± 0.87 kg DMI/d), respectively. There could have been seasonal influences, with hot summer temperatures impacting intakes for the CG2 heifers and altering FB to feed at cooler times of the day, as previously discussed, and therefore suppressing true expression of DMI and its relationships with FB variables.

4.4.5 Intake and feeding behaviour of yearling bulls

Effects of year were significant (*P* < 0.0001) for DMI, FED, FEF, FEL and ER (Table 19). Bulls in Year 1 consumed 23.9% less DMI, had 1.1% longer FED, 52.7% more FEF, 42.9% shorter FEL and 28.6% slower ER per day compared to the bulls in Year 2. Corn silage spoilage issues observed in Year 1 may have affected palatability and deterred animals from true expression of DMI. Furthermore, the increased ER and FEL seen in Year 2 may have been the driving FB variables that increased DMI in Year 2 compared to Year 1. Schwartzkopf-Genswein et al. (2002) proposed that ER could have a strong influence on the relationship between bunk attendance and DMI. This is apparent in our study, as longer FED did not result in increased DMI between years; rather, differences in ER and FEL seemed to be the variables of greater influence.

Weather may have also influenced DMI. When animals experience temperatures below their lower critical temperature (LCT), additional energy is required to maintain body temperature, thereby increasing nutritional demands and DMI (West, 2003; Young, 1981). The LCT for a growing bovine on an energy-based diet is -35°C (Young, 1981). While no feed days fell below the LCT in either year, 3% of feed trial days fell below -20°C in Year 1, whereas 10% fell below -20°C in Year 2. The slightly colder ambient temperatures in Year 2 may have increased DMI. Temperature fluctuations even on a day to day basis can confound DMI, and possibly FB.

Additionally, footing to access the feed bunks differed between Years 1 and 2. During the winter feeding period preceding our study in Year 2, ambient temperatures corrected for wind-chill were much colder (40% more days dropping below -20°C) compared to Year 1, and therefore, there was a continual problem with manure and ice build-up in front of the feed bunks. Until ice was removed, cattle were feeding on an incline. This awkward angle may have impacted their FB, due in combination to discomfort resulting from feeding at an unnatural angle, along with the icy ground and incline affecting their footing. Cattle are prey animals, and if they feel that their safety is compromised in a situation, including their ability to flee from perceived threats, they will do what they can to avoid or lessen their exposure to the situation. This could have been the reason the cattle in Year 2 spent less time overall accessing the feed bunks, and visited them less frequently, thereby compensating by increasing the rate in which they ingested the feed while accessing the bunks, in comparison to Year 1 when the grounding in front of the feed bunks was less inclined.

The effect of diet was significant for DMI, FED and ER ($P < 0.0001$), as well as FEF ($P = 0.07$). Feeding event head-down time and FEL were similar between treatments ($P > 0.1$). Bulls on the forage-based diet treatment consumed 16% less DMI per day, had 15.9% greater FED, 15.4% slower ER and tended toward a 13.5% increase in FEF compared to the grain-based diet treatment.

Differences in FB seen between diet treatments is expected given that the nature of the diet impacts both the manipulation of the feed during ingestion, as well as the metabolic receptors that are triggered by degree of rumen distention (Allen, 2000). Decreased intake associated with the forage-based diet may be attributed to increased NDF which was 58.1% and 40.2% in Year 1, and 39.9% and 27.3% in Year 2 for the forage-based and grain-based diets, respectively. Diets with increased NDF not only require more time to consume, but they will result in increased rumen fill and decreased rate of digestion compared to concentrate-based diets that are less. In addition, the grain-based diet had higher starch content compared to the forage-based diet. Starch is more readily digested, increasing the rate of passage and decreasing rumen retention time (Boadi et al., 2002). This may have led to increased intakes on the grain-based diet, as evidenced by grain-based bulls consuming 13.02 ± 0.25 kg DMI/d compared to the forage-based bulls ingesting 10.24 ±.030 kg DMI/d. Increased rumen retention time of the higher fibre forage-based diet resulted in a 13.5% increase in FEF compared with the grain-based bulls ($P = 0.07$). Golden et al. (2008) also reported increased FEF in cattle fed a forage-based diet compared to cattle fed a concentrate diet (14.5 vs. 11.0 events/d, respectively). However, there are differences in the literature regarding the impact of forage versus concentrate diets on FEF, as Schwartzkopf-Genswein et al. (2011) and Basarab et al. (2000) reported that concentrate-based diets decreased FEF (and FEL) compared to forage-based diets. Discrepancies in the literature are presumably related to differences in forage type. In our study, we fed a corn silage-hay TMR, which has a short fibre length and is highly palatable. Other studies may have fed a longer fibre, lower quality forage that is less palatable.

Similar to results obtained here-in, Schwartzkopf-Genswein et al. (2011) found that high concentrate diets increased the ER compared to high-fibre diets (149 vs. 98 g/min, respectively), due to the decreased time needed for mastication and manipulation of the concentrate-based diets compared to the longer fibre-length of the forage-based diets.

Effects of RFI group were significant ($P < 0.0001$) for DMI, FEF and FEHD, as well as FED ($P < 0.01$). There was no significance observed between RFI group for FEL and ER ($P > 0.1$). Overall, the low RFI grouped bulls had shorter FED by 10.4%, 22.1% fewer FEF, 32.4%

shorter FEHD, and consumed 13.2% less DMI/d when compared to the high RFI grouped bulls (Table 20).

Significant differences were observed between $\mathrm{RFI}_{\mathrm{fat}}$ groups ($P < 0.0001$) for DMI, FEF and FEHD, as well as FED and FEL ($P < 0.05$). Eating rate was not significantly different between $\mathrm{RFI}_{\mathrm{fat}}$ groups ($P > 0.1$). Low $\mathrm{RFI}_{\mathrm{fat}}$ bulls had shorter FED, fewer FEF, shorter FEHD and decreased DMI compared to the bulls in the high $\mathrm{RFI}_{\mathrm{fat}}$ group who spent longer durations at the feed bunks, had greater FEF, longer FEHD and increased daily DMI. The high grouped $\mathrm{RFI}_{\mathrm{fat}}$ bulls spent the least amount of time at the feed bunks per visit. The medium $\mathrm{RFI}_{\mathrm{fat}}$ bulls had the longest FEL, whereas the low $\mathrm{RFI}_{\mathrm{fat}}$ bulls had FEL that were on average 6.3% longer than high $\mathrm{RFI}_{\mathrm{fat}}$ bulls, but 7.6% shorter than the medium $\mathrm{RFI}_{\mathrm{fat}}$ bulls. The low $\mathrm{RFI}_{\mathrm{fat}}$ grouped bulls had 9.8% shorter FED, 20.1% fewer FEF, 32.6% shorter FEHD, and consumed 11.5% less DMI per day when compared to the high $\mathrm{RFI}_{\mathrm{fat}}$ grouped bulls.

Table 19. Significance of contemporary, RFI and RFI_{fat} groups and their interactions on DMI and feeding behaviour in yearling bulls.

Cattle Class	Parameter	Year (Y)	Diet (D)	RFI Group (G)	RFI_{fat} Group (FG)	Y*D	D*G	D*FG
Yearling Bulls								
	Intake (DMI), kg DMI/d	<0.0001	0.0001	<0.0001	<0.0001	0.8289	0.9104	0.5862
	Duration (FED), min/d	<0.0001	<0.0001	0.0057	0.0158	0.2763	0.2005	0.7476
	Frequency (FEF), events/d	<0.0001	0.0682	<0.0001	<0.0001	0.0012	0.2137	0.3002
	Head-down (FEHD), min/d	0.8475	0.5484	<0.0001	<0.0001	0.0478	0.7461	0.8147
	Length (FEL), min/event	<0.0001	0.6002	0.5760	0.0231	0.0001	0.0332	0.2899
	Eating rate (ER), kg DMI/min	<0.0001	<0.0001	0.8645	0.4890	0.0321	0.0389	0.2215

Table 20. Dry matter intake and feeding behaviour traits in yearling bulls categorized by contemporary, RFI and RFI$_{fat}$ groups.

Cattle Class	Parameter	Year			Diet			RFI Group				RFI$_{fat}$ Group			
		1	2	SE	Forage	Grain	SE	Low	Medium	High	SE	Low	Medium	High	SE
Yearling Bulls															
	Intake (DMI), kg DMI/d	10.24^{b}	13.02^{a}	0.25	10.70^{b}	12.56^{a}	0.30	10.94^{c}	11.48^{b}	12.48^{a}	0.27	11.02^{c}	11.59^{b}	12.37^{a}	0.25
	Duration (FED), min/d	171.47^{a}	152.97^{b}	3.75	175.12^{a}	149.32^{b}	4.40	153.21^{b}	162.54^{ab}	170.91^{a}	4.30	153.62^{b}	165.53^{a}	169.37^{a}	4.09
	Frequency (FEF), events/d	81.12^{a}	47.30^{b}	2.66	68.55	59.87	3.33	57.46^{c}	63.47^{b}	71.71^{a}	2.93	60.02^{b}	61.14^{b}	73.46^{a}	2.99
	Head-down (FEHD), min/d	83.75	82.89	4.39	85.59	81.05	5.33	68.99^{a}	85.28^{b}	95.69^{b}	4.93	68.74^{b}	85.98^{a}	95.52^{a}	5.05
	Length (FEL), min/event	2.21	3.40	0.13	2.75	2.86	0.16	2.83^{b}	2.87^{a}	2.72^{c}	0.14	2.77^{ab}	2.99^{a}	2.60^{b}	0.14
	Eating rate (ER), kg DMI/min	0.06^{b}	0.08^{a}	0.001	0.06^{b}	0.07^{a}	0.001	0.07	0.07	0.07	0.001	0.07	0.07	0.07	0.002

Least squares means with different superscripts within rows differ significantly ($P < 0.05$).
SEM varied very slightly from mean to mean, so simple averages are presented in this table.

Significant two-way interactions between factors are depicted in Figure 3. A significant interaction between year and diet was observed for FEF ($P < 0.01$), FEHD ($P < 0.1$), FEL ($P < 0.0001$) and ER ($P < 0.05$). The bulls in Year 1 had greater FEF on both the forage-based and the grain-based diets compared to FEF on the forage-based and grain-based diets in Year 2 (Figure 3A). Feeding event frequency between diets within each year did not differ in Year 1; however, the bulls fed the forage-based diet in Year 2 had increased FEF compared to the bulls fed the grain-based diet in Year 2.

Figure 3B demonstrates that the bulls fed the forage-based diet in Year 1 had shorter FEHD compared to the bulls on the forage-based diet in Year 2. The opposite effect was observed for the grain-based diet, where those bulls in Year 1 had longer FEHD as opposed to the bulls in Year 2 who had shorter FEHD. Feeding event head-down time comparisons between diets within each year demonstrated longer FEHD for the bulls fed the grain-based diet compared to the bulls fed the forage-based diet in Year 1, but the opposite was observed for Year 2, where the bulls fed the forage-based diet had substantially longer FEHD compared to the bulls fed the grain-based diet treatment.

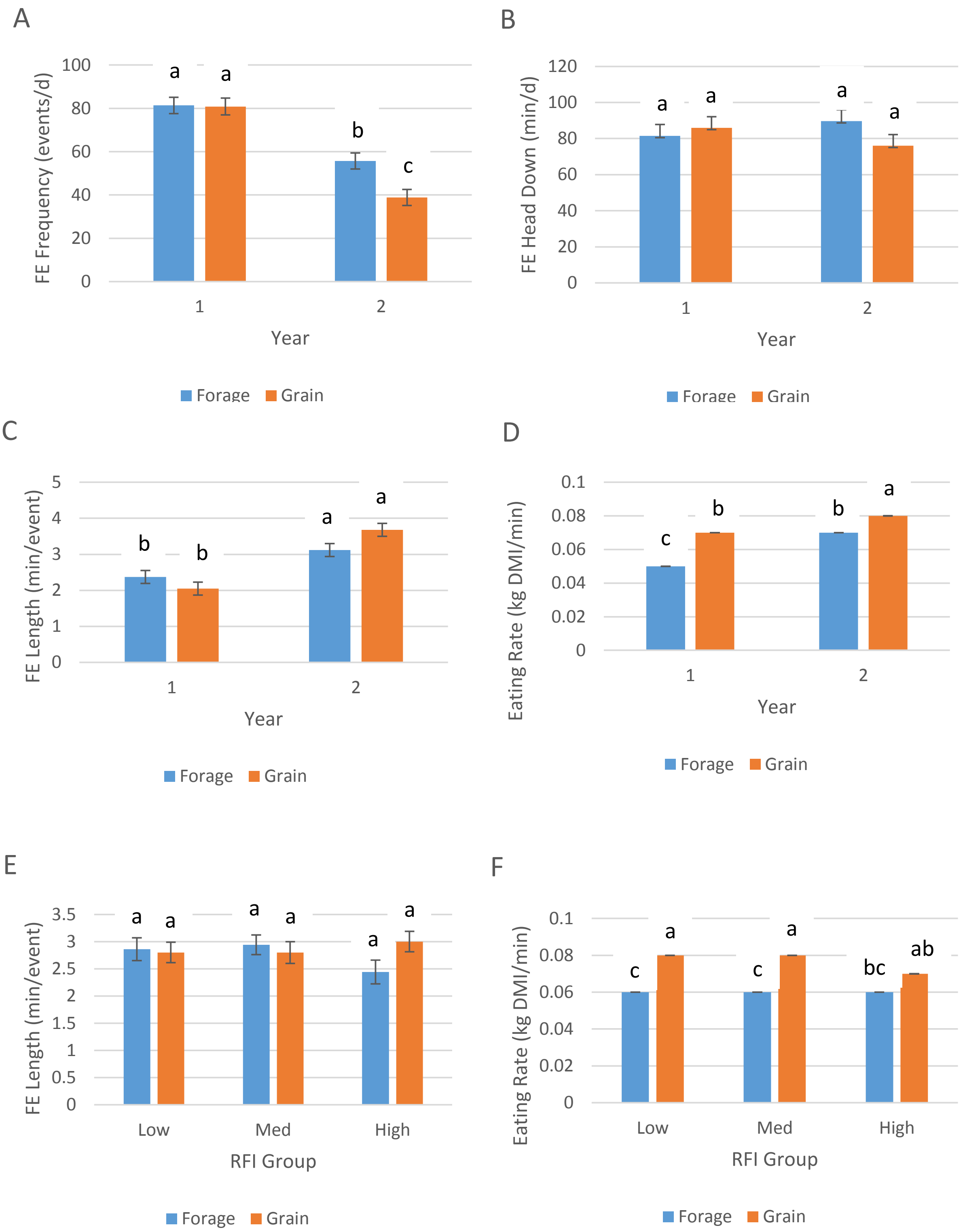
As depicted in Figure 3C, the bulls fed the forage-based diet in Year 1 had shorter FEL compared to the bulls fed the forage-based diet in Year 2. The bulls fed the grain-based diet followed a similar pattern to the forage-based diet treatment, where the bulls fed the grain-based diet in Year 1 had shorter FEL, compared to the bulls fed the grain-based diet in Year 2. Feeding event length comparisons between diets within each year revealed slightly longer FEL for the bulls on the forage-based diet compared to the bulls fed the grain-based diet in Year 1, but the opposite was observed for Year 2, where the bulls fed the forage-based diet had shorter FEL compared to the bulls fed the grain-based diet treatment.

As revealed in Figure 3D, in Year 1 the bulls fed the forage-based diet had a slower ER compared to the bulls in Year 2 fed the same diet. Similarly, the bulls fed the grain-based diet treatment in Year 1 had a slower ER compared to the bulls fed the same diet in Year 2. Eating rate comparisons between diets within each year indicate that bulls fed the grain-based diet had increased ER compared to the bulls fed the forage-based diet.

The medium RFI bulls fed the forage-based diet had longer FEL compared to the low RFI bulls fed the forage-based diet (Figure 3E). No difference was observed between FEL in the low and medium RFI groups fed the grain-based diet. The high RFI bulls fed the grain-based diet had the longest FEL compared to both the low and medium RFI groups fed the grain-based diet. The high RFI group fed the forage-based diet had a shorter FEL compared to the low and medium RFI groups fed the forage-based diet. Feeding event length comparisons between diets within each RFI group demonstrated that while FEL was similar between diet within the low and medium RFI groups, the bulls fed the grain-based diet in the high RFI group had a longer FEL compared to the bulls fed the forage-based diet in the high RFI group.

Bulls in the low, medium and high RFI groups fed the forage-based diet had comparable ER means across groups (0.06 kg DMI/min; Figure 3F). Bulls in the low and medium RFI groups fed the grain-based diet treatment had similar ER (0.08 kg DMI/min). Bulls in the high RFI group fed the grain-based treatment had a slower ER (0.07 kg DMI/min) compared to the other two RFI groups fed the grain-based diet. Eating rate comparisons between diets within each RFI group demonstrated that the bulls fed the grain-based diet within each RFI group had a faster ER compared to the bulls fed the forage-based diet within each RFI group.

Figure 3. Effect of year x diet interaction on **(A)** FEF, **(B)** FEHD, **(C)** FEL, **(D)** ER; and RFI group x diet interaction on **(E)** FEL and **(F)** ER for yearling bulls.



Pearson partial phenotypic correlation coefficients between RFI, $\mathrm{RFI}_{\mathrm{fat}}$, DMI and FB traits for the yearling bulls are displayed in Table 21. RFI and $\mathrm{RFI}_{\mathrm{fat}}$ were positively correlated ($P < 0.0001$) with FED ($r_{\mathrm{p}} = 0.37$; $r_{\mathrm{p}} = 0.35$), FEHD ($r_{\mathrm{p}} = 0.48$; $r_{\mathrm{p}} = 0.48$) and DMI ($r_{\mathrm{p}} = 0.37$; $r_{\mathrm{p}} = 0.36$), respectively. Residual feed intake was positively correlated ($P < 0.01$) with FEF ($r_{\mathrm{p}} = 0.24$), and $\mathrm{RFI}_{\mathrm{fat}}$ was positively correlated ($P < 0.05$) with FEF ($r_{\mathrm{p}} = 0.23$). Lancaster et al. (2009) reported a similar, moderate positive phenotypic correlation of FEF with RFI in growing yearling Angus bulls ($r_{\mathrm{p}} = 0.26$). Correlations of RFI and $\mathrm{RFI}_{\mathrm{fat}}$ with FEL and ER were non-significant ($P > 0.1$). Similarly, Lancaster et al. (2009) observed that RFI was moderately correlated both with DMI ($r_{\mathrm{p}} = 0.60$) and with FEHD ($r_{\mathrm{p}} = 0.38$).

Table 21. Pearson partial phenotypic correlations between RFI, RFI_{fat}, DMI and feeding behaviour traits for yearling bulls fed either forage-based or grain-based diets.

Traits	RFI, kg DMI/d	RFI_{fat}, kg DMI/d	Intake (DMI), kg DMI/d	FE duration, min/d	FE frequency, events/d	FE head-down, min/d	FE length, min/event	Eating rate, kg DMI/min
RFI, kg DMI/d	1.00	0.95 ***	0.37 ***	0.37 ***	0.24 **	0.48 ***	-0.02	-0.08
RFI_{fat}, kg DMI/d		1.00	0.36 ***	0.35 ***	0.23 *	0.48 ***	-0.02	-0.07
Intake (DMI), kg DMI/d			1.00	-0.26 **	-0.47 ***	0.10	0.46 ***	0.70 ***
FE duration, min/d				1.00	0.46 ***	0.60 ***	-0.04	-0.83 ***
FE frequency, events/d					1.00	0.17	-0.84 ***	-0.54 ***
FE head-down, min/d						1.00	0.16	-0.41 ***
FE length, min/event							1.00	0.23 **
Eating rate, kg DMI/min								1.00

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.0001$.

Feeding event duration was positively correlated ($P < 0.0001$) with FEF ($r_p = 0.46$) and FEHD ($r_p = 0.60$), negatively correlated ($P < 0.0001$) with ER ($r_p = -0.83$), and was negatively correlated ($P < 0.01$) with DMI ($r_p = -0.26$). Feeding event duration was not related to FEL ($P > 0.1$). These results indicate that the bulls who made more trips to the feed bunks and who spent longer time periods within scanner range (FEHD), had increased FED. However, the bulls who spent longer at the bunks consumed less DMI, presumably investing more time in other activities instead of feed consumption. Possible activities may have been scratching or licking the bunks, or backing out of the bunk for a short period of time before returning to the same bunk to resume the feed event, thereby increasing the FED without increasing the amount of feed consumed. The negative correlation between FED and ER further supports this possibility; bulls that spend more time during a feed event engaging in non-related feeding activities consume less feed/min during the duration of the feed event.

Feeding frequency was negatively correlated ($P < 0.0001$) with FEL ($r_p = -0.84$), DMI ($r_p = -0.47$) and ER ($r_p = -0.54$), indicating that those bulls who frequented the bunks more often spent less time at the bunk per visit, ate slower and consumed less DMI/d compared to the bulls who had longer FEL with increased ER, resulting in greater DMI. Dry matter intake was positively correlated with ER ($r_p = 0.70$, $P < 0.0001$). There were no significant correlations between FEF and FEHD ($P > 0.1$).

Feeding event head-down time was negatively correlated ($P < 0.0001$) with ER ($r_p = -0.41$), but was unrelated to FEL and DMI ($P > 0.1$). The negative correlation between FEHD and ER suggests that those bulls who consumed feed at a slower pace spent longer at the feed bunks. Since FEHD was unrelated to DMI, it stands to reason that another FB variable such as ER may have influenced FEHD as lower FEHD did not result in decreased DMI. Possibly, increased ER may have enabled those bulls with shorter FEHD to eat faster and still consume DMI that was comparable to the bulls who had lengthier FEHD but slower ER. Unlike the present study, Lancaster et al. (2009) found a weak to moderate positive correlation between FEHD and DMI in growing Angus bulls ($r_p = 0.36$, $P < 0.05$), which was indicative that those bulls who spent a longer in the feed bunk within scanner range consumed more feed.

Feeding event length was positively correlated ($P < 0.0001$) with DMI ($r_p = 0.46$) and was positively correlated ($P < 0.01$) with ER ($r_p = 0.23$).

4.4.6 Factors influencing feeding behaviour

In addition to the within-class differences observed in our study, electronic feed system differences in other studies may account for some of the variability when comparing these results to those existing in the literature. Methodologies to calculate FB traits continue to pose a challenge when making literature comparisons (Tolkamp et al., 2000). Some studies consider all bunk visits, including those when no feed was consumed, to constitute a feed event. Additionally, FEHD is calculated based upon the sum of transponder detections of an animal during a feeding event multiplied by the system's scanning time, and this scanning time ranges from 1.0-6.3 s, depending on the feeding system's configuration, suggesting caution is necessary when making comparisons of FEHD with other literature. Furthermore, bunk management strategies (*ad libitum* versus restricted feeding, head to feed bunk ratio), feed delivery times and frequencies (delivery of fresh feed is proven to stimulate feeding activity, as evaluated by DeVries and von Keyserlingk, 2005), test facilities and housing conditions (differences in cover from harsh weather elements in the form of wind break fences or open faced buildings, or shade from the sun), and cattle temperament can confound FB comparisons with other literature.

Physical characteristics of the diet may contribute to differences in FB variables (Tables 3 and 4). Mature cows had the fastest ERs compared to all other cattle classes (Table 6). The increased rate of intake may be attributed to the physical form of the diet. Given that the cows were fed a cubed diet, this would allow for easier manipulation of the feed and decrease the time required for mastication and rate of passage. Differences in FB traits associated with physical form of the diet are also apparent with the bull data sets. Diets higher in forage occupy greater surface area and bulk due to the larger particle size, thereby increasing rumen fill and limiting

DMI (Rode et al., 1985). Bulls fed the grain-based diet consumed 1.84 kg DMI/d more compared to the bulls fed the forage-based diet. Increase in DMI on grain-based diets may also in part be due to the faster rates of passage into the small intestine, in turn allowing the animal to consume more feed on a DM basis. Chemical composition of the diet may also influence FB indirectly. Studies by Carberry et al. (2012) and Fernando et al (2010) suggest that the differences in starch content will influence the shift in rumen microbial populations from fibrolytic bacteria to amylolytic bacteria when starch is the main energy source. Differences in rumen microbe diversity has been reported to impact RFI (Carberry et al., 2012).

Stage of estrous cycle, gestational differences and gender may presumably contribute to some of the observed FB variation within classes of beef animals. However, comparisons of FB between cattle classes are difficult given the heavily confounding effects of season across groups. Without available data to replicate season, it would not be meaningful to make statistical comparisons between cattle classes.

Onset of puberty in intact growing cattle is affected by various genetic and external parameters, particularly breed, nutrition and age, thereby resulting in differences at onset of puberty by as much as several months, with some animals reaching sexual maturity earlier (six months of age), and others by as late as eighteen to twenty months of age (Basarab et al., 2011; Schillo et al., 1992; Lunstra et al., 1978). Pubescent cattle are undergoing development of the reproductive system, and are expending energy in the form of sexual behaviour, as opposed to those pre-pubescent cattle who are not yet utilizing energy reserves for physiological and behavioural reproductive needs (Schillo et al., 1992). Those cattle that are sexually maturing or matured may exhibit an increased level of activity allocated toward expressing sexual behaviour, including signs of estrus in females (temporary pacing, distractedness, decreased feed intake and occasional aggressiveness) and reception in bulls (pacing, distractedness and increased aggression). These reproductive behaviours would likely interfere with FB variables. A study by Basarab et al. (2011) investigated effects of beef heifer puberty on RFI, and found that sexually maturing heifers consumed 4.7% more feed as opposed to the pre-pubescent heifers ($P < 0.0001$). Since it is believed that FB variables may govern feed intake to a degree, it is arguably plausible that FB variables are also altered if DMI is influenced by puberty. All test cattle in this thesis were a minimum of 260 d of age, thereby at least 60 d older than the suggested average six month onset of puberty reported by Schillo et al. (1992). Therefore, some animals in the yearling bull, replacement heifer and feeder heifer data sets may have reached puberty during the on-test period, while others had not, which may have impacted RFI ranking (Basarab et al., 2011) and possible DMI and FB expression both across and within CG.

Differences in beef cattle breed have been reported to have a significant effect on FEF. Nkrumah et al. (2007) examined the impact of breed and found that Charolais cattle had greater FEF (31.49 ± 0.86 events/d) compared to hybrid steers (28.70 ± 0.53 events/d) and Angus steers (28.86 ± 0.55 events/d); $P = 0.02$. Feeding event duration and FEHD were not significantly different between the three breed groups (Nkrumah et al., 2007). Bailey et al. (2011) examined significant effect of beef breed on RFI and DMI among Angus, Braford, Simbrah and Brangus beef heifers, and found significant differences between cattle breed and RFI, with Simbrah cattle being the most efficient compared to the other three breeds ($P < 0.01$). In the same study, these authors reported significant ($P < 0.01$) differences between beef breed and DMI while fed a grain-based diet, with Angus beef cattle having the greatest DMI (10.30 kg/d) and Braford cattle having the lowest DMI (9.52 kg/d). Elzo et al. (2009) reported a decreased RFI value (improved efficiency) in cattle that had a greater percentage of *Bos indicus* in their genetic make-up, as opposed to *Bos taurus*.

4.5 CONCLUSIONS

Limited studies have examined the phenotypic relationships between RFI and FB traits in commercial breeding stock (Fitzsimons et al., 2014; McGee et al., 2014; Lancaster et al., 2009), as most studies have been conducted in feedlot cattle. An examining of FB traits among all classes of beef cattle (breeding bulls, replacement heifers, mature cows and feeder cattle) under varying circumstances that included: time of year, age, breed, sex and diet type, demonstrates that the effect of, and relationship with RFI is similar. Low ranking RFI and RFI_{fat} cattle had significantly ($P < 0.05$) decreased FED, FEHD and FEF compared to high ranking RFI and RFI_{fat} cattle. Bulls fed the grain-based diet spent significantly less time acquiring feed, with faster ER and greater DMI, compared to bulls fed the forage-based diet. Feeding behaviour traits and DMI were phenotypically correlated with RFI and RFI_{fat}. High RFI cattle consumed more feed compared to low RFI cattle; since RFI is moderately heritable, selecting for low RFI cattle will favorably lead to decreased feed usage and costs. There is merit to further evaluating FB as a predictor of feed efficiency in beef cattle. Although automated feeding technology exits to measure daily intake in order to calculate RFI, feed trial time frame may not be ideal on cow/calf operations. Fully understanding the extent to which feed efficiency influences FB traits may validate alternative time-efficient and cost-effective methods to readily select for feed efficient cattle. Additionally, FB is predominantly measured in young growing cattle; however, assessing FB traits may be more important in mature cows. Feeding behaviour traits measured in growing cattle cannot be expected to be related to efficiency in mature cows as they are very different traits.

5. MANUSCRIPT II

Relationships between residual feed intake, temperament and feeding behaviour in growing yearling Angus beef bulls

L. Lippens, K.H. Ominski, G. Crow, K. Schwartzkopf-Genswein, F. Zvomuya, J.A. Basarab

Department of Animal Science, Faculty of Agricultural and Food Sciences, University of Manitoba, Winnipeg, Manitoba, Canada, R3T 2N2

5.1 ABSTRACT

Residual feed intake (RFI) is a measure of feed efficiency independent of growth traits, therefore bearing economic relevance to the cattle industry. Temperament and feeding behaviour (FB) may have economic value if they have potential to indicate feed efficient cattle. The objective of this study was to assess the relationships between beef cattle temperament, RFI, RFI_{fat} and FB in acclimated Angus beef bulls 355 ± 23 d of age fed either a forage-based ($n = 29$) or a grain-based ($n = 29$) diet. Cattle were grouped into low, medium and high RFI classes, and the effects of diet and RFI ranking on four temperament assessments including: chute score (CS), exit velocity (EV; m/s), flight distance (FD; m) and lying duration (LD; %/d) were assessed. Phenotypic correlations between the aforementioned temperament assessments, dry matter intake (DMI) and FB traits including: feeding event duration (FED; min/d), feeding event frequency (FEF; events/d), feeding event head-down time (FEHD; min/d), feeding event length (FEL; min/event) and eating rate (ER; kg DMI/min) were examined.

Lying duration was 7.24%/d greater for bulls fed the grain-based diet compared to bulls fed the forage-based diet ($P < 0.01$). Chute score and EV were significantly correlated ($r_{\text{p}} = 0.36$, $P < 0.01$). There was no observed relationship between temperament and RFI or RFI_{far} ranking ($P > 0.05$), indicating that temperament as measured by CS, EV, FD and LD on acclimated cattle is not associated with RFI ranking. Additionally, selecting for feed efficient (low RFI) cattle will not negatively impact temperament.

Abbreviations used in Manuscript II: **ADF**, acid detergent fibre; **ADG**, average daily gain; **AFD**, assigned feed disappearance; **CS**, chute score; **DM**, dry matter; **DMI**, dry matter intake (kg DMI/day); **ER**, eating rate; **EV**, exit velocity; **ENS**, entry score; **EXS**, exit score; **FBF**, final backfat thickness (mm); **FD**, flight distance; **FE**, feeding event; **FED**, feeding event duration (minutes/day); **FEF**, feeding event frequency; **FEHD**, feeding event head-down time (minutes/day); **FEL**, feeding event length (minutes/event); **MMW**, metabolic mid-weight; **NDF**, neutral detergent fibre; **RES**, restraint score; **RFI**, residual feed intake; **RFI**$_{\text{fat}}$, residual feed intake adjusted for final backfat thickness; **RFID**, radio frequency identification; **SDFI**, standardized daily feed intake; **TMR**, total mixed ration

Keywords: chute score, exit velocity, feeding behaviour, flight distance, lying duration, residual feed intake

5.2 INTRODUCTION

Residual feed intake is the difference between actual feed intake and expected feed intake determined from actual body weight and gain of animals within or across contemporary groups (Basarab et al., 2003). Efficient animals have a low or negative RFI and consume less feed, whereas inefficient animals have a positive or high RFI and consume more feed than expected (Basarab et al. 2003). Five major factors contributing to this variation in efficiency include: physical activity, feed intake, digestion of feed and associated energy costs, metabolism associated with body composition variation and biogenesis of energy, and thermoregulation (Herd, 2009). Of the 73% of variation in RFI that is accounted for, physical activity comprises 9% (Kelly et al., 2010; Richardson and Herd, 2004; Arthur et al., 2001), and is partly influenced by FB. Many factors affect feed intake patterns (feeding behaviour) in cattle, including but not limited to: weather conditions, bunk space (competition), animal health, diet type (high concentrate versus high fibre), and temperament (Schwartzkopf-Genswein et al., 2011; Herd, 2009; Basarab et al., 2003).

Temperament has been defined as a dynamic matrix of traits which impact response to, and perception of, environmental influences and their impact on behavioural and physiological systems (Lyons, 1989). Behaviours indicative of an animal's temperament include: aggression, docility, avoidance, boldness, excitability, environmental surveillance, hesitation and fearfulness (Hurnik et al. 1995; Sebastian et al. 2011). Degree of fearfulness appears to be highly related to temperament and therefore, the most common method of measure involves an animal’s response to handling (Schwartzkopf-Genswein et al. 2012; Sebastian et al. 2011). Understanding the extent to which behavioral traits are heritable will allow for improvement in temperament, enhancing animal welfare through the reduction of stress elicited by husbandry and production practices (Sebastian et al. 2011). Further, it has been postulated that high efficiency (low RFI) cattle are less susceptible to stress than cattle assigned a high RFI ranking (Sebastian et al., 2011). Studies indicate that cattle less susceptible to stress are more efficient at coping and adapting to a given stressor and allocating energy toward weight gain rather than investing energy in coping with perceived environmental stressors (Herd, 2009).

Research efforts need to continue advancing toward a more in-depth understanding of feed efficiency to improve profitability and reduce the cost of production. Knowledge of the phenotypic correlations between feed efficiency, FB and temperament of beef cattle will provide the basic information required to develop successful cattle selection and bunk management strategies in western Canadian beef cattle production systems. Further, most research conducted in this area has focused on initial temperament assessment of cattle within 0-28 d of arrival to a feedlot. Little research has examined temperament traits in beef cattle that were already acclimated to their surroundings, including handling facilities and handlers. There is merit in assessing temperament in cattle that have been acclimated to their surroundings, as is the case in cow-calf operations.

5.3 MATERIALS AND METHODS

5.3.1 Facilities and animal management

Fifty-eight purebred Angus yearling bulls obtained from several Manitoban producers with an average age of 355 (± 23) d and average body weight of 491 (± 44) kg at the start of the 67 d feed test were randomly assigned to four pens, two pens with 14 head each, and two pens with 15 head each. Each pen was equipped with four GrowSafe feed bunks (GrowSafe Systems Ltd., Airdrie, Alberta) and one automatic Ritchie heated watering bowl. The bulls were fed *ad libitum,* with two pens receiving a grain-based diet, and two pens receiving a forage-based diet (Table 22). All pens were transitioned onto their respective diet during a 21 d adaptation period prior to the start of the RFI feed trial. To prevent bedding material from impacting feed intakes, all pens were initially bedded with a straw base, and subsequent bedding consisted of lesser palatable flax shives that were added to the pens as required throughout the duration of the study.

Bulls were weighed on two consecutive days at the start and end of the feeding period, and weekly throughout the entire 67 d feeding period. Backfat, rump fat, ribeye area and intramuscular fat were measured once at the start and again at the end of the feeding period via an Aloka 500V diagnostic real-time ultrasound camera (Overseas Monitor Corporation Ltd., Richmond, BC). These measurements, coupled with daily intake data collected by the GrowSafe feeding system, allowed for collection of growth and intake data that would later be used to calculate RFI and RFI_{fat}, and to determine feeding event traits.

Bulls were further assessed during a 21 d temperament study which was initiated 50 days after the onset of the feeding period. Average age and body weight at the start of the 21 d temperament study were 405 (± 23) d and 585 (± 52) kg, respectively.

All test animals were cared for abiding by guidelines established by the Canadian Council on Animal Care (CCAC). All bulls had previously been vaccinated with Vision 8 (Merck Animal health, Summit, NJ) and Vista Once (Merck Animal Health, Summit, NJ), and treated with Noromectin (Norbrook Inc., Lenexa, KS) along the spine. Vitamin A and D injections were administered four months prior to the commencement of this trial, and vitamin boosters given every three months there-after.

5.3.2 Feed sample collection and analysis

Weekly feed samples of both TMRs were collected, dried at 60° C in a forced-air oven to a constant weight, ground, composited monthly and analyzed for nutrient composition. Acid detergent fibre (ADF) and neutral detergent fibre (NDF) were calculated using an ANKOM 200 fibre analyzer (Fairport, NY). Gross energy was derived by combusting a pelleted feed sample in a Par 6300 Automatic Isoperibol Calorimeter (Moline, IL). Crude protein (CP) was analyzed via the LECO NS 2000 analyzer (LECO Corporation, St. Joseph, MI) and calculated as 6.25 x N (AOAC 1996, Official Method 973.03). Mineral analysis (calcium, phosphorus, potassium and magnesium) was carried out by ashing 0.9 - 1.1 g in a furnace followed by inductively-coupled plasma emission spectroscopy (Vista MPX ICP, Varian Canada Inc., Mississauga, ON; AOAC 2005, method no. 985.01).

Table 22. Nutrient composition of forage- and grain-based diets fed to yearling beef bulls.

Item	Grain-based diet	Forage-based diet
Ingredient composition, % As Fed basis		
Grass Hay	-	17.9
Alfalfa Hay	-	-
Alfalfa Silage	33.1	-
Corn Silage	39	81.7
Corn Grain	27.5	-
Limestone	-	0.3
Mineral	0.2	0.1
Salt	0.2	0.1
Nutrient composition, % DM basis		
Dry Matter, %	53.4	51.3
Acid Detergent Fiber, %	14.9	21.9
Neutral Detergent Fiber, %	27	41.9
Total Digestible Nutrients, %	80.6	73.3
Metabolizable Energy, MJ/kg	12.2	11.1
Crude Protein, %	12.3	13
Starch (Enzymatic), %	32.3	22.1
Calcium, %	0.96	1.06
Phosphorus, %	0.56	0.58
Magnesium, %	0.45	0.56
Potassium, %	2.09	2.77

5.3.3 Feed data collection

Ad libitum intake data were collected and recorded daily by the GrowSafe feed intake and feeding behaviour monitoring system. The following FB variables were examined: FED (min/d); FEF (bunk visits/d); FEL (min/event); and an overall ER (kg DMI/min). Dry matter intake (kg DMI/d) was also examined. The GrowSafe System captured FED and FEF, including those visits where 0 g of feed was consumed. Whereas bunk visits encompass all visits including those when 0 g of feed are consumed (not examined in this thesis), feeding events only considered events where > 0 g were consumed. Total FEDs, FEFs and FEHDs were tabulated for the entire trial period, then divided by number of trial days to calculate a daily value for each trait. Eating rate was calculated by dividing total kg of feed consumed (DMI) over the trial duration, by minutes spent actively feeding (sum of FED with intake > 0 g) over the trial period. Feeding event length was calculated as the total minutes spent eating (sum of FED with intake > 0 g) divided by the frequency of events over the entire feeding period.

5.3.4 Temperament data collection

As described in Table 23, the 21 d temperament study consisted of four assessment techniques performed at the end of the RFI trial: LD, CS, EV and FD. Differences in handling and exposure backgrounds were eradicated to closely mimic a cow-calf operation scenario.

Table 23. Summary of temperament variables measured in yearling beef bulls over a 21 day assessment period.

Variable	Units	Measuring Device(s)	Frequency of Measure	Animals (n)	Parameter
Lying duration	%/day	HOBO Pendant G Acceleration Data Logger	3, 48-hr periods	48**	Lying behaviour (Y-axis)
Chute score	Scale of 3-10*	Subjective (visual) at 3 points	6	58	Entry, Restraint, Exit score
Exit velocity	Meters/ second	Objective (laser beam generators, reflectors, timer)	6	58	Exit time
Flight zone	Meters	Bosch Laser Distance Measurer, Model GLR 225	2	58	Flight distance

* Score of 3 = calm; score of 10 = highly reactive.
** 12 animals per pen across four pens.

5.3.4.1 Pen lying duration

Individual LD may be an indication of an animal’s capacity to endure environmental and social influences (MacKay et al., 2013). Three consecutive weekly 48 hr LD assessments were completed on 12 bulls selected from each of four pens for this study (80-86% of the animals in each pen). Bulls were selected based upon GrowSafe feeding data that demonstrated which animals had the most consistent DMI during the 50 d feeding period prior to LD assessment.

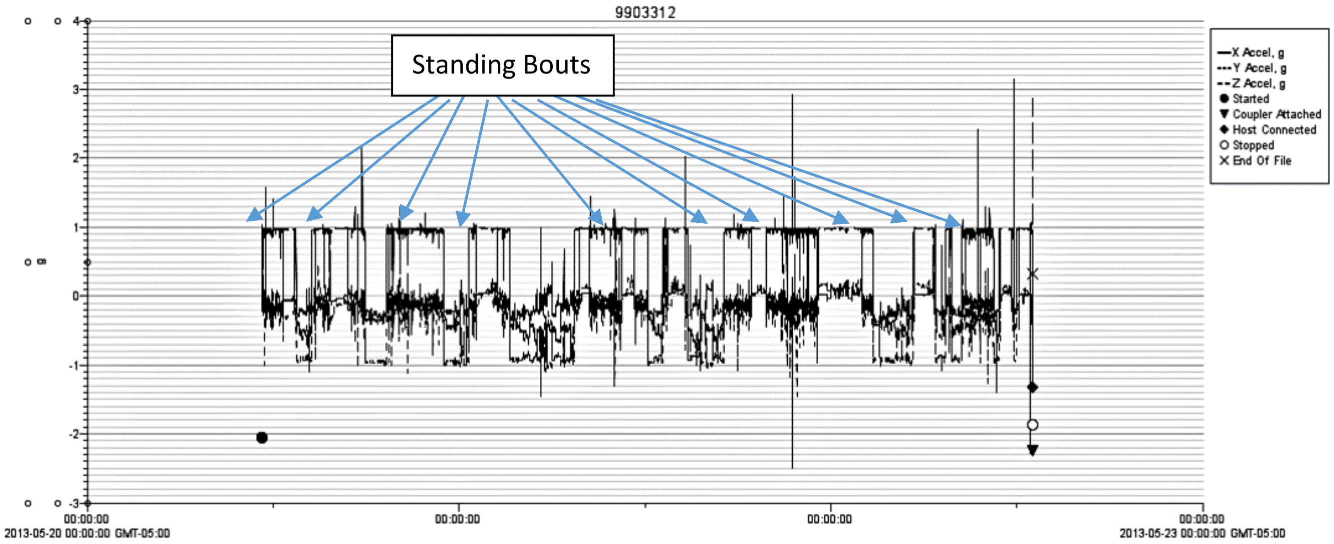
One accelerometer (HOBO Pendant G Accelerometer, Onset Computer Corporation, Bourne MA) contained in a waterproof pouch was attached to the medial side of the left hind leg of each bull with a Velcro strap and cohesive bandage (VetWrap). The attachment site was between the tarso-metatarsal joint and accessory digit (O'Driscoll et al. 2008). Attachment was in a position so that the x-axis was parallel to the ground, the y-axis perpendicular to the ground pointing upward, and the z-axis parallel to the ground pointing away from the sagittal plane (Figure 4), allowing the accelerometer to record the g-force on the x, y and z-axes at 30 s intervals for a 2 d collection period. According to Ito et al. (2009), one-min logging intervals allow for sampling days to be shortened from five to three days and still obtain accurate estimates of lying behaviour that provide sufficient estimates of the overall mean LD (R^2 = 0.94). Therefore, 30s logging intervals were recorded for three, 2-d periods.

Figure 4. HOBO Pendant G accelerometer enclosed within a waterproof casing and attached to the hind leg.

During each 48 hr data collection period, bulls were not disturbed. Animals were bedded at least two d prior to, to prevent any behaviour influenced by fresh bedding. Feed delivery times coincided with the norm that had occurred throughout the 50 d preceding HOBO Pendant G data logging.

Accelerometers were removed following the 2 d period and data downloaded using Onset HOBOware Pendant G Onset Corporation computer software, which allows for a conversion of the g-force readings into degrees of tilt to determine when the animal is standing up (Yunta et al., 2012; Ito et al. 2009) such that any y-axis readings less than 60° indicate an animal standing, and readings greater than or equal to 60° indicate the animal lying down (Ito et al. 2009). Figure 5 demonstrates a normal posture plot obtained by the HOBOware Pendant G Onset Corporation computer software for one bull during a 48 h period. The plateaus portray standing bouts.

Figure 5. Posture plot generated from an accelerometer depicting standing bouts during a 48 hr period.



Daily standing time (s/d) and bouts were calculated based on 86,440 observations from midnight until midnight the following day, as described by Ito et al. (2009). Any standing or lying bouts of less than two minutes were discounted to eliminate misinterpretation of exaggerated leg movements for standing or recumbent positions. Daily time spent in recumbency was calculated as the inverse of the standing time. The total LD was then converted into a percentage per day.

Mean LD values were calculated for every bull in each of the three 48 hr collection periods, and an overall mean was further calculated for the three period averages such that one average percentage value represented total LD for each animal, as described by MacKay et al. (2013).

5.3.4.2 Subjective (visual scoring) and objective (exit velocity) assessment

Bulls were subjected to a total of six (i) subjective measurements performed visually while restrained in the head gate (Table 24); and (ii) objective measurements upon release from the head gate, as described by Schwartzkopf-Genswein et al. (2012) and Sebastian et al. (2011).

The measurements were carried out over three consecutive weeks, twice a week on two consecutive days. Assessment was performed by one individual in the same sequence, at the same time each day, commencing on the day after removal of the HOBO Pendant G accelerometers.

(i) Subjective measurement series – chute score

A subjective CS was determined at three points by a single observer through visual assessment of the animal's reactivity during handling in the chute and head gate (Schwartzkopf-Genswein et al., 2012; Sebastian et al., 2011; Grandin, 1993) as described in Table 24.

Table 24. Chute score system (scale of 3-10) used to measure temperament in beef bulls. [1]

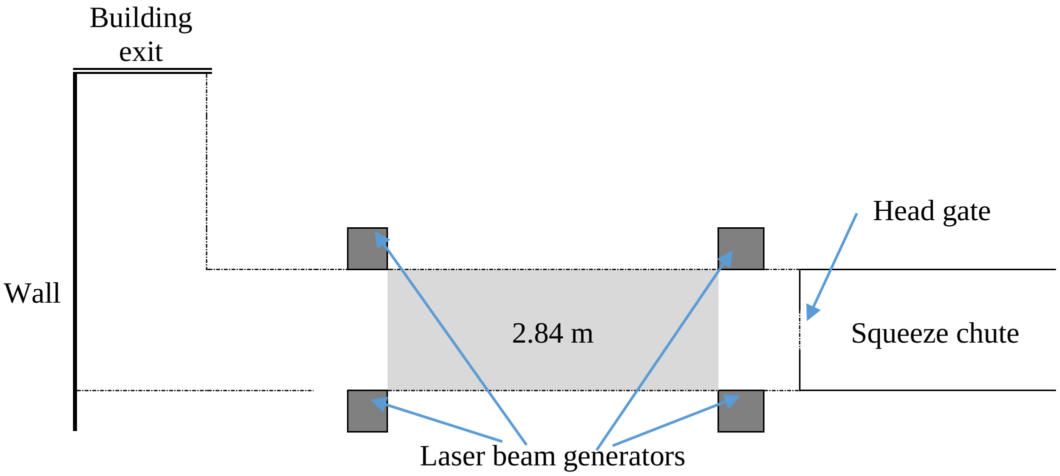
Entry Score (ENS)	1	Enters head gate calmly
	2	Coaxed in, enters head gate with moderate force
	3	Running entry, enters head gate with excessive force
Restraint Score (RES)	1	Little to no movement
	2	Restless, low amplitude movement
	3	Nervous, obvious forward and backward movement
	4	Nervous, continuous violent movements
Exit Score (EXS)	1	Calm exit
	2	Slow trot exit
	3	Running/jumping exit

[1] Modified from Grandin (1993).

(ii) Objective measurement – exit velocity

Exit velocity was assessed to obtain an objective and quantifiable measure of the speed of travel over a set distance when released from the head gate (Figure 6). As observed by Sebastian et al. (2011), calm animals leave the chute at a slower rate than more nervous animals. Therefore, the EV test was used to measure temperament of each bull by recording the elapsed speed to move a measured distance after exiting the confined area of the chute.

Figure 6. Diagram depicting the animal handling facility design in which CS and EV tests were performed.



The measuring apparatus consisted of two sets of laser beam generators, reflectors on a stand, and a timer. The first laser beam was situated 0.44 m from the exit of the head gate and the second laser beam was situated 2.84 m after the initial 0.44 m mark; ie: 3.28 m from the squeeze chute. The EV measured within the 2.84 m spanning between both sets of laser beam generators.

The clock timer was triggered when the bull broke the first laser beam and stopped when it broke through the second laser beam. The stands supporting the lasers measured 0.9 m each above ground in order to record the flight time of the animal at head level. Distance used is comparable to those describe by Black et al. (2013) of 1.83 m and Sebastian et al. (2011) of 2.9 m.

(iii) Overall sequence of subjective and objective measurements

Sequence of measurements was performed as described by Sebastian et al. (2011): (a) a subjective visual ENS score was assigned upon entry into the head gate; (b) once secured in the head gate, reaction was visually assessed for 30s and a subjective visual RES score was assigned; (c) during the second half of the 60s restraint period, the person operating the head gate handled each animal's left ear; (d) when released from the head gate, a subjective visual EXS score was assigned; (e) the bull travelled the 2.84 m distance dividing the two laser beams in succession, and the objective travel distance time was recorded.

5.3.4.3 Flight distance

Flight distance was measured at the same time each day, on two consecutive days, at the end of the feeding trial. As described by Schwartzkopf-Genswein et al. (2012), FD was determined using a commercially available Distometer laser device (Distometer; Leica DISTO plus 56, Leica Inc., Switzerland). Bulls were moved individually into an unfamiliar 10 m x 10 m (100 m^2) pen built of windbreak fences that obscured any distractions outside the test pen. Upon entry into the pen, each bull was given five minutes to settle before the FD test commenced.

Following the 5-min settling period, the unfamiliar person operating the Distometer laser device (Distometer; Leica DISTO plus 56, Leica Inc., Switzerland) approached the bull at a constant pace of one step/s from the same marked location, progressing toward the animal from the side, perpendicular to its shoulder. Flight distance measurement was obtained by marking the point of shoulder with the laser pointer when the bull attempted to move away from the operator.

5.3.5 Calculations and statistical analyses

5.3.5.1 Residual feed intake

Residual feed intake was calculated for each bull as described by Basarab et al. (2007). Total DMI was calculated by obtaining daily feed intake from the GrowSafe feeding system and multiplying by dry matter content of the diet and then by the total days on test (67 d) for each bull. Total standardized feed intake was then calculated by multiplying each animal's total DMI by the metabolizable energy content of the diet (Table 22), and then dividing the total metabolizable energy intake by 10 MJ ME/kg DM, and then by the total days on test to standardize intake to a uniform energy density (SDFI; kg DM/d) for each bull.

Residual feed intake, as well as RFI adjusted for final backfat thickness (FBF) measured at end of test (equations 1 and 2, respectively) for each bull were calculated as follows (Basarab et al., 2003):

$$(1)\ SDFI_i = \beta_O + \beta_1 ADG_i + \beta_2 MMW_i + +e_i$$

$$(2)\ SDFI_i = \beta_O + \beta_1 ADG_i + \beta_2 MMW_i + \beta_3 FBF_i + e_i$$

where i = SDFI for the i'th bull, β_O = regression intercept, β_1 = partial regression coefficient of SDFI on ADG, β_2 = partial regression coefficient of SDFI on MMW, β_3 = partial regression coefficient of SDFI on FBF in the case of RFI_{fat}, and e_i = the residual deviation (random error term) of SDFI for the i'th bull. Bulls were then sorted into either a low (RFI < -0.05), medium (within ± 0.05 SD) or high (RFI > 0.05) RFI or $\mathrm{RFI_{fat}}$ group.

Bulls were ranked by RFI within each of the four pens with *n* = 14, 15, 15, 14 for Pens 1 to 4, respectively, and placed into low (< 0.5 SD mean RFI), medium (within +/- 0.5 SD), and high (> 0.5 SD mean RFI) RFI groups.

5.3.5.2 Temperament model

Temperament traits were analyzed using the MIXED procedure of SAS (SAS Institute Inc., Cary, NC) to identify the influence of diet (forage and grain), RFI and $\mathrm{RFI_{fat}}$ group on the following four temperament parameters: CS, EV, FD and LD. The temperament traits were considered the dependent variables; diet, RFI and $\mathrm{RFI_{fat}}$ group were classified as the independent variables. The following models were used to calculate RFI (1), and $\mathrm{RFI_{fat}}$ (2):

$$(1)\ y_{ijkl} = \mu + \mathrm{RFIgroup}_i + \mathrm{diet}_j + \mathrm{pen}_{jk} + \mathrm{RFIgroup{*}diet}_{ij} + e_{ijkl}$$

$$(2)\ y_{ijkl} = \mu + \mathrm{RFI_{fat}group}_i + \mathrm{diet}_j + \mathrm{pen}_{jk} + \mathrm{RFI_{fat}group{*}diet}_{ij} + e_{ijkl}$$

where y_{ijkl} is the dependent temperament variables on the l'th bull with the i'th RFI or $\mathrm{RFI_{fat}}$ classification located in the k'th pen nested within the j'th diet; μ is the population mean; $\mathrm{RFIgroup}_i$ is the effect of the i'th RFI or $\mathrm{RFI_{fat}}$ group (i = -1, 0, 1, representing low, medium and high RFI values, respectively; fixed effect); diet_j is the effect of the j'th diet (j = forage-based, grain-based; fixed effect); pen_{jk} is the effect of the k'th pen nested within the j'th diet (k = 1, 2, 3, 4, representing pens 1, 2, 3, 4, respectively; random effect); $\mathrm{RFIgroup{*}diet}_{ij}$ is the interaction of RFI or $\mathrm{RFI_{fat}}$ group (low, medium or high; fixed effect) and diet (forage or grain; fixed effect);

and e_{ijkl} is the error (residual deviation) of the l'th bull. Pen was a random effect. Bull age was initially tested in the model as a covariate (excluded from the class statement), but was found to be non-significant ($P > 0.5$), so it was excluded from the model. Significance of the fixed effects was determined by F-values using Type 3 tests of fixed effects (diet, RFI and RFI_{fat} group). Mean values for CS, EV, FD and LD were tested using Tukey's range test (*t*-tests).

5.3.5.3 Pearson partial phenotypic correlations

The models as described above were used to generate residuals. The PROC CORR procedure of SAS was then used to determine partial pearson correlation coefficients for RFI, RFI_{fat}, DMI, FB traits (FED, FEF, FEHD, FEL, ER) and temperament traits (CS, EV, FD, LD). Statistical significance was reported when $P < 0.05$. Trends were reported when $P < 0.1$.

5.4 RESULTS

Means for the performance, FB and temperament traits are presented in Table 25. The omission of non-valid days and corresponding feeding event data occurred when either 1) the average feed disappearance (AFD) was less than 95% for the entire pen; or 2) the AFD was less than 90% for any bunk within the pen. Mean daily AFD throughout the trial was 99.1%. Six days of feed data were excluded due to loss of RFID ear tags, power outages and equipment malfunction.

Table 25. Descriptive statistics including means, standard deviations and coefficients of variation for performance, feeding behaviour and temperament traits in 58 yearling Angus beef bulls.

	Mean	SD	CV (%)
Age at start of feeding period, d	355	23	6.48
Performance			
ADG, kg/d	1.83	0.32	17.49
Metabolic mid-weight, kg	113.24	7.34	6.48
RFI, kg DMI/d	0.00	0.90	-
$RFI_{fat,}$ kg DMI/d	0.00	0.86	-
Intake (DMI), kg DMI/d	12.96	1.45	11.19
Feeding Behaviour			
Feeding event duration (FED), min/d	152.49	25.40	16.66
Feeding event frequency (FEF), events/d	46.26	12.50	27.02
Feeding event head-down time (FEHD), min/d	82.26	28.19	34.27
Feeding event length (FEL), min/event	3.44	0.75	21.80
Eating rate (ER), kg DMI/min	0.07	0.01	14.29
Temperament			
Age at start of temperament test, d	405	23	5.68
Body weight at start of temperament test, kg	585	52	8.94
Chute score, scale 3 (calm) -10 (reactive)	3.19	0.27	8.46
Exit velocity, m/s	0.67	0.22	32.84
Flight distance, m	1.94	0.91	46.91
Lying duration, %/d	36.6	3.28	8.96

Statistical significance of diet, RFI and RFI_{fat} group and their interactions with the temperament variables CS, EV, FD and LD, are presented in Table 26. Least squares means (LSM) for CS, EV, FD and LD, summarized by diet and RFI group, are provided in Table 27. The effect of diet was significant ($P < 0.01$) for LD, such that the bulls on the grain-based diet spent on average 2% more time in recumbency than those on the forage-based diet. Diet had no effect on other temperament variables ($P > 0.05$). Neither RFI nor RFI_{fat} was significant for any temperament traits ($P > 0.05$). Chute scores were comparable for all bulls, indicating consistently calm animals during this test. Likewise, no significant differences were observed between diet treatment, RFI and RFI_{fat} group ($P > 0.05$) for CS or EV.

Table 26. Significance of diet and RFI ranking and their interactions on temperament variables measured in yearling Angus beef bulls.

Parameter	Diet (D)	RFI Group (G)	RFI_{fat} Group (FG)	D*G	D*FG
Temp Variable					
Chute score, 3-10	0.7205	0.2853	0.6607	0.5592	0.5343
Exit velocity, m/s	0.5532	0.4726	0.6712	0.6152	0.9667
Flight distance, m	0.6293	0.7662	0.6357	0.0262	0.4060
Lying duration, %/d	0.0187	0.2413	0.2290	0.4842	0.8571

Statistical significance reported when $P < 0.05$.

Table 27. Temperament traits in relation to diet, RFI group and RFI_{fat} group for yearling Angus beef bulls.

	Diet			RFI Group				RFI_{fat} Group			
Parameter	Forage	Grain	SE	Low	Medium	High	SE	Low	Medium	High	SE
Temperament Variable											
Chute score, 3-10	3.18	3.20	0.05	3.21	3.23	3.10	0.06	3.24	3.16	3.17	0.06
Exit velocity, m/s	0.66	0.68	0.04	0.68	0.70	0.61	0.05	0.69	0.68	0.62	0.05
Flight distance, m	1.81	2.02	0.30	1.88	2.03	1.84	0.27	1.88	2.03	1.84	0.26
Lying duration, %/d	35.24^{b}	37.89^{a}	0.68	37.58	35.77	36.51	0.80	37.50	35.59	36.61	0.80

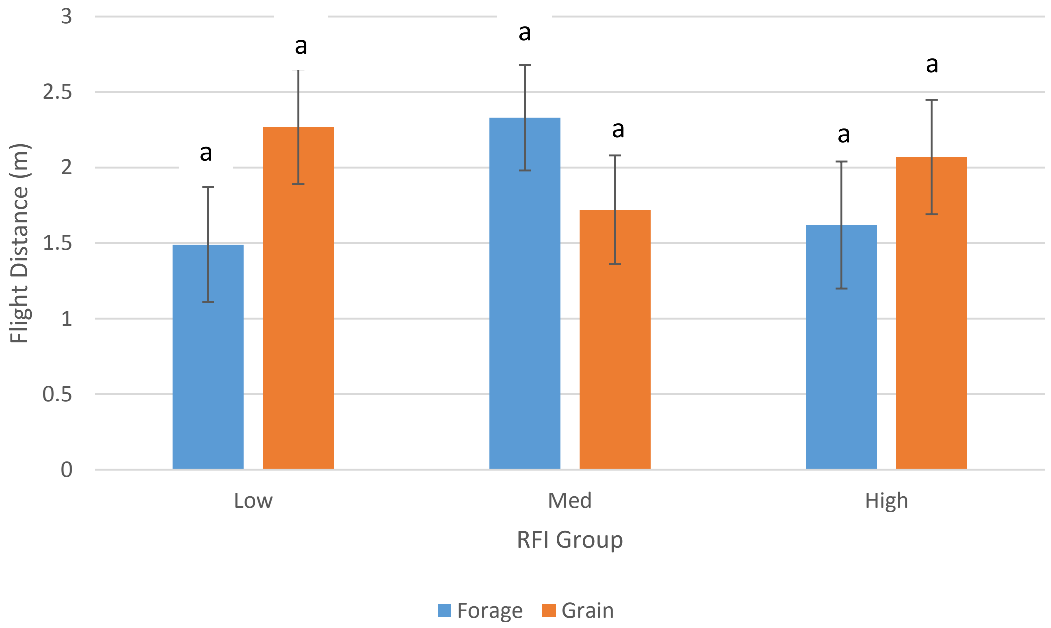
Least squares means with different superscripts within rows differ significantly ($P < 0.05$).
Standard error (SE) simple averages are depicted.

As displayed in Table 26, a significant two-way interaction between RFI group and diet was observed for FD ($P < 0.05$). Low RFI bulls fed the forage-based diet had a smaller flight zone (less reactive to the presence of an approaching human), compared to the high RFI bulls fed the forage-based diet, indicating that low RFI bulls moved away from the approaching handler sooner. Interestingly, the bulls fed the grain-based diet exhibited the reverse, with low RFI bulls avoiding the approaching human sooner (more reactive) compared to the high RFI grouped bulls.

Differences in FD were apparent between the forage- and grain-based diet treatments (Figure 7) in that low and high RFI bulls fed the grain-based diet had increased flight zones compared to the low and high RFI bulls fed the forage-based diet, indicating that the bulls fed the grain-based diet tended to be more reactive to the approaching human when compared to the bulls fed the forage-based diet.

Two-way significant interactions between RFI and diet were also apparent, with the smallest FD observed in the forage-fed, low RFI (1.49 ± 0.38 m) and high RFI (1.62 ± 0.42 m) bulls. The largest FDs occurred in the medium RFI forage-fed bulls. The grain-based diet treatment had FD means of 2.27 ± 0.38 m for the low RFI group, 1.72 ± 0.36 m for the medium RFI group and 2.07 ± 0.38 m for the high RFI group.

Figure 7. Effect of RFI group x diet (forage- and grain-based) interaction on flight distance for yearling bulls.



Correlations between temperament traits are presented in Table 28. A significant positive correlation between EV and CS ($r_p = 0.36$, $P < 0.01$) was observed. This is not surprising, given that an animal that is struggling to escape confinement during the CS test would likely exit the chute when released at an increased speed compared to a calm animal that is demonstrating no form of resistance or motivation to escape. There were no other significant correlations ($P < 0.05$) or trends ($P < 0.1$) found between temperament traits. In addition, there were no significant correlations ($P > 0.05$) for temperament traits with FB traits. However, LD tended to be negatively correlated with FED and FEF ($r_p = -0.26$, $P = 0.09$ and $r_p = -0.25$, $P = 0.08$), respectively. Flight distance tended to be positively correlated with FEHD ($r_p = 0.23$, $P = 0.08$).

Table 28. Pearson partial phenotypic correlations between temperament traits and feeding behaviour traits for yearling Angus beef bulls fed forage- and grain-based diets.

Trait	FE duration, min/d	FE frequency, events/d	FE head-down, min/d	FE length, min/event	FE intake, kg DMI/d	Eating rate, kg DMI/min	Exit velocity, m/s	Flight distance, m	Lying duration, %/d
Chute score, 3-10	0.00	0.06	0.12	-0.09	-0.10	-0.04	0.36**	0.20	0.10
Exit velocity, m/s	-0.05	-0.09	0.19	0.03	-0.14			0.16	0.21
Flight distance, m	0.16	-0.09	0.23	0.19	0.07				0.07
Lying duration, %/d	-0.26	-0.25	-0.22	0.13	0.18				

**P* < 0.05; ***P* < 0.01; ****P* < 0.0001.

The extent to which CS, EV, FD and LD were influenced by RFI and RFI_{fat} group was examined by using a stepwise regression in SAS. However, no temperament variable met the 0.1500 significance level for entry into the model.

5.5 DISCUSSION

Temperament assessment during a three-week period on 58 purebred Angus yearling bulls found no significant effect of RFI, $\mathrm{RFI}_{\mathrm{fat}}$ or diet on CS, EV or FD. This suggests that bulls selected as feed efficient (low RFI) will not necessarily result in inadvertent selection for, or against particular reactions toward the specific temperament traits of assessment in this study. These results further indicate that habituation over a six month period prior to the commencement of the temperament study will acclimate cattle to stock personnel, environmental surroundings including handling facilities, and routine handling, thereby potentially reducing if not altogether removing reaction response through learning, providing that the handling experience is positive for the animal. It is worth noting that, if handling experiences are negative, this may result in cattle that are more resistant, reactive and fearful of handling, thereby affecting temperament assessment. Secondly, this study was performed on producers' breeding bulls that were selected for desirable characteristics by the producers prior to the start of the trial, thereby possibly increasing the likelihood that any bulls with highly excitable reactive responses would have been culled through the selection process. This would have resulted in reduced variation in temperament in this study. Lastly, temperament assessments were done on bulls at the end of a feeding period, where they were at their heaviest in terms of body weight. It is speculated that heavier animals may have lower energy levels and reduced reaction speed, potentially affecting reaction response particularly during the EV test, as opposed to their reaction had they been tested at the start of the feeding period when they were lighter in body weight.

Most temperament studies (Black et al., 2013; Elzo et al., 2009; Nkrumah et al., 2007; Fox et al., 2004) assess the reaction response of cattle in a feedlot setting at specific time intervals over an established time frame, commencing upon arrival to new surroundings. The cattle come from varied backgrounds with varied levels of human exposure and handling. Cattle that have been handled more, or have had positive experiences associated with humans, may respond differently to temperament assessments than cattle who have been handled less or have had negative experiences associated with humans, regardless of temperament. Therefore, previous acclimation to handling and humans may interfere with the true expression of temperament. Nkrumah et al. (2007) and Fox et al. (2004) have reported no significance between flightier animals, as measured by EV, and feed efficiency (RFI or ADG) when assessing cattle that have come from varied backgrounds. It is speculated that acclimation differences may have been a factor. Therefore, in order to contribute to the robust repertoire of temperament research performed in all aspects of beef production, it is also worth examining temperament under conditions that are more relatable to commercial cow-calf production scenarios, where cattle have often received the same degree and method of handling prior to assessing temperament, as was the case in this study. Curley et al. (2006) proposed that the most accurate time to assess cattle temperament may be after the animals have received a period of uniform acclimation.

5.5.1 Residual feed intake and temperament

Neither RFI nor RFI_{fat} were significantly different for any temperament traits (Table 26). These findings are in agreement with Black et al. (2013) and Nkrumah et al. (2007), who reported no significant relationship ($P > 0.05$) between RFI and CS, EV and FD in 74 beef mixed breed heifers, and RFI and EV in 302 composite beef steers, respectively. Similarly, Elzo et al. (2009) found no relationship between CS and RFI ($P > 0.05$). However, Rolfe et al. (2011) reported a small and negative phenotypic correlation of RFI with EV ($r_p = -0.09$). Since RFI is adjusted for maintenance and growth, this may be inadvertently eliminating any undesirable effects of more reactive animals on feed efficiency, as suggested by Black et al. (2013).

Measuring temperament as a behavioural response to varying scenarios requires further examination. According to Richardson and Herd (2004), there may be a difference between behavioural response and physiological response to stress. These authors observed that high RFI cattle had a higher blood neutrophil:lymphocyte ratio and a higher cortisol concentration than low RFI cattle, suggesting high RFI cattle may be more physiologically responsive to stress. Knott et al. (2005) examined the relationship between RFI and physiological response in sheep as measured by levels of cortisol as a blood indicator of stress, found that there was a positive association between cortisol response and RFI ($r_p = 0.42$). These data combined, lend support to the possibility that physiological responses to stress may provide a more reliable assessment of temperament than behavioural responses. Van Reenen et al. (2005) postulated the concept of "passive coping", in which some animals may elicit very little behavioural reaction response to a stressful scenario, even though they may be experiencing a high level of internal stress relative to the behaviour they are exhibiting. Behavioural temperament testing has no way to distinguish these "passive copers" from those animals that display active behavioural responses indicative of disposition. Validating the method(s) of measuring temperament (behavioural versus physiological) warrant further research in light of the potential for differences between behavioural and physiological measures.

5.5.2 Diet treatment and temperament

The objective of the temperament test is to measure the animal's degree of reactivity in response to a perceived threat or novel stimuli. However, it may be speculated that there may be another intervening variable(s) that indirectly affects the animal's innate reactive response to the particular temperament test. Greater energy density of the grain-based ration may inadvertently increase the level of reactivity, not necessarily out of fear or avoidance of the test assessment itself, but because consumption of a denser energy diet may have in turn resulted in bulls with more energy to expend. While there were no significant interaction effects for diet and the behavioural temperament traits CS, EV and FD ($P > 0.1$), the bulls on the grain-based diet were slightly more reactive during subjective temperament assessment, as they had slightly increased CS, EV and FD means (3.18 ± 0.05, 0.68 ± 0.04 m/s and 2.02 ± 0.30 m, respectively), compared to the forage-based bulls who tended to have slightly decreased CS, EV and FD means (3.20 ± 0.05, 0.66 ± 0.04 m/s and 1.81 ± 0.30 m, respectively). To the author's knowledge, this is the first study to date to simultaneously compare temperament measures on two groups of bulls, same age and breed, on different diet treatments.

Interestingly, MacKay et al. (2013) proposed that degree of fitness may be a possible intervening variable that may indirectly affect an animal's reactive response to a temperament test. Degree of fitness may impact the agility of the animal; thereby, it is speculated that the heavier animals (those with higher ADGs) may be more sedentary in comparison to the lighter conditioned animals that may possibly be quicker to respond to a stressful stimulus. This was not the case in this thesis, as the bulls on the grain-based diet who were slightly more reactive during temperament tests had a higher mean ADG of 2.00± 0.31 kg/d compared to the bulls on the forage-based diet that had a lower mean ADG of 1.66 ± 0.23 kg/d.

In this study, there was a significant difference (*P* < 0.01) between diet and LD, with grain-based bulls spending a larger percentage (5%) of their day recumbent (37.89 ± 0.68 %/d), in comparison to the forage-based bulls who spent 35.24 ± 0.68% of their day lying. This significance is not surprising, given that animals consume more energy per feed event on higher concentrate diets, leading to a decrease in feeding frequency compared to cattle on a forage-based diet (Schwartzkopf-Genswein et al., 2011; Golden et al., 2008; Basarab et al., 2000). Concentrate-based diets also require less time for mastication and rumination given the nature of the diet (silage and grain), thereby increasing eating rate compared to forage-based diets that have a longer fibre length (Schwartzkopf-Genswein et al., 2011). Therefore, it is not unexpected that less time is required for bulls fed the concentrate-based diet to acquire feed to meet their maintenance and growth requirements compared to bulls on forage-based diet treatment, thereby allowing allocation of time toward other natural pen behaviours, such as lying down.

5.5.3 Temperament trait phenotypic correlations

As previously discussed, the behavioural assessment of temperament on this project more closely mimicked a commercial cow/calf operation in Western Canada, where cattle are acclimated to the stock person(s) and handling facilities. Beef cow/calf operations place emphasis on temperament of their livestock, since cows and breeding bulls are kept for years as replacement and breeding stock, and therefore, temperament holds merit in terms of both human safety and animal welfare. Hence, assessing temperament in an environment that closely mimics a cow/calf operation versus the more frequently studied feedlot setting has merit.

Similar to this study, MacKay et al. (2013) reported a moderate correlation between CS and EV ($r_p = 0.34$, $P = 0.005$), but found no significant correlation ($P > 0.184$) of CS with pen activity ($r_p < 0.17$) as measured by activity monitors. However, these researchers found a trend between EV and pen activity ($r_p < 0.24$, $P = 0.055$), where the flightier steers were more variable in their step count as measured by the activity monitors. This could indicate that CS and EV may be indirectly influenced by different underlying variables (eg: fear of humans, resistance to restraint, motivation to return to the pen). Chute score may be a measure of the animal's degree of acclimation to handling. Additionally, CS may directly reflect the handler's chute operating ability, rather than the animal's disposition. Exit velocity may be a measure of the animal's innate response to avoid fear via escape (MacKay et al., 2013), suggesting that EV would tend toward a stronger correlation with natural cattle behaviour during pen activity, rather than comparing CS to pen activity.

These results indicate that temperament traits require further evaluation with large data sets under varying conditions, in order to derive a less generalized and more consistent method of assessing temperament (Elzo et al., 2009).

5.5.4 Temperament and feeding behaviour

The results of the present study indicate that all measured temperament variables bear no significant phenotypic correlations to FB variables and DMI. In fact, FD only tended toward a positive phenotypic correlation to FEHD time ($r_p = 0.23$, $P = 0.08$). Lying duration tended toward a weak negative phenotypic correlation to FED and FEF ($r_p = -0.26$, $P = 0.08$ and $r_p = -0.25$, $P = 0.09$), respectively, suggesting that those bulls who spent less time standing also spent less time actively engaging in feed bunk activity. These results are in agreement with MacKay et al. (2013) and Nkrumah et al. (2007), who found no significant phenotypic correlations between temperament variables and FB variables ($P > 0.05$). Nkrumah et al. (2007) found that FED was unrelated phenotypically to EV, but there was an observed weak negative phenotypic correlation between FEHD and EV ($P < 0.10$). These authors conducted an EV assessment on a larger body of cattle ($n = 302$ steers) compared to this study ($n = 58$ bulls), and although the steers had no previous acclimation to the facilities, similar results were observed when comparing EV to FB within both studies. They observed a mean EV of 2.52 ± 0.73 m/s (Nkrumah et al., 2007), whereas the mean EV for the bulls in our study was 0.67 ± 0.22 m/s, indicating that the bulls were less motivated to travel the set distance quickly, likely attributed to their habituation to the handling procedure prior to the temperament testing. Therefore, the results of this study further contributes to the robustness of literature examining phenotypic correlations among FB and temperament variables, proving that habituation (a common scenario on commercial cow-calf production operations) may not diminish efficacy of EV assessments when comparing to particular FB traits.

Llonch et al. (2016) reported a significant phenotypic correlation between DMI and EV on 84 Charolais-Luing crossbred steers, where animals with faster EVs had lower DMI ($P < 0.05$). Their study was in agreement with Rolfe et al. (2014), Nkrumah et al. (2007) and Fox et al. (2004), who observed weak negative phenotypic correlations between EV and DMI ($r_p = -0.22$, -0.35 and -0.34, respectively). It is speculated that cattle who consumed larger quantities of feed exited the chute more slowly (Elzo et al., 2009). These authors reported a significant ($P < 0.001$) negative regression estimate of daily feed intake on mean EV (-0.29 ± 0.09 kg of DM/d), where calves which consumed more feed appeared to be more sluggish coming out of the chute, resulting in a slower EV. They suggested two possibilities: this may be an indication of temperament, or it may be the result of animals that consume more feed are heavier, and may be slower. Body condition scoring cattle to assess degree of fatness may allow for comparisons between degree of fat cover and EV. Black et al. (2013) found no significant correlations among EV and DMI, or CS and DMI in heifers or cows. Their findings are in agreement with that obtained herein, which also found no significant correlation of either EV or CS with DMI. It is reasonable to conclude that EV appears to be more reliable in predicting FB traits compared to CS; however, while there is potential, there is not enough consistency among research to warrant EV as a reliable indicator trait of FB, given that underlying variables may be indirectly factoring into the equation.

5.6 CONCLUSIONS

Most of the literature on cattle temperament in relation to RFI has assessed temperament on naïve animals. Results from this study contribute to the existing literature by providing data on cattle acclimated to facilities and handlers prior to assessment. There were no significant differences due to RFI and diet on CS, EV, FD or LD. Significance between diet treatment and LD ($P < 0.01$) was reported, with bulls fed the grain-based diet engaging in longer lying bouts overall (37.89 ± 0.68 %/d) compared to bulls fed the forage-based diet (35.24 ± 0.68 %/d). There was a significant interaction effect between diet and RFI ($P < 0.05$) for FD, with the low RFI and RFI_{fat} bulls fed the forage-based diet having a decreased flight zone compared to bulls fed the grain-based diet. Lack of significance between RFI and temperament traits indicate that temperament, as assessed by CS, EV, FD and LD, does not predict RFI ranking. No significance suggests that selecting for feed efficiency will not have negative consequences on temperament.

6. GENERAL DISCUSSION

The overall objective of this thesis was to evaluate FB traits measured by the GrowSafe automated feeding system, and temperament traits assessed both objectively and subjectively, and their relationships to feed efficiency. Residual feed intake was used as the measure of feed efficiency in cattle given that it is independent of growth and body size, thereby providing an opportunity to examine underlying variation in feed efficiency since it allows for meaningful comparisons among cattle within and across CG. More specifically, the first manuscript assessed FB traits in five different classes of cattle divided into low, medium and high RFI groups, as well as phenotypic correlations among them. The second manuscript focused on assessing temperament in previously acclimated yearling beef bulls using a subjective CS, an objective EV and FD, and LD. The primary objective was to relate the outcomes of the temperament techniques and FB traits to RFI to assess potential to predict RFI ranking.

6.1 Relationship between temperament, feeding behaviour and RFI ranking

In western Canada, feed costs account for 55-80% of the total costs on a beef cow-calf production operation (Lamb and Maddock, 2009; Arthur et al., 2004; Basarab et al., 2002). Selecting for feed efficient cattle has coveted growing interest and become paramount in the beef industry due to the increase in feed costs since 2007 (Larson, 2010). It is the current reality that feed costs are one of the challenges facing the beef industry, partly resulting from animal selection objectives that were primarily focused on selecting for outputs (post-weaning gain, carcass characteristics) with little emphasis on selecting for input/output (feed efficient cattle that can produce the same quality end product, but with lower feed consumption). However, selecting for faster growing cattle inadvertently resulted in selecting larger-framed animals that consumed more feed due to greater maintenance requirements. Basarab et al. (2003) comparatively assessed the economic impact of feeding high efficiency steers in relation to the lower efficiency steers with similar gain, and the feed consumption difference equated to a $45.60/head reduction in feed costs over a 120 d finishing period.

Residual feed intake has been recognized as a superior measure of feed efficiency, as it is independent of growth and body size. However, the underlying physiological mechanisms contributing to the variation in RFI are not fully understood, and require further research. A portion of that variation can be attributed to physical activity, including FB and temperament of the animal (Kelly et al., 2010; Richardson and Herd, 2004; Arthur et al., 2001a). Along with the innovation of computerized RFID feeding systems came the capability of individually assess daily feed intake and FB variables on an unlimited number of cattle, increasing number of observations within data sets to provide for robust analysis of individual FB. Historically, feed intake data were obtained from group averages within pens, or on animals penned individually, thereby limiting either the number of animals comprising a data set, or removing the individual FB variation that is not obtainable from pen averaged data (Lancaster et al., 2009; Nkrumah et al., 2007). However, although technology exists to measure individual DMI and calculate RFI, it is a costly investment for many cattle operations. The beef industry would benefit from alternative cost-effective approaches to identify feed efficient cattle. Feeding behaviour traits, in particular FED, FEHD and FEF as determined in our study, have the potential to provide for a better understanding regarding the underlying physiological variation associated with differences in RFI. In Manuscript I, regardless of cattle age, breed, sex, diet type or season, all classes of cattle except replacement heifers differed significantly ($P < 0.05$) in FB traits across RFI groups, with the low RFI cattle investing in fewer trips to the feed bunks, spending less time at the feed bunks and consuming less feed, compared to the high RFI cattle. The reduced time and energy the low RFI cattle invested in acquiring feed may suggest that their physical activity levels are lower due to decreased energy expenditure to acquire the feed, partly contributing to a more efficient animal. Given that this was observed for four of the five cattle classes, it validates the statement by Tolkamp et al. (1998) that FB is not random and is repeatable.

None of the temperament assessments were related to RFI or $\mathrm{RFI}_{\mathrm{fat}}$, and there was a weak to moderate positive phenotypic correlation ($r_{\mathrm{p}} = 0.23$, $P = 0.08$) between FD and FEHD, where the flightier cattle spent more time at the feed bunks. The cattle that spent a larger percentage of the day lying down spent less time at the feed bunks (shorter FED and fewer FEF), suggesting that cattle who spend less energy acquiring feed are able to engage in other behaviours, presumably ruminating while recumbent, as supported by Schirmann et al. (2012) who found that Holsteins that spent less time feeding spent longer periods ruminating (r = -0.34) and lying down. Although our study found no correlation between RFI and the four temperament assessments, it provides assurance that selecting for low RFI cattle will not have a negative impact on temperament.

6.2 Current challenges and limitations to assessing feeding behaviour and temperament in beef cattle

While the poultry and swine industries have made great strides in terms of reducing feed costs and maintaining a high quality end product, the beef industry has developed at a substantially slower pace in selecting for feed efficient cattle that can reduce costs of production associated with feeding (Shike, 2013). These authors suggest that since cattle are uniparous and generally yield one calf per dam each year as opposed to the multiparous swine and poultry species, selecting calves with desirable phenotypic and genetic attributes cannot be accomplished as rapidly as in the swine and poultry sectors. Ideally, the beef industry would progress more rapidly in selection for feed efficient cattle if farms had the capacity and capability of measuring individual intake. High costs of RFI testing equipment such as the GrowSafe feeding system or the Broadbent Calan gates (American Calan, Northwood, NH) pose economic barriers for many beef producers. Without automated feed equipment, feed intake data collection on individual animals becomes laborious and restrictive in terms of animal numbers being tested, since animals need to be penned separately to determine individual feed consumption. Likewise, cattle are social beings, and solitary confinement can alter natural cattle behaviour, thereby potentially impacting true expression of natural FB patterns.

In addition to FB traits, cattle temperament was evaluated for its efficacy at predicting feed efficient cattle via low-cost, easy-to-repeat assessments that can be carried out on-farm. It may be deduced that, given its broad scope, a few confounding scenarios may impact true assessment of temperament: 1) Cattle temperament is highly complex in nature, and it is therefore unlikely that a single assessment technique will embody the true temperament of the animal in relation to the trait(s) of interest. The vast scope of behavioural responses that define temperament deem it challenging to accurately assess by a single test (Nkrumah et al., 2007). For example, with the exception of a moderate phenotypic correlation between CS and EV ($r_p = 0.36$, $P < 0.01$), the temperament assessments in Manuscript II were not correlated, indicating that they may be measuring different aspects of the animal's temperament (Ferguson et al., 2014). Therefore, there may be other assessment criteria that are better indicators of temperament in relation to RFI. Understanding that temperament is not only inherited, but is also influenced by acclimation (Curley et al., 2006) and surrounding environment, assessing temperament using one technique alone may not portray an accurate embodiment of the animal's true disposition. 2) Possible relationships between production traits and cattle temperament require highly repeatable, standardized temperament assessments. For example, this thesis used the popular subjective CS as one method of assessing temperament, where an overall score is assigned based upon a numerical scale, relative to the animal's degree of aversion toward the handler and restraint in the head-gate. Three challenges associated with this technique may include lack of observer observation usually due to over-looking very subtle body language indicative of a stressed animal, a previous negative encounter with the handling facility influencing reactivity, and although more commonly seen in *Bos indicus* cattle as opposed to *Bos taurus* breeds, tonic immobility - a state of immobility in response to a fearful situation (Grandin, 1989) – being misinterpreted for docility and calmness. These challenges impact interpretation of CS within and amongst bodies of research; ambiguity will not yield repeatable and reliable, standardized assessments of temperament and a true evaluation of temperament and its relationship(s) with RFI or other production traits. 3) The six month habituation period in our study provided all bulls with the same handling experiences and exposure to facilities and handlers prior to the start of the temperament trial, acting as a standardization technique to remove any varying previous experiences. However, if animals become too habituated to a particular level of handling prior to the test period, this may suppress any significant behavioural (and possibly physiological) responses to temperament tests (Elzo et al., 2009), thereby diminishing any significance of RFI and $\mathrm{RFI}_{\mathrm{fat}}$ or other measures of efficiency with temperament. Contrarily, Curley et al. (2006) indicate that this may be the ideal time to assess temperament, because it can be reasoned that those cattle who express aversion toward tests after habituation to positive handling and human encounters are more reactive due to their innate capacity to cope with handling or stress, thereby providing a true assessment of temperament. Contradicting results in the literature warrant further investigation.

6.3 Direction of future research

Previously, measuring RFI required a 76 d feeding period. In the last several years, the RFI feeding period has been shortened to 63 d (Wang et al., 2006) and 40-55 d (Manafiazar et al., 2015). If FB traits can be incorporated into the RFI calculation, there may be potential to shorten the feeding period even further, thus reducing time and associated feed costs required to calculate RFI. The significant phenotypic relationships between RFI and FB traits lends merit to the potential of using FB traits, in combination with daily intake and animal weights, to more readily derive RFI. To the author's knowledge, there is no published literature that examines the time period required to obtain accurate FB trait data. Furthermore, future research efforts should continue a thorough examination of FB traits under a variety of situations, with greater emphasis placed on mature cows fed forage-based diets since this is most lacking in the literature. As new advancements are made in automated feeding technology, having an extensive understanding of FB will provide opportunity to investigate alternative methods of assessing feed efficiency that may be more cost-effective to implement on a larger scale: at the farm level.

Until recently, the majority of RFI research has focused on growing, feedlot-housed cattle in backgrounding or finishing phases prior to slaughter that are receiving high quality energy rations targeted to bring them to a desired slaughter weight. The lack of RFI research on mature beef cows on a lower quality forage-based diet is disconcerting given that 65-85% of the feed is delivered to the mature cow herd (Montano-Bermudez et al., 1990). As evidenced in Manuscript I, the nature of the diet alters FB, with forage-based (longer fibre length) diets resulting in lower

DMI, slower ER and increased FED compared to concentrate-based diets. Feeding strategies, such as feedlot versus rangeland grazing, could affect individual cattle differently in terms of expression of feed efficiency (Manafiazar et al., 2015). As these authors indicate, expecting that the same RFI outcomes obtained in the feedlot will prevail in cattle on pasture that experience different environmental pressures cannot be assumed; RFI research needs to examine how repeatable RFI ranking and FB characteristics are in environments beyond the dry lot. Given that grazing cattle on land constitutes the bulk of feeding strategies in beef cow-calf operations, whether that be pasture grazing, bale grazing or swath grazing, the question worthy of addressing is if those cattle who are superior in feed efficiency in a feedlot setting will perform similarly in a rangeland grazing setting.

7. CONCLUDING STATEMENTS AND RECOMMENDATIONS

From this study, it can be concluded that:

- Low RFI replacement heifers consumed 10.2% less DMI ($P < 0.05$) compared to the high RFI group.
- Low RFI_{fat} replacement heifers consumed 8.1% less DMI ($P < 0.0001$) compared to the high RFI_{fat} group.
- Low RFI cows had 37.7% shorter FED ($P < 0.05$), 34.6% fewer FEF ($P < 0.01$), 49.9% shorter FEHD ($P < 0.05$), 30.8% slower ER ($P < 0.05$), and consumed 22.9% less DMI ($P < 0.01$) compared to the high RFI cows.
- Low RFI_{fat} cows had 29.9% fewer FEF ($P < 0.01$) and consumed 13.8% less feed ($P < 0.05$) than high RFI_{fat} ranked cows.
- Low RFI feeder heifers had 30% shorter FED ($P < 0.0001$), 17.7% fewer FEF ($P < 0.01$), 34.9% shorter FEHD ($P < 0.0001$), 17% faster ER ($P < 0.01$) and consumed 13.6% less DMI ($P < 0.0001$) compared to high RFI feeder heifers.
- Low RFI_{fat} feeder heifers had 20% shorter FED ($P < 0.0001$), 17.2% fewer FEF ($P < 0.0001$), 26.2% shorter FEHD ($P < 0.0001$), 8% faster ER ($P < 0.01$) and consumed 11.4% less DMI ($P < 0.0001$) compared to high RFI_{fat} heifers.
- Low RFI feeder steers had 18.4% shorter daily FED ($P < 0.0001$), 18.1% fewer FEF ($P < 0.01$), 20.7% shorter FEHD ($P < 0.01$) and 16.2% less DMI ($P < 0.0001$) compared to high RFI steers, respectively.
- Low RFI_{fat} feeder steers had 7.6% shorter daily FED ($P < 0.01$), 13.2% fewer FEF ($P < 0.01$), 9.7% shorter FEHD ($P < 0.05$) and 11.8% less DMI ($P < 0.0001$) compared to the high RFI steers.

    - Low RFI bulls had shorter FED by 10.4% ($P < 0.01$), 22.1% fewer FEF ($P < 0.0001$), 32.4% shorter FEHD ($P < 0.0001$), and consumed 13.2% less DMI ($P < 0.0001$) when compared to the high RFI bulls.
    - Low $\mathrm{RFI}_{\mathrm{fat}}$ bulls had 9.8% shorter FED ($P < 0.05$), 20.1% fewer FEF ($P < 0.0001$), 32.6% shorter FEHD ($P < 0.0001$), consumed 11.5% less DMI ($P < 0.0001$), and had FEL longer by 6.3% longer ($P < 0.05$) when compared to the high $\mathrm{RFI}_{\mathrm{fat}}$ bulls.
- Feeding behaviour traits are phenotypically correlated with RFI and $\mathrm{RFI}_{\mathrm{fat}}$, and with one another, indicating potential that selecting for one FB trait may lead to favorable selection for other desirable traits:
    - Replacement heifers:
        - Residual feed intake and $\mathrm{RFI}_{\mathrm{fat}}$ were significantly and positively correlated with FED, FEHD and DMI (0.23 to 0.36, $P < 0.01$). While RFI was weakly and positively correlated with FEL (0.18, $P < 0.05$), $\mathrm{RFI}_{\mathrm{fat}}$ only tended to be positively correlated with FEL (0.13, $P = 0.09$).
        - Feeding event duration was positively correlated with FEHD, FEL and DMI (0.29 to 0.64, $P < 0.01$), and negatively correlated with ER (-0.54, $P < 0.0001$). Feeding event frequency was positively correlated with FEHD (0.19, $P < 0.05$), and was negatively correlated with FEL and DMI (-0.20 to -0.81, $P < 0.05$). Feeding event head-down time was positively correlated with FEL and DMI (0.17 to 0.36, $P < 0.05$), and was negatively correlated with ER (-0.19, $P < 0.05$). Dry matter intake was positively correlated with ER (0.64, $P < 0.0001$).

- Mature cows:
    - Residual feed intake and RFI_{fat} were significantly and positively correlated with FED, FEF, FEHD and DMI (0.38 to 0.62, $P < 0.01$), and negatively correlated with ER (-0.25, $P < 0.05$).
    - Feeding event duration was positively correlated with FEF FEHD, FEL and DMI (0.32 to 0.93, $P < 0.01$) and negatively correlated with ER (-0.86, $P < 0.0001$). Feeding event frequency was positively correlated with FEHD and DMI (0.36 and 0.40, $P < 0.01$) and negatively correlated with FEL and ER (-0.28 and - 0.29, $P < 0.05$). Feeding event head-down time was positively correlated with FEL and DMI (0.69, $P < 0.0001$) and negatively correlated with ER (-0.79, $P < 0.0001$). Dry matter intake was negatively correlated with ER (-0.50, $P < 0.0001$).
    - Under *ad libitum* conditions, as ER increased, DMI also increased. Under restricted feed access, as DMI increased, ER decreased.
- Feeder heifers:
    - Residual feed intake and RFI_{fat} were significantly and positively correlated with FED, FEF, FEHD, DMI (0.27 to 0.48, $P < 0.0001$), and negatively correlated with ER (-0.19 and -0.21, $P < 0.01$).
    - Feeding event duration was positively correlated with FEF, FEHD, FEL and DMI (0.16 to 0.87, $P < 0.05$), and negatively correlated with ER (-0.68, $P < 0.0001$). Feeding event frequency was negatively correlated with DMI, FEL and ER (-0.24 to -0.65, $P < 0.01$). Feeding event head-down time was positively correlated with FEL (0.18, $P < 0.01$) and negatively

    correlated with ER (-0.65, $P < 0.0001$). Feeding event length was positively correlated with DMI and ER (0.18 and 0.38, $P < 0.01$). Dry matter intake was positively correlated with ER (0.56, $P < 0.0001$).

- Feeder steers:
    - Residual feed intake and RFI_{fat} were significantly and positively correlated with FED, FEF, FEHD and DMI (0.25 to 0.31, $P < 0.0001$).
    - Feeding event duration was positively correlated with FEF, FEHD, FEL and DMI (0.32 to 0.77, $P < 0.0001$), and negatively correlated with ER (-0.53, $P < 0.0001$). Feeding event frequency was positively correlated with FEHD (0.41, $P < 0.0001$) and was negatively correlated with DMI, FEL and ER (-0.36 to -0.71, $P < 0.0001$). Feeding event head-down time was negatively correlated with ER (-0.66, $P < 0.0001$). Feeding event length was positively correlated with DMI and ER (0.26 and 0.60, $P < 0.0001$). Dry matter intake was positively correlated with ER (0.61, $P < 0.0001$).
- Yearling bulls:
    - Residual feed intake and RFI_{fat}, were significantly and positively correlated with FED, FEF, FEHD and DMI (0.23 to 0.48, $P < 0.05$).
    - Feeding event duration was positively correlated with FEF and FEHD (0.46 and 0.60, $P < 0.0001$), and was negatively correlated with ER and DMI (-0.26 and -0.83, $P < 0.01$). Feeding frequency was negatively correlated with FEL, ER and DMI (-0.47 to -0.84, $P < 0.0001$). Dry matter intake was positively correlated with ER (0.70, $P < 0.0001$). Feeding event head-down time was negatively correlated with ER (-0.41,

    $P < 0.0001$). Feeding event length was positively correlated with ER and DMI (0.23 and 0.46, $P < 0.01$).

- Diet type will influence FB:
    - The bulls on the forage-based diet treatment had longer FED by 15.9% ($P < 0.0001$), 15.4% slower ER ($P < 0.0001$), consumed 16% less DMI ($P < 0.0001$) and tended to have a 13.5% increase in FEF ($P = 0.07$) compared to the grain-based diet treatment.
- There was no observed difference in temperament ($P > 0.1$) among high and low RFI and $\mathrm{RFI}_{\mathrm{fat}}$ cattle when assessed using the CS, EV and FD techniques, suggesting that selection for feed efficient cattle will not result in selection for, or against, a specific temperament in relation to human handling.
- Diet type influenced LD in the pen, with the bulls fed the grain-based diet spending less time acquiring feed and spending a larger percentage of the day recumbent (37.89 ± 0.68 %/d) compared to the bulls on the forage-based diet (35.24 ± 0.68 %/d).
- Chute score and EV were phenotypically correlated (0.36, $P < 0.01$), indicating that those cattle who are more resistant to head gate restraint are more inclined to flee the handling facility upon release. However, there are about 87% of animals that do not follow this general assumption, indicating much need for further refinement of temperament traits.
- There were no significant phenotypic correlations between temperament traits and FB traits, but those bulls who spent longer periods of the day recumbent in the pen tended to spent less time acquiring feed, with decreased FED (-0.26, $P = 0.08$) and decreased FEF (-0.25, $P = 0.09$).

From this study, it can be recommended that:

- Given the cow-calf sector constitutes 70% of the Canadian beef industry and the cows are often grazed and fed poorer quality forages, feed efficiency (RFI) research should direct greater emphasis onto examining FB and RFI in mature cows fed a comparable forage diet in a dry lot setting, and cows in a grazing scenario.
- Further assessment of cattle temperament is warranted to better understand the complexity of the behavioural and physiological responses toward differing external stimuli that may be perceived as stressful.
    - Until a standardized and easily repeatable assessment of temperament is established, the beef industry will continue to experience a large variation in cattle temperament, and likewise, a compromised understanding of the potential relationships between temperament and feed efficiency.

8. REFERENCES

Allen, M. S. 2000. Effects of diet on short-term regulation of feed intake by lactating dairy cattle. J. Dairy Sci. 83: 1598-1624.

Archer, J. A., Arthur, P. F., Herd, R. M., Richardson, E. C. and Burton, D. A. 1999a. Potential for reducing the length of net feed intake test by weighing cattle more frequently. Proc. 13th Conf. Assoc. Advmt. Anim. Breed. Genet., Mandurah, Australia. 247-249.

Arthur, P. F., Archer, J. A. and Herd, R. M. 2004. Feed intake and efficiency in beef cattle: Overview of recent Australian research and challenges for the future. Aust. J. Exp. Agric. 44: 361-369.

Arthur, P. F., Archer, J. A., Herd, R. M. and Melville, G. J. 2001a. Response to selection for net feed intake in beef cattle. Proc. 14th Conf. Assoc. Advancement Anim. Breed. Genet., Queenstown, New Zealand. 135-138.

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

Arthur, P. F., Herd, R. M., Wright, J., Xu, G., Dibley, K., and Richardson, E. C. 1996. Net feed conversion efficiency and its relationship with other traits in beef cattle. Proc. Aust. Soc. Anim. Prod. 21: 107-110.

Bailey, J. C., Tedeschi, L. O., Mendes, E. D. M., Sawyer, J. E. and Carstens, G. E. 2012. Evaluation of bimodal distribution models to determine meal criterion in heifers fed a high-grain diet. J. Anim. Sci. 90:2750-2753.

Bailey, J. C., Carstens, G. E., Tedeschi, L. O. and Sawyer, J. E. 2011. Thesis. Feed intake and feeding behaviour associations with performance and feed efficiency of feedlot cattle fed a corn-based diet. Office of Graduate Studies, Texas A & M University.

Basarab, J. A., Beauchemin, K. A., Baron, V. S., Ominski, K. H., Guan, L. L., Miller, S. P. and Crowley, J. J. 2013. Reducing GHG emissions through genetic improvement for feed efficiency: effects on economically important traits and enteric methane production. Animal. Suppl 2: 303-315.

Basarab, J. A., Colazo, M. G., Ambrose, D. J., Novak, S., McCartney, D. and Baron, V. S. 2011. Residual feed intake adjusted for back fat thickness and feeding frequency is independent of fertility in beef heifers. Can. J. Anim. Sci. 91: 573-584.

Basarab, J.A., Colazo, M.G., Ambrose, D.J., Novak, S., Robertson, K., McCartney, D. and Baron, V. 2008. Relationship between residual feed intake and age at puberty and pregnancy rate in replacement heifers. Alberta Bovine Genomics Program meetings, May 3-6, Banff, AB, Canada, Abstr. A-03.

Basarab, J. A., McCartney, D., Okine, E. K. and Baron, V. S. 2007. Relationships between progeny residual feed intake and dam productivity traits. Can. J. Anim. Sci. 87: 489-502.

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

Basarab, J. A., Price, M. A. and Okine, E. K. 2002. Commercialization of net feed efficiency. Memo. Western Forage Group, Alberta Agric. Food and Rural Development Ctr. Lacombe, Alberta, Canada: p. 12.

Basarab, J. A., Milligan, D. N., Okine, E. K. and Hand, R. 2000. Early detection of low growth performance in feedlot steers using feeding and watering behaviours. Technical report. Alberta Agriculture, Food and Rural Development, Lacombe Research Centre, Lacombe, Alberta, Canada.

Basarab, J. A. and Ominski, K. 2014. Beef Cattle Research Council (BCRC): Using Residual Feed Intake to Improve Lifetime Productivity of Beef Cows in Forage-Based Beef Cattle Production Systems. Website. http://www.beefresearch.ca/factsheet.cfm/feed-efficiency-on-pasture-216.

Beef Cattle Research Council (BCRC). 2017. Beef cattle research council – genetic improvements in feed efficiency. http://www.beefresearch.ca/research-topic.cfm/genetic-improvements-in-feed-efficiency-57?language=&print.

Bellows, R. A. and Short, R. E. 1994. Reproductive Losses in the Beef Industry. In: Fields, M. J. and Sand, R. S., (Eds.), Factors Affecting Calf Crop, 109-134. CRC Press LLC, Boca Raton, FL, United States.

Bishop, S. C. 1992. Phenotypic and genetic variation in body weight, food intake and energy utilization in Hereford cattle II. Effects of age and length of performance test. Livest. Prod. Sci. 30: 19-31.

Black, T. E., Bischoff, K. M., Mercadante, V. R. G., Marquezini, G. H. L., DiLorenzo, N., Chase, Jr., C. C., Coleman, S. W., Maddock, T. D. and Lamb, G. C. 2013. Relationships among performance, residual feed intake, and temperament assessed in growing beef heifers and subsequently as 3-year-old, lactating beef cows. J. Anim. Sci. 01: 2254-2263.

Boadi, D., Witternberg, K. and McCaughey, W. 2002. Effects of grain supplementation on methane production of grazing steers using the sulphur (SF_6) tracer gas technique. Can. J. Anim. Sci. 82: 151-157.

Boivin, X., Le Neindre, P., Garel, J. P and Chupin, J. M. 1994. Influence of breed and rearing management on cattle reactions during human handling. Appl. Anim. Behav. Sci. 39: 115-122.

Brinks, J. S. 1995. Genetic studies of reproduction in beef cattle in the U.S.A. Proc. Aust. Assoc. Anim. Breed. Genet. 11: 329-340.

Britton, R. A. and Stock, R. A. 1987. Acidosis, rate of starch digestion and intake. Okla. Agric. Exp. Sta. Res. Rep. MP-121: 125-137.

Burdick, N. C., Carroll, J. A., Randel, R. D., Willard, S. T., Vann, R. C., Chase Jr., C. C., Lawhon, S. D., Hulbert, L. E., and Welsh Jr., T. H. 2011. Influence of temperament and transportation on physiological and endocrinological parameters in bulls. Livestock Sci. Doi10.1016/j.livesci.2011.01.013.

Burdick, N. C., Carroll, J. A., Hulbert, L. E., Dailey, J. W., Willard, S. T., Vann, R. C., Welsh, Jr., T. H. and Randel, R. D. 2010. Relationships between temperament and transportation with rectal temperature and serum concentrations of cortisol and epinephrine in bulls. Livestock Sci. 239: 166-172.

Burdick, N. C., Banta, J. P., Neuendorff, D. A., White, J. C., Vann, R. C., Laurenz, J. C., Welsh Jr., T. H. and Randel, R. D. 2009. Interrelationships among growth, endocrine, immune, and temperament variables in neonatal Brahman calves. J. Anim. Sci. 87: 3202-3210.

Burrow, H. M. and Dillon, R. D. 1997. Relationships between temperament and growth in a feedlot and commercial carcass traits of *Bos indicus* crossbreds. Aust. J. Exp. Agric. 37: 407-411.

Burrow, H. M., Seifert, G. W. and Corbet, N. J. 1988. A new technique for measuring temperament in cattle. Proc. Austr. Soc. Anim. Prod. 17: 154-157.

Byerly, T. C. 1941. Feed and other costs of producing market eggs. Bull. A1. Maryland Agriculture Experimental Station, Univ. Maryland, College Park, MD.

Cafe, L. M., Robinson, D. L., Ferguson, D. M., McIntyre, B. L., Geesink, G. H. and Greenwood, P. L. 2011. Cattle temperament: Persistence of assessments and associations with productivity, efficiency, carcass and meat quality traits. J. Anim. Sci. 89: 1452-1465.

Carberry, C. A., Kenny, D. A., Han, S., McCabe, M. S. and Water, S. M. 2012. Effect of phenotypic residual feed intake and dietary forage content on the rumen microbial community of beef cattle. Appl. Environ. Microbio. 78: 4949-4958.

Carstens, G. E. and Tedeschi, L. O. 2006. Defining feed efficiency in beef cattle. Proceedings of the Beef Improvement Federation 38th Annual Research Symposium and Annual Meeting, April 18-21, Choctow, MS, USA, 12-21 pp.

Chen, L., Mao, F., Crews, D. H., Vinsky, M., and Li, C. 2014. Phenotypic and genetic relationships of feeding behaviour with feed intake, growth performance, feed efficiency, and carcass merit traits in Angus and Charolais steers. J. Anim. Sci. 92: 974-983.

Cooke, R. F., Bohnert, D. W., Cappellozza, B. I., Mueller, C. J. and Delcurto, T. 2012. Effects of temperament and acclimation to handling on reproductive performance of *Bos Taurus* beef females. J. Anim. Sci. 90: 3547-3555.

Cooke, R. F., Bohnert, D. W., Meneghetti, M., Losi, T. C. and Vasconcelos, J. L. M. 2011. Effects of temperament on pregnancy rates to fixed-time AI in *Bos indicus* beef cows. Livest. Sci. 142: 108-113.

Crews, Jr., D. H. 2005. Genetics of efficient feed utilization and national cattle evaluation: A review. Genet. Mol. Res. 4:152-165.

Crowley, J. J., McGee, M., Kenny, D. A., Crews, D. H. Jr., Evans, R. D. and Berry, D. P. 2010. Phenotypic and genetic parameters for different measures of feed efficiency in different breeds of Irish performance-tested beef bulls. J. Anim. Sci. 88:885-894.

Culbertson, M. M., Speidel, S. E., Peel, R. K., Cockrum, R. R., Thomas, M. G. and Enns, R. M. 2015. Optimum measurement period for evaluating feed intake traits in beef cattle. J. Anim. Sci. 93 (5): 2482-2487.

Curley Jr., K. O., Paschal, J. C., Welsh, Jr., T. H. and Randel, R. D. 2006. Technical note: Exit velocity as a measure of cattle temperament is repeatable and associated with serum concentration of cortisol in Brahman bulls. J. Anim. Sci. 84: 3100-3103.

de Haer, L. C. M., Luiting, P and Aarts, H. L. M. 1993. Relations among individual (residual) feed intake, growth performance and feed intake pattern of growing pigs in group housing. Liv-est. Prod. Sci. 36: 233-253.

de Haer, L. C. M. and Merks, J. W. M. 1992. Patterns of daily food intake in growing pigs. Anim. Prod. Sci. 54: 95-104.

DeVries, T. J. and von Keyserlingk, M A. G. 2005. Time of feed delivery affects the feeding and lying patterns of dairy cows. J. Dairy Sci. 88:625-631.

Durunna, O. N., Mujibi, F. D.N., Goonewardene, L., Okine, E. K., Basarab J. A., Wang, Z. and Moore, S. S. 2011. Feed efficiency differences and re-ranking exist in beef steers fed grower and finisher diets. J. Anim. Sci. 89: 158-167.

Elzo, M. A., Riley, D. G., Hansen, G. R., Johnson, D. D., Myer, R. O., Coleman, S. W., Chase, C. C., Wasdin, J. G. and Driver, J. D. 2009. Effect of breed composition on phenotypic residual feed intake and growth in Angus, Brahman, and Angus x Brahman crossbred cattle. J. Anim. Sci. 87: 3877-3886.

Ferguson, D. M., Johnston, D., Burrow, H. A. and Reverter, A. 2014. Relationships between temperament, feedlot performance and beef quality. Australian Beef – the Leader Conference. 161-165.

Fernando, S. C., Purvis II, H. T., Najar, F. Z., Sukharnikov, L. O., Krehbiel, C. R., Nagaraja, T. G., Roe, B. A. and DeSilva, U. 2010. Rumen microbial population dynamics during adaptation to a high-grain diet. Appl. Environ. Microbio. 76: 7482-7490.

Ferrell, T. C. and Jenkins, T. G. 1998. Body composition and energy utilization by steers of diverse genotypes fed a high-concentrate diet during the finishing period. 1. Angus, Belgian Blue, Hereford, and Piedmontese sires. J. Anim. Sci. 76: 637-646.

Fitzsimons, C., Kenny, D. A., Fahey, A. G. and McGee, M. 2014. Feeding behaviour, ruminal fermentation, and performance of pregnant beef cows differing in phenotypic residual feed intake offered grass silage. J. Anim. Sci. 92(5): 2170-2181.

Forbes, J. M. 1985. The importance of meals in the regulation of food intake. Proc. Nutr. Soc. Aust. Vol. 10: 14-24. Proceedings of the Nutrition Society of Australia Tenth Annual Conference, Blacktown, Australia.

Fordyce, G., Dodt, R. M. and Wythes, J. R. 1988. Cattle temperaments in extensive beef herds in northern Queensland. 1. Factors affecting temperament. Austr. J. Exp. Agric. 28: 683-687.

Fordyce, G., Goddard, M. E., Tyler, R., Williams, G. and Toleman, M. A. 1985. Temperament and bruising of *Bos indicus* cross cattle, Austr. J. Exp. Agric. 25: 283-288.

Fox, D. G., Tedeschi, L. O. and Guiroy, P. J. 2001. Determining feed intake and feed efficiency of individual cattle fed in groups. Proceedings of the 2001 Beef Improvement Federation Meeting, San Antonio, TX.

Francisco, C. L., Cooke, R. F., Marques, R. S., Mills, R. R. and Bohnert, D. W. 2012. Effects of temperament and acclimation to handling on feedlot performance of *Bos taurus* feeder cattle originated from a rangeland-based cow-calf system. J. Anim. Sci. 90: 5067-5077.

Gaspers, J. J., Stokka, G. L., Swanson, K. C. and Young, J. M. 2014. Relationships between animal temperament and growth performance, feeding behaviour, and carcass characteristics in feedlot steers. North Dakota Beef Report, Animal Sciences Department, NDSU. Pp 13-15.

Gibb, D. J., McAllister, T. A., Huisma, C. and Wiedmeir, R. D. 1998. Bunk attendance of feedlot cattle monitored with radio frequency technology. Can. J. Anim. Sci. 78: 707-710.

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

Grandin, T. 2003. Transferring results of behavioural research to industry to improve animal welfare on the farm, ranch, and the slaughter plant. Appl. Anim. Behav. Sci. 81: 214-228.

Grandin, T. 1993. Behavioural agitation during handling of cattle is persistent over time. Appl. Anim. Behav. Sci. 36: 1-9.

Grandin, T. 1989. Pages 1-11 in Behavioral Principles of Livestock Handling. American Registry of Professional Animal Scientists. Colorado State University, Fort Collins, Colorado.

Hahn, G. L. 1995. Environmental influences on feed intake and performance of feedlot cattle. Pages 207-225 in Proc. Intake in Feedlot Cattle, Stillwater, OK. Oklahoma Agric. Exp. Sta., Stillwater.

Haley, D. B., Rushen, J. and de Passille, A. M. 2000. Behavioural indicators of cow comfort: activity and resting behaviour of dairy cows in two types of housing. Can. J. Anim. Sci. 80: 257-263.

Henken, A. M., W. van der Hel, H. A. Brandsma, and M. W. A. Verstegen. 1991. Differences in energy metabolism and protein retention of limit-fed growing pigs of several breeds. J. Anim. Sci. 69:1443–1453.

Hennessy, D. W., and Arthur, P. F. 2004. The effect of preweaning restriction on the feed intake and efficiency of cattle on a grain-based diet before slaughter. Aust. J. of Exp. Agric. 44:483-488.

Herd, R. M. 2009. Residual feed intake. Resource Allocation Theory Applied to Farm Animal

Production. CAB International. ed. W. M. Rauw.

Herd, R. M., Oddy, V. H. and Richardson, E. C. 2004. Biological Basis for Variation in Residual Feed Intake in Beef Cattle. 1. Review of potential mechanisms. Australian J. of Exp. Agric. 44: 423-430.

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

Herd, R. M. and Bishop, S. C. 2000. Genetic variation in residual feed intake and its association with other production traits in British Hereford cattle. Livest. Prod. Sci. 63: 111-110.

Hurnik, J. F., Webster, A. B. and Siegel, P. B. 1995. Dictionary of farm animal behaviour. 2nd ed. Iowa State University Press, Ames, IA. Pp. 183-184.

Ito, K., Weary, D. M. and von Keyserlingk, M. A. G. 2009. Lying behavior: assessing within- and between- herd variation in free-stall-housed dairy cows. J. Dairy Sci. 92: 4412-4420.

Kelly, A. K., McGee, M., Crews, D. H. Jr., Sweeney, T., Boland, T. M. and Kenny, D. A. 2010. Repeatability of feed efficiency, carcass ultrasound, feeding behaviour, and blood metabolic variables in finishing heifers divergently selected for residual feed intake. J. Anim. Sci. 88: 3214-3225.

Keys, J. E., Person, R. E. and Thompson, P. D. 1978. Effect of bunk stocking density on weight gains and feeding behaviour of yearling Holstein heifers. J. Dairy Sci. 61: 448-454.

Kilgour, R. J., Melville, G. J. and Greenwood, P. L. 2006. Individual differences in the reaction of beef cattle to situations involving social isolation, close proximity of humans, restraint and novelty. Appl. Anim. Behav. Sci. 99: 21-40.

Knott, S. A., Leury, B. J., Cummins, J. J. and Dunshea, F. R. (2005). An adrenocorticotropin hormone (ACTH) induced stress challenge can be used to identify rams, which are different in net feed intake and feed conversion efficiency. Adv. Anim. Nutr. 15: 12A.

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

Lamb, C. G. and Maddock, T. 2009. Feed efficiency in cows. Cash, Cows, and Calves. 35-42.

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

Lancaster, P. A., Schilling, B. R., Carstens, G. E., Brown, E. G., Craig, T. M. and Lunt, D. K. 2005. Correlations between residual feed intake and carcass traits in finishing steers administered different anthelmintic treatments. J. Anim. Sci. 83(Suppl. 1): 263. (Abstr.).

Larson, K. 2010. 2008 Saskatchewan cow/calf cost of production analysis. http://www.wbdc.sk.ca/pdfs/fact_sheets/2010/2008_SK_Cow_Calf_COP_%20Analysis.pdf.

Le Neindre, P., Trillat, G., Sapa, J., Menissier, F., Bonnet, J. N. and Chupin, J. M. 1995. Individual differences in docility in Limousin cattle. J. Anim. Sci. 73: 2249-2253.

Llonch, P., Somarriba, M., Duthie, C-A., Haskell, M. J., Rooke, J. A., Troy, S., Roehe, R. and Turner, S. P. 2016. Association of temperament and acute stress responsiveness with productivity, feed efficiency, and methane emissions in beef cattle: an observational study. Front Vet Sci. 3: 43.

Lunstra, D. D., Ford, J. J. and Echternkamp, S. E. 1978. Puberty in beef bulls: hormone concentrations, growth, testicular development, sperm production and sexual aggressiveness in bulls of different breeds. J. Anim. Sci. 46: 1054-1062.

Luiting, P. J., Schrama, W., Van der Hel, W. and Urff, E. M. 1991. Metabolic differences between white leghorns selected for high and low residual food consumption .Br. Poult. Sci. 32: 763-782.

Lyons, D. M. 1989. Individual differences in temperament of dairy goats and the inhibition of milk ejection. Appl. Anim. Behav. Sci. 22: 269-282.

MacKay, J. R., Turner, S. P., Hyslop, J., Deag, J. M. and Haskell, M. J. 2013. Short-term temperament tests in beef cattle relate to long-term measures of behavior recorded in the home pen. J. Anim. Sci: 10: 4917-4924.

Manafiazar, G., Basarab, J. A., Baron, V. S., McKeown, L., Doce, R. R., Swift, M., Undi, M., Wittenberg, K. and Ominski, K. 2015. Effect of post-weaning residual feed intake classification on grazed grass intake and performance in pregnant beef heifers. Can. J. Anim. Sci. 95(3): 369-381.

Manitoba Agriculture, Food and Rural Development (MAFRD). 2017. Guidelines for estimating beef cow-calf production costs. Pp 2.

McGee, M., Ramirez, J. A., Carstens, G. E., Price, W. J., Hall, J. B. and Hill, R. A. 2014. Relationships of feeding behaviors with efficiency in RFI-divergent Japanese Black cattle. J. Anim. Sci. 92: 3580-3590.

McKinnon, John. 2015. A Colorado low you say – only in Manitoba: understanding heat stress in beef cattle and the ‘thermal neutral zone’. Canadian Cattlemen 2015.

Montano-Bermudez, M., Nielson, M. K. and Deutscher, G. H. 1990. Energy requirements for maintenance of crossbred beef cattle with different genetic potential for milk. J. Anim. Sci. 68: 2279-2288.

Mousel, M. R. (1998). Daily activity and core body temperature of mice selected for high and low heat loss. M. Sc. Thesis. University of Nebraska, Lincoln, Nebraska.

Muller, R. and von Keyserlingk, M. A. G. 2006. Consistency of flight speed and its correlation to productivity and to personality in *Bos taurus* beef cattle. Appl. Anim. Behav. Sci. 99: 193-204.

Nkrumah, J. D., Crews Jr., D. H., Basarab, J. A., Price, M. A., Okine, E. K., Wang, Z., Li, C. and Moore, S. S. 2007. Genetic and phenotypic relationships of feeding behaviour and temperament with performance, feed efficiency, ultrasound, and carcass merit of beef cattle. J. Anim. Sci. 85: 2382-2390.

Nkrumah, J. D., Okine, E. K., Mathison, G. W., Schmid, K., Li, C., Basarab, J. A., Price, M. A., Wang, Z. and Moore, S.S. 2006. Relationships of feedlot feed efficiency, performance, and feeding behavior with metabolic rate, methane production, and energy partitioning in beef cattle. J. Anim. Sci. 84: 145-153.

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

NRC. 2000. Nutrient Requirements of Beef Cattle. 7th ed. Natl. Acad. Press, Washington, DC, USA.

Oddy, V. H. and Herd, R. M. 2001. Potential mechanisms for variation in efficiency of feed utilization in ruminants. Pages 30-34 in Feed Efficiency in Beef Cattle. Proc. Feed Efficiency Workshop. CRC for Cattle and Beef Qual. Univ. New England, Armidale, Australia.

Oddy, V. H., R. M. Herd, M. B. McDonagh, R. Woodgate, C. A. Quinn, and K. Zirkler. 1998. Effect of divergent selection for yearling growth rate on protein metabolism in hind-limb muscle and whole body of Angus cattle. Livest. Prod. Sci. 56:225– 231.

Oddy, V. H., P. A. Speck, H. M. Warren, and P. C. Wynn. 1995. Protein metabolism in lambs from lines divergently selected for weaning weight. J. Agric. Sci. Camb. 124:129–137.

O'Driscoll, K., Boyle, L. and Hanlon, A. 2008. A brief note on the validation of a system for recording lying behaviour in dairy cows. Appl. Anim. Behav. Sci. 111: 195-200.

Patterson, D. J., Wood, S. L. and Randle, R. F. 2002. Procedures that support reproductive management of replacement beef heifers. Proceedings, The Applied Reproductive Strategies in Beef Cattle Workshop, pp 204-227.

Petherick, J. C., Holroyd, R. G., Doogan, V. J. and Venus B. K. 2002. Productivity, carcass and meat quality of lot-fed *Bos indicus* cross steers grouped according to temperament. Austr. J. Exp. Agric. 42: 389-398.

Proudfoot, K. L., Veira, D. M., Weary, D. M and von Keyserlingk, M. A. 2009. Competition at the feed bunk changes the feeding, standing, and social behaviour of transition dairy cows. 92(7): 3116-3123.

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

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

Richardson, E. C., Kilgour, R. J., Archer, J. A. and Herd, R. M. 1999. Pedometers measure differences in activity in bulls selected for high or low net feed efficiency. Proc. Aust. Soc. Study Anim. Behav. 26: 16 (Abstr.).

Richardson, E. C., Herd, R. M., Arthur, P. F., Wright, J., Xu, G., Dibley, K. and Oddy, V. H. 1996. Possible physiological indicators for net feed conversion efficiency in beef cattle. Proceedings for the Australian Society of Animal Production. 21: 103-106.

Robinson, D. L. and Oddy, V. H. 2004. Genetic parameters for feed efficiency, fatness, muscle area and feeding behaviour of feedlot finished beef cattle. Livest. Prod. Sci. 90: 255-270. SAS Institute, Inc. 2005. SAS/STAT user's guide. Version 9 and 9.1. Volumes 1-5. SAS Institute, Inc., Cary, NC.

Rode, L. A., Weakley, D. C. and Satter, L. D. 1985. Effect of forage amount on particle size in diets of lactating dairy cows on site of digestion and microbial protein synthesis. Can. J. Anim. Sci. 65: 101-111.

Rolfe, K. M., Snelling, W. M., Nielsen, M. K., Freetly, H C., Ferrell, C. L. and Jenkins, T. G. 2011. Genetic and phenotypic parameter estimates for feed intake and other traits in growing beef cattle, and opportunities for selection. J. Anim. Sci. 89:3452-3459.

SAS Institute, Inc. 2005. SAS/STAT user's guide. Version 9 and 9.1, Volumes 1-5. SAS Institute, Inc., Cary, NC.

Schillo, K. K., Hall, J. B. and Hileman, S. M. 1992. Effects of nutrition and season on the onset of puberty in the beef heifer. J. Anim. Sci. 70: 3994-4005.

Schirmann, K., Chapinal, N., Weary, D. M., Heuwieser, W. and von Keyserlingk, M. A. 2012. Rumination and its relationship to feeding and lying behaviour in Holstein dairy cows. J. Dairy Sci. 95 (6): 3212-3217.

Schmutz, S. M., Stookey, J. M., Winkelman-Sim, D. C., Waltz, C. S., Plante, Y. and Buchanan, F. C. 2001. A QTL study of cattle behavioural traits in embryo transfer families. J. Hered. 92: 290-292.

Schutt, K. M., Arthur, P. F., and Burrow, H. M. 2009. Brahman and Brahman crossbred cattle grown on pasture and in feedlots in subtropical and temperate Australia. 3. Feed efficiency and feeding behaviour of feedlot-finished animals. Anim. Prod. Sci. 49: 452-460.

Schwartzkopf-Genswein, K. S., Shah, M. A., Church, J. S., Haley, D. B., Janzen, K., Truong, G., Atkins, R. P. and Crowe, T. G. 2012. A comparison of commonly used and novel electronic techniques for evaluating cattle temperament. Can. J. Anim. Sci. 02: 21-31.

Schwartzkopf-Genswein, K. S., Hickman, D. D., Shah, M. A., Krehbiel, C. R., Genswein, B. M. A., Silasi, R., Gibb, D. G., Crews, D. H. and McAllister, T. A. 2011. Relationship between feeding behaviour and performance of feedlot steers fed barley-based diets. J. Anim. Sci. 89: 1180-1192.

Schwartzkopf-Genswein, K. S., Atwood, S. and McAllister, T. A. 2002. Relationship between bunk attendance, intake and performance of steers and heifers on varying feeding regimens. Appl. Anim. Behav. Sci. 76: 179-188.

Sebastian, T., Watts, J. M., Stookey, J. M., Buchanan, F. and Waldner, C. 2011. Temperament in beef cattle: methods of measurement and their relationship to production. Can. J. Anim. Sci. 91: 557-565.

Shabi, Z., Murphy, M. R. and Moallem, U. 2005. Within-day feeding behaviour of lactating dairy cows measured using a real-time control system. J. Dairy Sci. 88: 1848-1854.

Shaffer, K. S., Turk, P., Wagner, W. R. and Felton, E.E. D. (2011). Residual feed intake, body composition, and fertility in yearling beef heifers. J. Anim. Sci. 89: 1028-1034.

Shike, D. W. 2013. Beef Cattle Feed Efficiency in Driftless Region Beef Conference. University of Illinois at Ubana-Champaign.

Snelling, W. M., Cushman, R. A., Fortes, M. R. S., Reverter, A., Bennett, G. L., Keele, J. W. and Kuehn, L. A. 2012. Physiology and endocrinology symposium: how single nucleotide polymorphism chips will advance our knowledge of factors controlling puberty and aid in selecting replacement beef females. J. Anim. Sci. 90: 1152-1165.

Standing Committee on Agriculture. 2000. Feeding Standards for Australian Livestock. Ruminants. Standing Committee on Agriculture. CSIRO Publications, East Melbourne, Australia.

Streeter, M. N., Branine, M., Whitley, E. and McCollum, F. T. 1999. Feeding behaviour of feedlot cattle: Does behavior change with health status, environmental conditions and performance level? Pp 36-47 in Proc. Plains Nutrition Council, San Antonio, TX.

Thompson, S., Schaefer, A., Crow, G., Basarab, J., Colyn, J., Wittenberg, K., Baron, V., Fitzsimmons, C. and Ominski, K. 2013. Predicting residual feed intake in beef bulls by measuring radiated heat loss through infrared thermography. Proceedings of the CSAS-CMSA Joint Annual Meeting, 18-20 June 2013, Banff, Alberta. Canadian Society of Animal Science – Canadian Meat Science Association (Symposium June 18-20).

Tolkamp, B. J., Schwietzer, D. P. N. and Kyriazakis, I. 2000. The biologically relevant unit for the analysis of short-term feeding behaviour of dairy cows. J. Dairy. Sci. 83: 2057-2068.

Tolkamp, B. J., Allcroft, D. J., Austin, E. J., Nielsen, B. L and Kyriazakis, I. I. 1998. Satiety splits feeding behaviour into bouts. J. Theor. Biol. 194(2): 235-250.

Vann, R. C., Loyd, A. N., Burdick, N. C., Carroll, J. A., Welsh, Jr., T. H. and Randel, R. D. 2009. Temperament assessment provides insight into future health and growth performance of beef cattle. Mississippi Agriculture and Forestry Experiment Station-Brown Loam Experiment Station, Mississippi State, Raymond, MS. Pp 75-81.

Van Reenen, C. G., O-Connell, N. E., Van der Werf, J. T. N., Korte, S. M., Hopster, H., Jones, R. B. and Blokhuis, H. J. 2005. Responses of calves to acute s tress: Individual consistency and relations between behavioural and physiological measures. Physiol. Behav. 85: 557-570.

Von Felde, A. 1996. Genetische Analyse der Futteraufnahme-Information von Jungebern aus Gruppenprufung mit automatischen Futterungsanlagen. Ph D thesis no. 90, Christian-

Alberchts University, Kiel, Germany.

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

Webster, A. J. F., Osuji, P. O., White, R. and Ingram, J. F. (1975). The influence of food intake on portal blood flow and heat production in the digestive tract of the sheep. The British J. of Nutrition. 34: 125-139.

West, J. W. 2003. Effects of heat-stress on production in dairy cattle. J. Dairy Sci. 86(6): 2131-2144.

Yeates, M. P., Tolkamp, B. J., Allcroft, D. J., and Kyriazakis, I. 2001. The use of mixed distribution models to determine bout criteria for analysis of animal behaviour. J. Theor. Biol. 213: 413-425.

Young, B. A. 1981. Cold stress as it affects animal production. J. Anim. Sci. 52(1): 154-163.

Young, J. M. and Dekkers, J. C. M. 2012. The genetic and biological basis of residual feed intake as a measure of feed efficiency. J. F. Patience (ed.), *Feed efficiency in swine.* 153-166.

Yunta, C., Guasch, I. and Bach, A. 2012. Short communication: lying behavior of lactating dairy cows is influenced by lameness especially around feeding time. J. Dairy Sci. 95: 6546-6549.