The effect of diet type on residual feed intake and the use of infrared thermography as a method to predict efficiency in beef bulls

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List of Abbreviations

ADG	=	Average daily gain
ATP	=	Adenosine triphosphate
BF	=	Backfat
BW	=	Body weight
CH_4	=	Methane
Ck_{HH}	=	Cheek surface temperature calculated from handheld camera images
Ck_S	=	Cheek surface temperature calculated from stationary camera images
CO_2	=	Carbon dioxide
DM	=	Dry matter
DMI	=	Dry matter intake
EFI	=	Expected feed intake
Ey_{HH}	=	Eye surface temperature calculated from handheld camera images
Ey_S	=	Eye surface temperature calculated from stationary camera images
FCR	=	Feed conversion ratio
HPA	=	Hypothalamic-pituitary-adrenal
IMF	=	Intramuscular fat
IRT	**=**	Infrared thermography
KR	=	Kleiber ratio
LCT	=	Lower critical temperature
ME	=	Metabolizable energy
MEI	=	Metabolizable energy intake
MMWT	=	Metabolic mid-test weight
MWT	=	Mid-test weight
NFE	=	Net feed efficiency
NFI	=	Net feed intake
O_2	=	Oxygen

RE	=	Retained energy
REA	=	Ribeye area
RF	=	Rumpfat
RFI	=	Residual feed intake
RFI_{Fat}	=	Residual feed intake adjusted for backfat thickness
SD	=	Standard deviation
SFI	=	Standardized feed intake
TNZ	=	Thermoneutral zone
UCT	=	Upper critical temperature
WW	=	Weaning weight
YW	=	Yearling weight

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Abstract

Thompson, Sean. M.Sc., The University of Manitoba, 2015. The effect of diet type on residual feed intake and the use of infrared thermography as a method to predict efficiency in beef bulls. Advisors: K. H. Ominski and A. L. Schaefer.

Residual feed intake (RFI) is a recognized measure of biological efficiency in beef cattle. However, RFI determination is expensive, time consuming and not well studied in animals fed forage-based diets. The objectives of this experiment were to investigate infrared thermography (IRT) as method for determining RFI ranking in yearling beef bulls, and to evaluate the effect of diet type on RFI repeatability in consecutive feeding periods. No significant correlations ($P > 0.05$) were observed between eye or cheek surface temperatures measured using handheld or within-pen stationary infrared camera systems with RFI. Reranking was observed for RFI in all diet treatments, however significant repeatability estimates occurred for the forage and grain diet treatments ($r=0.58$ and 0.64 respectively; $P < 0.01$) but not the diet switch treatment ($r=0.24$; $P > 0.05$). Extreme cold temperatures experienced in Western Canada influence IRT measurements and energy partitioning, indicating the need for standardized performance testing procedures.

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, 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.

1.0 General introduction

The performance of beef cattle has traditionally been evaluated using traits that measure total output (i.e. weight gain or lean meat carcass yield) without consideration for inputs such as feed requirements. Costs associated with feed represent more than 50% of the total costs in a cow/calf operation (Manitoba Agriculture Food and Rural Development, 2013), signifying a major component for improvement and potential to increase farm profitability. The feed conversion ratio (FCR) has historically been a useful measure of feed efficiency, however, selection for this ratio trait (Gunsett, 1984) results in heavier mature cattle weights (Koots et al., 1994) which leads to increased feed requirements and therefore is an ineffective method to improve biological efficiency (Archer et al., 1999; Johnson et al., 2003). Residual feed intake (RFI) was first proposed for beef cattle by Koch et al. (1963); expected feed intake (EFI) was calculated by regressing average daily gain (ADG) and metabolic mid-test weight (MMWT) on standardized feed intake (SFI), and the difference of this value from actual feed intake provided a "residual" or RFI value. The initial limitations to adopting this methodology for predicting feed efficiency on a large-scale basis was the inability to accurately measure feed intake in a feedlot setting. Advancements of individual feed intake recording systems, such as GrowSafe® Feeding Systems (GrowSafe Systems Ltd., Airdrie, Alberta), have made accurate feed intake monitoring possible, giving way to use of RFI to estimate efficiency in cattle.

A benefit of RFI over traditional efficiency measures is its ability to assess biological efficiency while maintaining phenotypic independence from most production traits (Arthur et al., 1997; Archer et al., 1999; Basarab et al., 2003). Even so, industry-wide adoption of the RFI concept has been limited, presumably due to cost associated with individual animal feed intake monitoring systems and the time necessary to collect intake and growth data for determination of

RFI. A less expensive, indirect method for determining RFI ranking would benefit the beef industry. Infrared thermography (IRT) has recently shown utility to predict RFI ranking in beef bulls (Montanholi et al., 2009), heifers (Colyn, 2013), cows (Schaefer et al., 2005) and steers (Montanholi et al., 2010).

Body surface temperatures measured through IRT have successfully predicted radiant heat dissipated from homeothermic animals (Cena and Clark, 1973; Turner, 2001; McAfferty, 2007), with radiant heat losses representing lost energy while an animal is within their thermoneutral zone (TNZ). As well, Nkrumah et al. (2006) found that a significant portion of the variation in RFI can be associated with differences in energy partitioning, including but not limited to heat production. As well, thermoregulation has been considered a factor contributing to the underlying variation in RFI, although its contribution has yet to be quantified (Richardson and Herd, 2004; Herd et al., 2004). This indicates the potential relationship between surface temperatures of extremity tissues as measured by IRT and RFI. This methodology has been successfully applied to beef cattle under the assumption that the relative biological efficiency among individuals could be predicted by measuring the radiant heat loss from specific anatomical regions, including the side of the animal (Scott et al., 2002), the dorsal region (Scott et al., 2002; Schaefer et al., 2005), the hind region (Montanholi et al., 2006), the back of the front hooves (Montanholi et al., 2009), the snout (Montanholi et al., 2010), and the eye and cheek regions (Montanholi et al., 2009, 2010; Colyn, 2013).

There are aspects associated with RFI that require further research before widespread adoption in the beef industry can occur. At present, RFI is typically measured during a small portion of the growing phase of a young beef animal's life, similar to most other growth and carcass traits. Performance during this time frame is assumed to be reflective of the animal's

biological efficiency throughout its entire life. However, repeatability estimates of RFI have been variable; moderate to high repeatabilities were reported in beef heifers with evidence of reranking (Kelly et al., 2010) while Durunna et al. (2011) observed that over half of the steers in both the control and feed-swap groups changed RFI by more than 0.5 SD in consecutive feeding periods. Similarly, Durunna et al. (2012) observed 51% of heifers change RFI class when fed the same diet in successive feeding periods. This implies that further research is needed to investigate repeatability of RFI and potential factors that may influence values. One such factor is diet type.

Historically, beef performance evaluations have been conducted with concentrate-based diets and are assumed to reflect animal performance regardless of diet composition. Typically, central test stations have evaluated bull performance, including RFI, when fed high-energy diets. A lack of literature involving bulls fed forage-based diets limits the comparison of feed intake, growth, carcass traits or biological efficiency for bull performance under different regimes. Recent RFI studies with bulls have utilized corn grain as the primary carbohydrate source (Lancaster et al., 2005; Montanholi et al., 2009). This may not be the best methodology for determining performance as bulls, and most often their offspring, spend the rest of their lives in a forage-based feeding system. Assessing the variation in biological efficiency for an individual beef animal receiving a forage-based diet followed by a grain-based diet, or vice versa, would improve our understanding of RFI and the effectiveness of selecting more efficient animals to increase the future profitability in cow-calf operations.

The information from this thesis will provide evidence for the use of IRT as an indirect method for predicting RFI in beef bulls within a Western Canadian feedlot setting. As well, this experiment will present a unique opportunity to evaluate the effect of forage and grain-based

diets containing similar energy densities on the repeatability of RFI. This data may lead to recommendations for standardizing IRT collection methods and animal management guidelines in future studies.

2. Review of literature

2.1 History of feed efficiency measures

Livestock performance has long been characterized by measuring quantitative traits which are deemed economically beneficial (e.g., average daily gain (ADG) and body weight (BW)) at time of weaning (WW) or one year of age (YW)). Advancements in feed intake monitoring systems along with an increased understanding of biological processes has shifted the focus of evaluation from output only to output for given levels of input. Growth traits like the feed conversion ratio (FCR) or the Kleiber ratio (KR) are efficiency measures, albeit simplified measures, which provide an opportunity to examine energy utilization from consumed feed. While these ratios offer an opportunity to measure the biological efficiency of livestock, there are challenges that limit their use as a selection tool. Improvement in our understanding of thermodynamic concepts and our ability to measure individual animal intake has advanced measurement of biological efficiency. A look back at the evolution of our understanding of energy transformation will demonstrate how current biological efficiency measures can be utilized to select animals for improved feed efficiency.

2.1.1 Animal energetics

The partitioning of feed energy has and continues to be an area of interest for scientists in biological studies. Leonardo da Vinci (1452-1519) was one of the first individuals to examine energy utilization by animals. Da Vinci noticed that animals could not survive in an environment that could not support a flame, but it would be over two centuries following this observation before the phenomenon was explained. Similarly, Kleiber (1975) describes the work of Scheele, Priestly, and Lavoisier which helped to develop the concept that life is primarily a combustion process, which could be applied to metabolic processes. Lavoisier and Laplace (1780)

established a fundamental principle in thermochemistry which states that the heat required in the combustion of glucose into carbon dioxide and water is equal to the heat required for the reverse process. Their work also established the first relationship between oxygen use, carbon dioxide production, and heat production, declaring that at least a major source of the heat produced by animals originates from the combustion of organic substances (Kleiber, 1975). New objectives arose as advancements were made in pursuit of knowledge of animal energetics, including establishing relationships between gas exchange and heat production, developing a system of guidelines to evaluate foods which could be related to energy requirements and expenditures, and to investigate the possible causes for energy expenditures (Johnson et al., 2003).

Research by Mayer in the 1840's led to the declaration of the law of conservation of energy (the first law of thermodynamics). The first law of thermodynamics is applied to all chemical reactions and makes possible many of the calculations used in the study of animal nutrition. This law allows us to accept the equation ME=RE + HE, where ME represents metabolizable energy, RE refers to retained energy not lost in feces, urine, or gases, and HE is heat produced by the animal. Historically, considerable efforts were made to quantify the metabolizable energy in feeds and to measure heat production, with very little focus on the retained energy. The influential comparative slaughter technique by Lawes and Gilbert (1861) provided a direct measure of energy retention in cattle, limited only by analytical accuracy and the assumption that both animals being used in the experiment had the same initial heat of combustion (Blaxter, 1967). The comparative slaughter technique showed for the first time that energy from carbohydrates was the primary source for fat synthesis.

Hess's Law, or the law of constant heat sums, states the total amount of heat produced or consumed when a chemical system changes from an initial state to a final state is independent of

the way in which the change is brought about. Through calorimetry testing at the end of the 19th century, Rubner (1894) and Laulanie (1896) confirmed the law of constant heat sums and its application to animal metabolism. The second law of thermodynamics, which states that all forms of energy can quantitatively be converted to heat, along with Hess's Law, form the basis for all measurements made in nutritional energetics (Ferrell and Oltjen, 2008).

Calorimetry experiments intensified in the late 1800's with the use of live animal species as thermochemistry theories became accepted. Consequently, calorimetry trials performed on a variety of species over a wide range of conditions, such as that by Atwater and Benedict (1903), confirmed many of those theories and allowed scientists to form the concept of basal metabolic rate. Indirect calorimetry—measuring the heat production of an animal based on chemical changes—contributed a great deal towards our understanding of animal metabolism. Likewise, measurements of sensible and evaporative heat losses from an animal (direct calorimetry) utilized instrumentation founded on many of the aforementioned principles. Adding this knowledge to established energetic models culminated in the derivation of net energy-based feeding systems by Kellner (1919) and Armsby and Fries (1915), which was further partitioned into net energy for maintenance and net energy for gain by Lofgreen and Garrett (1968).

2.1.2 Current measures of efficiency

2.1.2.1 Relative growth rate

Animal performance is typically determined by measuring total output or production, regardless of input, e.g. body weight, rate of gain, milk production or carcass weight. However, it was also known that many different factors directly affect animal production. The energy density and quality of feed being offered (McCarthy et al., 1985; Helferich et al., 1986), management practices including handling techniques and pen density (Voisinet et al., 1997; Mader and

Colgan, 2007) and the environmental conditions under which an animal is housed, including but not limited to wind speed, temperature, precipitation, and pen conditions (Morrison et al., 1970; Holmes et al., 1978; Mitlöhner et al., 2001), all have the potential to affect animal performance.

Genetic merit also affects animal performance traits. Several studies have estimated the genotypic and phenotypic variances of performance traits in beef cattle (Gregory et al., 1995; Koots et al., 1994; Mohiuddin, 1993). A strong positive relationship exists for both the genotypic and phenotypic variance of ADG, as well as genotypic and phenotypic variance of standard interval weights commonly reported (weaning weight, yearling weight, and mature weight). Most growth traits in beef cattle are moderately heritable (Knapp et al., 1950; Shelby et al., 1955). Historically, the positive genetic correlations found in these growth traits were assumed not to handicap selection for carcass traits and efficiency of gain (Carter and Kincaid 1959).

Average daily gain can be used as a selection criterion which influences the time required to reach a target weight, reducing time on feed and total feed requirements. However, it does not account for daily feed intake nor how efficiently animals are using that feed. Individual variation in metabolic processes between animals (such as protein turnover) make calculating biological efficiency much more complex than simply measuring weight gain as an output from feed intake. A greater understanding of use of feed energy by the animal following consumption, including energy partitioning, is necessary to more accurately characterize biological efficiency.

2.1.2.2 Feed conversion ratio

For many years animal performance was primarily measured by examining output (weight, milk production, carcass weight) for given levels of input (feed intake). “Efficiency in meat animal production is measured by the gain in body weight per unit of feed consumed” (Brody, 1945). Thus, FCR was the most commonly used standard for feed efficiency in beef

cattle. The ratio of feed consumed to body mass gained and its inverse, body mass gain to feed consumption (known as gross feed efficiency), has shown utility for many years. Selecting for low FCR animals was traditionally shown to improve most other growth traits with few if any setbacks (Brelin and Brannang, 1982; Koots et al., 1994b). In fact, reviews by Korver (1988) and Cameron (1998) suggested that selecting for increased production (e.g. growth rate in beef cattle or milk production in dairy cattle) will result in a corresponding improvement in gross efficiency, which eliminates the need for calculating individual animal feed intake to improve FCR. Mrode et al. (1990) observed a line of Hereford cattle where the response in gross efficiency obtained by selecting for increased lean meat yield was greater compared to the direct response of selecting for improved lean conversion ratio. Moderate heritability for gross efficiency (Crews, 2005) also makes it possible to realize genetic improvement in this trait by selecting for low FCR animals.

However, despite favourable heritability and indirect responses to other production traits, FCR has limited value in the beef industry. Koots et al. (1994b) showed high negative correlations between FCR and growth rate/body size. From this we can assume selecting for improved gross efficiency will result in increased growth rate as well as mature cow size. The corresponding increase in mature cow size would be expected to increase the feed requirements for maintaining the breeding female (Barlow, 1984). Along with the increased body size, it has been shown that FCR patterns are largely based on maturity (Salmon et al., 1990). This poses a potential problem where gross efficiency improvements in the growing phase may be offset by increased feed requirements from mature animals; essentially resulting in no change for the production system feed efficiency (Archer et al., 1999). Similarly, FCR is a gross measure of efficiency comparing production to input costs in a ratio which does not separate energy

requirements into those needed towards maintenance and those needed for production. The failure to partition feed requirements may result in breeding females who do not retain the phenotypic expression of that trait for which they were selected (Carstens and Tedeschi, 2006). Given that maintenance functions of the beef cow may account for 70-75% of the total annual energy requirements (Ferrell and Jenkins, 1985), it has been proposed by Montano-Burmudez et al. (1990) that 65-75% of the total energy required in beef production is used by the cow herd. Therefore, approximately 50% of the total energy needed in a beef production system is used to maintain the beef cow.

Gunsett (1984) has suggested that since FCR is a ratio, selecting for improved gross efficiency could result in divergence of its component traits (feed intake or growth rate). This divergence and unpredictable response in the component traits applies only if the genetic variances of these traits are different, which is typically the case. He proposed that a disproportionate selection pressure could be placed on one of the component traits when selecting based on FCR which may not result in an actual improvement of feed efficiency. Although most breeds of cattle have seen genetic improvements in growth rate in the last 20 years, the correlated response in FCR has not been as large (Crews 2005).

Another challenge associated with FCR use is accurately measuring individual animal feed intake, in a cost-effective way (Arthur and Herd, 2008), despite advancements in automatic feed intake recording. Gross efficiency has traditionally been calculated using pen averages to estimate an individual animal's feed consumption. This is not ideal, however, as it results in the loss of individual animal variation which ultimately forms the basis of comparisons between animals and the ability to select superior breeding stock. The ratio of feed intake to growth

known as FCR appears to be simple, however multiple confounding factors make it difficult, if not impossible, to precisely determine the actual feed efficiency of cattle (Johnson et al. 2003).

2.1.2.3 Kleiber ratio

Max Kleiber (1936) described an efficiency trait which measured the rate of gain of an animal compared to its metabolic weight (weight$^{0.75}$) in a ratio (ADG/ weight$^{0.75}$). The Kleiber ratio (KR) was meant to be used as an indirect measure of efficiency. Bergh et al. (1992) suggested that indirect selection based on the KR would result in more rapid genetic improvement of feed efficiency rather than selecting for FCR alone as the heritability for KR (0.52) was much higher than FCR (0.19), while also having a practical advantage over FCR as it does not require the measurement of individual feed intake. However, studies have shown slightly positive (Bergh et al., 1992) and moderately positive (Nkrumah et al., 2004; Mello et al., 2010) correlations with KR and feed intake (FI), signifying increases in FI despite increased efficiency. As well, Nkrumah et al. (2004) suggested two shortcomings with using KR as a feed efficiency measure: 1) KR may not recognize different energy efficiencies between animals, and 2) the phenotypic relationship of KR with animal performance and efficiency may not be any different than reported relationships with FCR. As KR values increase in magnitude, there is a larger dilution of maintenance energy requirements which implies ADG can increase at the same metabolic weight without a corresponding increase in maintenance energy cost (Tedeschi et al., 2006). Lastly, KR fails to account for differences in the fat and protein content of gain. The difference in primary tissue deposition must be considered as larger, faster gaining animals are likely to be leaner at a particular weight, requiring less feed per unit of gain (Tedeschi et al., 2006). This creates the illusion that feed efficiency has increased, when in actual fact using this

selection criteria results in larger-framed animals without necessarily changing growth efficiency (Tedeschi et al., 2006).

2.1.3 Calorimetry

2.1.3.1 Direct Calorimetry

As previously mentioned, early concepts of energy exchange were successfully studied and validated with the use of calorimeters. Direct calorimetry is a way in which the heat loss from an animal can be measured. Although current technology is much more advanced than the systems first employed, the methodology founded by Lavoisier, Atwater, Armsby, and Blaxter still stands today (Johnson et al., 2003). The functionality of direct calorimeters depends on the ability to isolate the heat chamber or box from the outside environment. Any heat gained or lost from the system would ultimately affect the results. Popularity of calorimeters increased at the turn of the 20th century when the first respiration calorimeter large enough to study cattle was built at the Pennsylvania State University by Armsby (1904). Sensible heat transfer from the chamber to or from the environment was minimized by maintaining the same temperature within the triple walls of the calorimeter, effectively eliminating any temperature gradient and possibility for heat exchange (Braman, 1933). The calorimeter used in this example is known as a respiration calorimeter. Sensible heat is trapped in some type of heat sink, such as water, which can then be measured to estimate heat production.

Another type of direct calorimeter is known as the gradient layer calorimeter. A gradient layer calorimeter allowed for the measurement of temperature gradients across thermoelectric heat flow meters. Advantages of this calorimeter were being able to partition sensible heat loss into radiation and convection, as well as its sensitivity to changes in sensible heat loss of the animal (Nienaber et al., 2009). Stewart (1957) was the first to use the gradient level calorimeter

for farm animal experiments while another such calorimeter was built at the Hannah Research Institute in Scotland for large animal trials, described by MacLean and Tobin (1987). However, most of the gradient layer calorimeters are no longer in use today.

More recently, spot calorimeters have been developed to measure temperature and humidity of air over defined areas of a cow. Hillman et al. (2001) constructed a spot calorimeter at Cornell University where sensible and latent heat loss can be deduced from these values. The use of an infrared transducer to measure longwave radiation exchange between the surface and the environment allows a surface temperature to be calculated. Ambient air is pulled through the area of interest by vacuum pumps and a flow rate is established. Relative humidity, ambient air temperature, and atmospheric pressure are used in concert with the air flow rate and surface temperature to predict heat loss from an animal. Direct calorimetry, regardless of the method, has shown utility in farm animal experiments. However, an easier method for predicting heat loss uses heat production measurements from indirect calorimetry.

2.1.3.2 Indirect Calorimetry

Indirect calorimetry relies on the measurement of energy exchange within animal tissues, e.g. metabolism and catabolism. Since stoichiometric relationships provide the amount of energy that is transformed into heat during chemical reactions, measurements of oxygen consumption and carbon dioxide, methane, and waste nitrogen production provide evidence of heat production (Nienaber et al., 2009). Many years of intense research attempted to establish the relationship between gas exchange and heat production. An open circuit respiration apparatus was used by Carl Von Voit to conduct extensive energy balance experiments during the latter half of the 1800's. His students, Armsby, Atwater, Kellner, and Rubner, furthered his research thereafter, as described by Johnson et al. (2003).

The simple closed circuit calorimetry principle originating from Regnault and Reiset (1849) was further developed by Atwater and Benedict (1905), but wasn't applied to large animal experiments until 1954 by Blaxter, Graham, and Rook, as described by MacLean and Tobin (1987). Closed circuit respiration calorimeters were used less extensively for predicting whole animal energy expenditures, particularly for larger animals. Nevertheless, the cumulative work in this field led to the publication of the Brouwer equation (Brouwer, 1965), which found the relationship between heat production (H, kcal) and oxygen consumption (O_2, L), carbon dioxide production (CO_2, L), methane production (CH_4, L), and urinary nitrogen output (N, g). The equation,

$$H=3.866 \times O_2 + 1.200 \times CO_2 - 0.518 \times CH_4 - 1.431 \times N$$

has been the standard equation used for the calculation of heat production under indirect calorimetry methods since it was originally published in 1965.

While many direct (isothermal, heat-sink, convection, and differential) and indirect (confined, open-circuit, closed circuit) calorimetry systems exist (MacLean and Tobin, 1987), the most common and practical method used in cattle trials is the open-circuit indirect calorimetry technique, either whole animal (Young et al., 1975; Johnson, 1986) or ventilation hood/head-box designs (Delfino et al., 1988; Kelly et al., 1994; Nkrumah et al., 2006; Montanholi et al., 2009). Although technology has improved the accuracy of input (O_2) and output (CO_2, CH_4) measurements, the principles for open-circuit calorimetry remain the same. Outside air is circulated through the area surrounding a cow's muzzle as an O_2 supply, and respired air is collected either continuously or periodically for analysis (MacLean and Tobin,

1987). Air flow is calculated from inlet and outlet air sources, and respiratory exchange is determined by the difference in gas concentrations from inspired and expired air.

Regardless of the system, whole animal open-circuit indirect calorimetry is expensive (Johnson, 1986). Fortunately, it is also possible to use output measurements of CO_2 and CH_4, or in some cases, CO_2 measurements alone that are produced through the oxidation of feed energy and translate these quantities into a heat production equivalent (MacLean and Tobin, 1987). This allows utilization of ventilation hoods and head boxes, which are less expensive than whole animal respiration chambers. Unfortunately, regardless of the calorimeter technique sample size is limited due to the time and labour involved with individual animal respiration measurements.

These challenges, coupled with those associated with an accurate measure of individual animal intake needed to measure biological efficiency, have limited progress in determining feed efficiency. It wasn't until such automated feeding technologies were developed that researchers were able to collect individual feed intake with significant accuracy and to compare biological efficiency between several animals at one time.

2.2 Measurement of individual animal feed intake

The race to create an automated system which gathered individual animal intakes began in the 1970's with the Calan Individual Feeding System. This innovative feeding system was initially developed by Broadbent et al. (1970) and made use of head gates which were electronically unlocked by keys that cattle wore around their necks. Unlocking a head gate would allow an animal to push gates open and access feed. Feed intake was recorded and the feed supply was replenished when the remaining feed was thought likely to affect the animals' intake. In 1981, the Pinpointer feeding system (Gonyou and Stricklin, 1981) became another multiple animal feeding system option. The system used individual stalls rather than head gates and

consisted of a feed hopper which supplied the feed and microprocessor which recorded feeding information. Animal were identified by transponders worn around their neck. Feeding time, feed consumed, and feeding duration information was collected by the microprocessor and used to determine daily feed intakes.

While each feeding system had their own advantages and disadvantages, as reviewed by Cole (1994), the main problem associated with both systems was the frequency of electronic malfunctions due to incorrect animal identification and adverse weather effects caused by direct exposure to the elements. To minimize such malfunctions, constant monitoring of the feeding system was required (Cole, 1994) so that problems could be corrected immediately, minimizing data loss. These systems required a 7-21 day adaptation period for animals to adjust to the feeders. As well, group size was also limited because of the relatively low number of animals that each feed bunk could sustain.

The GrowSafe® Feeding System (GrowSafe Systems Ltd., Airdrie, Alberta), which does not require visual surveillance, was established shortly after Cole's review of current group fed systems (1994). The feeding system provides accurate feed intake and feeding behaviour information for individual cattle in large groups (Gibb et al., 1998; Schwartzkopf-Genswein et al., 1999) and is practical for commercial settings as well as large-scale research trials because it utilizes antennas and radio frequency identification (RFID) ear tags to distinguish the different animals present at feed bunks (Schwartzkopf-Genswein et al., 1999). As well, the feed bunks which GrowSafe® uses more closely reflect designs commonly used in feedlots, while allowing animals to eat without being isolated in a stall or head gate. The Insentec feeding system is another feed monitoring system which relies on the same principal of a feed bunk placed on load

cells (Tolkamp et al., 2000; Chapinal et al., 2007) is commercially available with useful applications for cattle housed indoors.

2.3 Residual Feed Intake

2.3.1 Concept and history of residual feed intake

The concept of measuring biological efficiency as residual energy above maintenance and production energy requirements was developed by Titus (1928) for chickens, and applied to beef cattle by Koch et al. (1963). Koch et al. (1963) utilized records from 1324 individually fed bull and heifer calves to determine a suitable measure of feed efficiency. Use of metabolic mid-test weight (MMWT) simultaneously in the regression analysis for feed intake and weight gain served to remove any differences in maintenance requirements when predicting expected feed intake. Residual feed intake (RFI), uses the assumption that feed intake be partitioned into two portions: a portion which goes towards basal energy requirements and production (e.g. growth or milk production), and a residual portion (Koch et al., 1963). In more simple terms, RFI can be defined as the difference between actual feed intake (FI) and expected feed intake (EFI) based on maintenance and production requirements, with a positive or negative residual intake representing a less or more efficient animal, respectively. The residual feed portion gives an indication of true metabolic efficiency (Crews, 2005). Although Koch et al. (1963) deemed the most accurate and heritable measure of efficiency to be that of gain adjusted for differences in feed consumption (deviations from the regression of gain on consumption) they suggested that selecting for weight gain should be just as effective as selecting for feed efficiency, with increases in both feed efficiency and feed consumption. This assumption may have lead subsequent feed efficiency studies to continue using FCR as a measure of biological efficiency instead of RFI (Smith et al., 1976; Brelin and Brannang, 1982; Cundiff et al., 1984) even though

improvements in FCR were eventually later correlated to greater cow size and increased feed requirements, as previously mentioned.

2.3.2 Calculation of RFI

Residual feed intake is typically calculated using phenotypic regression of feed intake on measured traits, as described in experiments by Archer et al. (1997) and Basarab et al. (2003). For accurate measures of feed efficiency, animals should not experience any nutritional restrictions and the same ration should be supplied ad-libitum for the entire feeding period to reflect true intake. Additionally, animals must remain healthy to avoid any variation in feed intake which could bias their daily intake average or relative growth rate. Young growing animals which grow normally should exhibit a linear growth curve which is not influenced by any of the aforementioned negative effects of nutrition or morbidity. Each animal's growth curve is determined by performing a linear regression of weight on time. Weight measurements should be taken at the beginning and end of the feeding period, as well as intermittently during the feeding period. The frequency of measurements will depend on the length of the trial, typically weekly or biweekly (Wang et al. 2006). Average daily gain, initial body weight, mid-test weight (MWT), and final body weight are determined using regression coefficients from each animal's own growth curve. Feed intake is monitored using automated feeding systems, such as the GrowSafe® system, and daily averages can be determined for each animal. Daily feed intake is multiplied by the dry matter percentage to derive a daily dry matter intake, and then multiplied by the metabolizable energy content of the ration. It is divided by 10 to standardize intake to an energy density of 10 MJ ME kg d^{-1} DM. The daily feed intake value is then converted back to an as-fed value for a standardized daily feed intake (SFI). Expected feed intake is estimated by

using ADG and metabolic MWT ($MWT^{0.75}$) to model SFI. The model fitted, using the regression analysis, was:

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

where Y_i= SFI for animal i, β_O= regression intercept, β_1=partial regression coefficient of SFI on average daily gain, β_2=partial regression coefficient of SFI on metabolic mid-test weight, and e_i=the residual error of SFI for the i'th animal. This general model is typically used in most RFI experiments, however when other phenotypic traits measured influence RFI measurement, it may be appropriate to correct for these traits by adding them into the model. Basarab et al. (2007) recommend that RFI be adjusted for backfat (BF) measurements in young, growing cattle to avoid any negative impacts on carcass quality when selecting for efficient cattle. Regardless of the model used in the regression, EFI will be predicted for each animal, and RFI can be calculated as the difference between SFI and EFI (RFI=SFI-EFI). Efficient animals will therefore have a lower RFI value, while inefficient animals will exhibit higher RFI values.

2.3.3 Association of performance traits with RFI

2.3.3.1 Growth

The majority of RFI studies following those conducted by Koch et al. (1963), investigated the genetic and phenotypic variation of residual feed intake and the relationship with the component traits used to calculate expected feed intake (e.g. ADG and MMWT). By definition, RFI is phenotypically independent of these component traits (Jensen et al., 1992; Herd and Bishop, 2000; Arthur et al., 2001a, d; Nkrumah et al., 2004), and therefore it is likely to reflect variation in basic metabolism rather than differences in performance (Crews, 2005). This correlation is reported when EFI is calculated by regression analysis. However, Fan et al. (1995) observed phenotypic correlations of -0.74 for RFI and ADG in Angus bulls when EFI was

predicted using feed intake formulae from the 1984 NRC. Arthur et al. (2001b) also found RFI and ADG to be phenotypically correlated (r=-0.38) when using feeding standards formulae to predict EFI. As well, Kennedy et al. (1993) theoretically showed that when RFI is determined by regression, genetic correlations between RFI and component traits were not independent. Significant positive genetic correlations of 0.33 and 0.39 in production periods 1 and 2, respectively between RFI and ADG were shown by Jensen et al. (1992), while Herd and Bishop (2000) reported a positive genetic correlation of 0.22 between RFI and metabolic mid-weight. Arthur et al. (2001b) suggest that genetic variance and covariance should be incorporated into the genetic regression model in order to achieve genetic independence between RFI and its component traits. Fortunately, phenotypic and genetic RFI are highly correlated (Hoque et al., 2006) which makes genetic improvement through selection for phenotypic RFI possible.

Comparisons of RFI and FCR to measure feed efficiency have been explored by several researchers. Fan et al. (1995) reported phenotypic correlations between RFI and FCR of 0.64 and 0.74 for Hereford and Angus cattle, respectively. Using 540 offspring from Hereford sires, Herd and Bishop (2000) reported a phenotypic correlation of 0.61 and a genetic correlation of 0.70 for RFI and gross efficiency, while Arthur et al. (2001b) found similar phenotypic (0.85) and genetic (0.57) correlations. More recent studies (Nkrumah et al., 2004; Hoque et al., 2006; Durunna et al., 2012) have demonstrated highly positive phenotypic and genetic correlations between RFI and FCR. This would suggest that selection for low RFI livestock would create an indirect response of improving FCR without seeing an increase in cow size that is normally associated with direct selection on FCR (Herd and Bishop, 2000). The calculation of the Kleiber ratio does not involve feed intake data as is the case for RFI and FCR, suggesting that KR should be independent of RFI. This has recently been demonstrated by Kelly et al. (2010) as no

correlations between KR and RFI were observed in 56 Friesan x Limousin heifers. Selecting for more efficient beef animals (low RFI) and the resulting impact on carcass and reproductive traits has also been recently studied.

2.3.3.2 Carcass

There appears to be conflicting results when investigating correlations between carcass traits and RFI. However, this may be attributed to sex and breed of animal, whether that animal is purebred or crossbred, and the technique used to measure live animal carcass quality (Hoque and Suzuki, 2009). Fifty four purebred Angus steers exhibited no differences in backfat, ribeye area, or marbling between low, medium and high RFI animals in a study by Baker et al. (2006). However, Basarab et al. (2003) reported a significant ($P<0.01$) negative correlation between carcass lean yield and RFI in 148 crossbred steers, and Arthur et al. (2001a) reported a positive genetic correlation of 0.17 between RFI and ribfat thickness for Angus bulls and heifers. Herd and Bishop (2000) reported a genetic correlation in Hereford bull calves for RFI and carcass lean content of -0.47, which supported the findings of Arthur et al. (2001a). With composite calves originating from Angus, Charolais, and Alberta Hybrid cattle lines, Nkrumah et al. (2007) described low positive genetic correlations for RFI with marbling and backfat; phenotypic correlations for RFI with backfat were significant ($P < 0.01$). Robinson and Oddy (2004) reported a similar small positive genetic correlation between RFI and marbling, but larger positive correlations for RFI with rump and rib fat measures. This suggested that downward selection for RFI may result in decreased subcutaneous fat deposition and less intramuscular fat, which was also reported by Richardson et al. (1998) in both Angus and crossbred cattle where a single generation of selection for low RFI cattle produced offspring with less subcutaneous fat

than offspring from high RFI parents. Conversely, Hoque et al. (2005, 2006) observed negative genetic correlations for RFI of bulls with the marbling and subcutaneous fat of their progeny,

2.3.4 Association of reproductive performance with RFI

The decreased percentage of carcass fat described by Richardson et al. (2001) and Basarab et al. (2003) suggests a potential antagonism of RFI with reproductive fitness, and examples from other species (mice, poultry and swine) suggest that selecting for efficient animals may result in negative effects on reproductive efficiency (Pitchford, 2004). Increased fat deposition, regardless of RFI ranking, has also been observed to negatively affect reproduction traits. Coulter and Kozub (1984) reported that beef bulls consuming a high energy diet had more backfat than bulls consuming a medium energy diet but exhibited decreased sperm motility, an increased percentage in sperm defects, and lower epididymal sperm reserves. However, Basarab et al. (2003) suggested that the differences in RFI are not entirely due to subcutaneous and intramuscular fat, but also intermuscular and internal fat deposition, maintenance and heat increment of feeding, and inherent differences in metabolic processes affecting metabolizable energy intake. The complexity of factors contributing to biological efficiency has presumably led to conflicting studies relating reproductive fitness to RFI.

Awda et al. (2013) reported decreased sperm motility, sperm viability and scrotal circumference in low RFI bulls compared to high RFI bulls, however there were no significant differences in subcutaneous or body cavity fat between efficiency classes. This suggests that decreased fertility in low RFI beef bulls is not confounded by fatness as measured by subcutaneous fat (typically backfat) and that reasons for this decreased fertility are due to some other factor. Wang et al. (2012) also reported slightly lower sperm motility in more efficient bulls, but no other negative reproductive effects related to increased efficiency. Several studies

have found no significant correlations between scrotal circumference and RFI (Arthur et al., 2001b; Schenkel et al., 2004; Van der Westhuizen et al., 2005; Fox et al., 2004) which is commonly used as an indicator of reproductive efficiency (Gipson et al., 1985). Fox et al. (2004) also found no significant differences for semen consistency, sperm motility, abnormalities, and overall breeding soundness between efficiency classes.

Studies have shown no significant differences in pregnancy, calving, or weaning rates between low and high RFI females measured postweaning (Arthur et al., 2005) or from cows which produced low and high RFI progeny (Basarab et al., 2007). While these studies displayed no negative reproductive effects with selection for improved feed efficiency, Blair et al. (2013) reported a trend of low RFI heifers to have a lower first-service conception rate when compared to less efficient females. However, the authors also showed that when RFI was estimated from a breeding group average, calves sired from low RFI bulls were born earlier in the year—a desirable trait in the beef industry. Donoghue et al. (2011) also demonstrated a negative relationship between RFI and reproductive fitness where low RFI heifers carried less subcutaneous fat and reached puberty later than high RFI heifers.

There have been possibilities suggested for reasons why low RFI animals may have decreased reproductive fitness. Basarab et al. (2007) first proposed that the FI procedure used to calculate RFI favours later maturing animals. This could lead to animals having immature reproductive tracts during the experiment, resulting in expected decreased performance when breeding soundness exams and reproductive traits are measured because of the delayed onset of puberty. Pre-pubescent cattle, both male and female, will also expend a reduced amount of energy by exhibiting less sexual activity and having a later development of the reproductive system which favours the RFI phenotype (Awda et al., 2013). Although these examples may

account for some of the negative reproductive effects when selecting for more efficient beef cattle, the inconsistency of results from such studies suggest more work needs to be done in this area.

2.3.5 Repeatability and heritability of RFI

2.3.5.1 Diet differences

While RFI is commonly measured during the growing phase of an animal's life, the question arises whether or not this efficiency trait is retained as the animal matures. The effect of diet has been investigated in beef steers and heifers (Crews et al., 2003; Kelly et al., 2010; Durunna et al., 2011) by comparing RFI in both grower and finisher diets in successive feeding periods. Crews et al. (2003) suggested that RFI, also known as net feed efficiency (NFE), measured in both feeding periods were genetically associated with each other and thus, biologically similar traits. However, the genetic correlation between NFE measured during the grower and finisher periods was 0.55, and the authors indicated that animals may rank differently when being fed a roughage-based grower diet compared to a grain-based finisher diet. Kelly et al. (2010) estimated repeatability to be even greater (R=0.62) between RFI in the grower versus finisher stages with crossbred heifers. Although close to one quarter (24%) of the heifers reranked by more than 1 SD of the original RFI, 54% changed rank by less than 0.5 SD, providing evidence that RFI is a consistent trait when measured in the growing and finishing phase of an animal's life, and regardless of whether the diet is roughage or grain-based.

More significant reranking has been reported by Durunna et al. (2011). The majority of beef steers consuming the grower diet, consuming the finisher diet, and switching from a grower to finisher diet (58%, 51% and 51%, respectively) changed RFI by at least 0.5 SD in successive feeding periods. This frequency of reranking between RFI measured in two different feeding

periods for the feed swap group suggests that diet type may affect feed efficiency, while reranking in the two control groups imply that feeding period effects, including ambient temperature, growth phase and/or stage of maturity of the animal, will influence feed efficiency measurements. The observed reranking suggests that RFI measured using different diets or at different life stages may be separate measures of efficiency altogether (Durunna et al., 2011).

2.3.5.2 Stage of growth

Few studies have determined RFI for beef cattle in consecutive feeding periods. Arthur et al. (2001b) measured feed intake and performance in Charolais bulls over several months and partitioned the entire feeding period into a period that began immediately after weaning (mean=274 days old) followed by a second feeding period that began the following spring (mean=470 days old). RFI was calculated for each feeding period, with a highly positive genetic correlation (r=0.75) and a lesser, but still positive phenotypic correlation (r=0.43). Evidence supporting observed differences in RFI measured at different stages of an animal's life was reported by Durunna et al. (2012). Of the 190 crossbred heifers fed the same diet in successive feeding periods, 51% changed their RFI group (low, medium and high based on ±0.5 SD of the mean) in the second feeding period, while 59% of heifers changed their RFI value in the second feeding period by at least 0.5 SD from the first feeding period measurement. These results indicate that RFI measured postweaning and as a yearling beef animal should be considered different traits, perhaps due to the differences in tissue deposition during each phase with primarily lean tissue growth in the weaner phase versus fat tissue deposition as yearlings (Berg and Butterfield, 1976). However, the positive relationship shown between RFI calculated at different ages suggests improvements came be made in biological efficiency through downward selection on RFI (Arthur et al., 2001b).

2.3.5.3 Adolescence versus maturity

Just as differences in RFI repeatability have been observed with changes in diet and growth phase, the effect of stage of maturity has also been studied. However, there has been limited research in this area, possibly due to the high costs associated with measuring RFI. During one of the early studies in this area, Nieuwhof et al. (1992) showed low phenotypic correlations between RFI measured in dairy heifers and again as lactating cows (r=0.07), but estimated genetic correlations were much higher (r=0.58).

At the Trangie Agricultural Research Centre in Australia, Herd et al. (1998) evaluated 56 cows of known feed efficiency to determine if heifers that ranked high in net feed efficiency measured postweaning remained efficient as three year old cows. Intraruminal alkane boluses were used to estimate dry matter intake while on pasture, and cows and calves were weighed to determine initial weight, calf weight gain, and final weight. Efficiency was measured using a ratio of calf weight sustained by the cow divided by the dry matter intake of the cow. It was reported that the more efficient dams produced 15% more calf weight per kg of intake than less efficient dams, but although the difference was numerically large the results were not significant. However, problems were identified with correctly identifying the preferred vegetation that the cows consumed through observation, and it was noted that failing to account for individual diet selection of each cow could result in erroneous values being used for the calculation of intake (Herd et al., 1998).

Archer et al. (2002) calculated the RFI of beef females just after weaning and again as three year old cows. Phenotypic correlations for RFI measured postweaning and at maturity was moderate (r=0.40), although RFI showed a higher repeatability than ADG or FCR (r=0.28 and 0.10, respectively). However, genetic correlations of the component traits of RFI were very high

between postweaning and mature measurements (ADG, r=0.72; $MidWt^{0.73}$, r=82; daily feed intake, r=0.94). As well, the genetic correlation between RFI measured at different life stages was close to 1 (r=0.98), suggesting that selecting low RFI heifers will result in a more efficient cow herd (Archer et al., 2002). Differences in the magnitude of phenotypic and genetic correlations from the previously mentioned studies can possibly be attributed to different cow types (dairy versus beef), age at which RFI was calculated on cows, and conditions under which the cows were maintained (lactating versus dry cows).

Meyer et al. (2008) calculated RFI on Hereford heifers and grouped them into low and high RFI classes. After calving, these females were housed by RFI group on pasture and average forage dry matter intake was estimated using grazing enclosures, weekly rising plate meter readings, and forage harvests every 21 days. The low RFI cows with their calves consumed less feed than the high RFI pairs in experiments 1 and 2 (21% and 11% less, respectively), however neither result was significant. The authors concluded that either forage intake did not differ between low and high RFI cattle on pasture, or that methodology and the small sample size used in the experiment limited their ability to detect any noticeable differences (Meyer et al., 2008).

2.3.5.4 Progeny

Heritability estimates for RFI range from 0.21-0.47 and indicate that genetic improvement through selection may be possible for beef cattle (Table 1). While most of the feed requirements for beef production can be attributed to the cow herd (Montano-Burmudez et al., 1990), the majority of RFI studies measured feed efficiency in young, growing animals. Moderate heritability estimates for biological efficiency have been reported extensively in a feedlot or bull test setting (Koch et al., 1963; Arthur et al., 2001b; Nkrumah et al., 2007). These heritability estimates derived from phenotypic and genetic variance are useful; however, more

meaningful values can be determined using progeny records. Herd et al. (1997) used multiple years of progeny data to compare dam and sire efficiency to subsequent progeny efficiency. Heifers and bulls were evaluated for net feed intake (NFI; synonymous with RFI) after weaning and animals were divided into two separate herds based on high or low efficiencies. The efficient bulls were mated with the efficient heifers, and vice-versa, to establish two NFI lines. Progeny from the efficient cows and bulls were significantly more efficient than progeny from inefficient parents, providing results that confirm a moderate heritability estimate for biological efficiency (Herd et al., 1997).

In a similar study evaluating residual feed intake of cow progeny, Basarab et al. (2007) showed that dams producing more efficiency calves (low RFI group) consumed 1.31 kg d^{-1} DM ($P<0.05$) less than cows producing inefficient offspring, with similar progeny weights and preweaning ADG. The dams of more efficient progeny correspondingly exhibited lower RFI values than cows producing inefficient calves ($P<0.05$). This evidence suggests that biological efficiency is a trait that can be inherited and expressed by progeny (Basarab et al., 2007) Moderate heritabilities have been consistent, with few exceptions, whether RFI is measured while the animals are growing, or when progeny are compared to their parents.

2.3.6 Potential sources of variation using RFI

Although feed efficiency can be predicted with RFI using relatively simple measurements of feed intake, body weight, and relative growth rate, the underlying physiological and whole animal factors regulating are much less understood. A number of authors have attempted to outline these plausible mechanisms behind variation in efficiency of nutrient use in beef cattle (Herd et al., 2004; Richardson and Herd, 2004; Swanson and Miller, 2008; Herd and Arthur, 2009). Herd et al. (2004) identified 5 major processes likely associated with differences in RFI.

Variation in feed intake (as measured by heat increment of feeding) accounted for 9% of the RFI variation, digestion of feed and the associated energy costs was estimated to contribute 14% of the variation in RFI, metabolism (catabolism and anabolism associated with and including variation in body composition) accounted for 5%, and 5% could be attributed to differences in physical activity. These mechanisms were hypothesized to account for approximately one third of the variation in RFI, with the remaining two thirds likely attributed to heat loss due to variation in other processes, such as protein turnover and ion transport (Herd et al., 2004). Thermoregulation was mentioned as a factor that influences the variation of RFI yet there were no suggested estimates for its contribution, presumably due to the difficulty in measuring heat production, heat loss and RFI.

Richardson and Herd (2004) used two lines of beef cattle divergently selected for low and high RFI to further explain plausible factors associated with variation in RFI. Differences in body composition (5%) and heat increment of feeding (9%) were observed to be the same as those described by Herd et al. (2004), with more contribution from differences in activity (10%) and less for differences in digestion (10%). By using blood protein and cortisol profiles from each divergent line, the authors suggest 37% of the variation in RFI is due to differences in protein turnover, tissue metabolism, and stress. Feeding patterns (2%) had a minimal contribution to variation in biological efficiency, while other unidentified processes (e.g. ion transport) were assumed to be associated with the remaining 27% (Richardson and Herd, 2004). Again, estimates were not made for the possible contribution of thermoregulation, though it was mentioned as a likely mechanism responsible for variation in RFI.

2.4 Infrared thermography

There is a growing interest in the use of low cost strategies such as infrared thermography (IRT) to measure radiant heat losses from an animal's skin surface as a method for predicting feed efficiency, relative to individuals in their contemporary group. Whole animal calorimetry was at one time the only way to directly measure the heat produced by an animal. However, our knowledge of the electromagnetic spectrum and the technological developments that followed has offered alternative methodologies to predicting energy lost as measurable heat. Infrared thermography is a term that describes the creation of an image depicting thermal surface property variation of objects (thermography) with energy in a portion of the electromagnetic spectrum that is just beyond the border of visual perception (infrared spectral band). Before exploring the application of IRT to current biological studies, it is necessary to understand the concept and factors affecting thermal imagery.

2.4.1 Thermal imaging fundamentals

Electromagnetic radiation is a form of energy derived from oscillating magnetic and electrostatic fields, and is emitted by all objects that have a surface temperature above absolute zero (Lloyd, 1975). Every molecule possesses a certain amount of "internal" energy with most of this energy associated with electrons orbiting their nucleus. However, some of this internal energy is related to the vibration of atoms in their molecular structure as well as the rotation of the molecule. For molecules, the energy of radiation originates from this vibration and rotation of individual atoms within their molecular structure (Monteith and Unsworth, 2008). The movement of atoms releases radiation in the form of photon particles. Since the energy associated with the release of photons is related to its wavelength and frequency we can measure the surface temperature of an object by detecting electromagnetic radiation emissions, without

physical contact (Holmann, 1986). Thermal radiation at terrestrial temperatures, though primarily due to self-emitted radiation from vibrational and rotational quantum energy level transitions in molecules, also includes the effects of reflected radiation from other heat sources (Lloyd, 1975).

The electromagnetic spectrum is arbitrarily divided into "bands", characterized by different wavelengths of the radiation within each region of the spectrum and the methods used to detect and produce such radiation. Infrared radiation is found in the region spanning wavelengths approximately 0.75-1000 μm in length, found between the visible light and microwave bands. To measure the temperature of objects on the surface of our earth within -10^0C to 50^0C, the most appropriate wavelengths are around 9-11 μm because this is the region of peak spectral emission and falls within the infrared range of the electromagnetic spectrum (Speakman and Ward, 1998).

There are several factors which complicate the measurement of surface temperatures of an object using the intensity of their emitted radiation. The intensity of emitted radiation largely depends upon the nature of the surface of the emitting material (Speakman and Ward, 1998). In contrast, imperfect emitters emit less radiation than black bodies at the same temperature. In order to quantify the degree to which an imperfect emitter material will emit radiation, it is given a value that expresses its emission as a proportion of that possible by a black body at the same wavelength, defined as the emissivity (Speakman and Ward, 1998). Stefan-Boltzmann's law changes for imperfect emitters to account for a material's emissivity, shown by:

$$\varphi=\epsilon\sigma T^4$$

where the radiation emitted from a plane surface is equal to the product of the emissivity (ϵ), Stefan-Boltzmann's constant (σ), and the absolute temperature (T) to the fourth power (Monteith

and Unsworth, 1990). The emissivity of a black body is therefore equal to 1.0, and constant at all wavelengths, while any material that does not emit radiation perfectly has an emissivity between 0 and 1. In the wavelength range of 9-11 μm, the emissivity of infrared radiation by biological material has been found to be 0.9-0.97 and is independent of surface color in the visual spectrum range (Porter and Gates, 1969).

The images that we as human beings perceive are primarily caused by reflection and reflective differences of objects illuminated by radiation with wavelengths ranging 0.4-0.7 μm. In contrast, thermal images are produced predominantly by self-emission of electromagnetic radiation in the infrared spectrum, thus making it more relevant to utilize infrared technology for measuring surface temperature (Lloyd, 1975). Several factors will influence the ability to accurately measure surface temperature variation through the thermal imaging process and they must be known to allow an operator to adjust the thermal image accordingly. For an object to be detected and subsequently recognized, an object-to-background apparent temperature difference must exist in sufficient magnitude to distinguish the object from its background (Lloyd, 1975). Atmosphere between the infrared camera and the object being measured must not excessively blur or attenuate the signal (Lloyd, 1975). For example, modern infrared cameras typically have the option to input current air humidity as a means of adjusting emitted radiation for potential distortion caused by aerosols. If the relative humidity during image collection is high there will be radiation absorbed in the atmosphere between the source and the camera; humidity should be measured and accounted for in such a case (FLIR Systems AB, 2003). As well, as the distance separating the camera operator and the object of interest increases, there is a corresponding decline in transmittance with a portion of the radiation being scattered or absorbed by gas molecules in the atmosphere (FLIR Systems AB, 2003). Speakman and Ward (1998) suggest that

under normal environmental conditions the effect of distance on infrared radiation transmission is trivial for distances less than 10 m.

2.4.2 IRT applied to livestock production

Infrared thermography technology (IRT) can be applied in animal agriculture due to physiological processes involving thermoregulation or heat-inducing responses from various stimuli, as well as the ability for infrared cameras to detect surface temperature variations of biological tissues. This methodology has been successfully utilized in animal studies associated with evaluating diagnostic, welfare and production related measurements (Luzi et al., 2013). One advantage of using IRT compared to conventional thermometry is continuously collected observations of unconstrained subjects that is not destructive, from distances ranging a few centimeters to several hundred meters away from the subject with improved accuracy (Cena and Clark, 1973). The non-invasive nature of IRT makes this technology especially suited for animal production research where traditionally the close proximity and physical contact necessary for many measurements invokes certain safety concerns. Minimizing the disturbance to the animal ensures that natural behaviours are maintained without inducing any fear or stress responses which could influence thermoregulatory processes. While both IRT and conventional thermometry methods still depend on the skill of the operator and willingness of the animal to remain stationary for a few seconds, the development of thermal imaging systems has improved the accuracy of surface temperature readings.

Infrared thermography has been used to detect increased radiant heat losses from cattle due to increased immune response as an indicator of disease and lameness. Berry et al. (2003) measured the surface temperature of the posterior udder for lactating dairy cows using a thermal scanner to evaluate inflammatory responses to predict the presence of mastitis, while Haley et al.

(2005) used IRT to detect lameness in dairy cattle. Hurnik et al. (1984) reported an increased area enclosed by the 37^0C isotherm on the gluteal region of cows that were ill due to pneumonia, mastitis, kidney infections, or minor injuries and swelling. These authors concluded that IRT showed promise for early detection of disease or leg injuries in dairy cattle. In addition, the presence of bovine respiratory disease in young growing beef cattle has been reported to increase the surface temperature of several anatomical regions, especially the orbital region, as measured through infrared thermography (Schaefer et al., 2004; 2007; 2012). Therefore, the use of an automated thermal detection system was suggested as an efficacious tool for identifying calves suffering from the early stages of respiratory disease (Schaefer et al., 2012).

Additionally, radiated heat from the orbital region of livestock was shown to be a predictor of stress as eye temperature and cortisol levels in horses were positively correlated following adrenocorticotropic hormone injections (Cook et al., 2001). This suggests that the activation of the hypothalamic-pituitary-adrenal (HPA) axis may be associated with higher temperatures. Stewart et al. (2007) used dairy cattle in a similar experiment inducing an HPA response with injections of varying levels corticotropin-releasing hormone but did not see a corresponding elevation in eye temperature. The authors, however, suggest that cognitive recognition of the attempted stress-induction was not evident in their test animals, and that a psychological aspect of stress is necessary to produce responses to stress (sympathetic activation does not produce a stress response on its own).

The evaluation of infrared technology for the purpose of estrus detection was explored by Hurnik et al. (1985) in their work with dairy cattle. It was discovered that the area enclosed by the 37^0C isotherm found on the gluteal region of dairy cattle increased in the association with the occurrence of estrus, becoming statistically significant after the third postpartum estrous cycle.

However, there was a 33% incidence of false positives around the third postpartum estrus, limiting the effectiveness of IRT as an indicator of estrus-onset. As well, estrus could not be detected in 7% of the cattle regardless of the number of days following parturition (Hurnik et al., 1985).

Another application for infrared imaging systems in livestock production is to determine meat quality. Infrared thermography has been used as a screening tool for the presence of darker cutting feeder cattle pre-slaughter (Schaefer et al., 1988). As well, it was shown that pigs exhibiting localized hot spots over the dorsal neck and lumbar regions corresponded to the halothane-positive genotype, indicating susceptibility to pale-soft-exudative pork, while pigs with cooler mean side temperatures measured by IRT tended to have a higher percentage drip loss and a paler color of muscle meat (Schaefer et al., 1989). Tong et al. (1995) also reported that beef cattle with cooler side temperatures and a less variable temperature distribution produced a less desirable carcass with dark firm dry-cut meat after processing. There are many examples where body surface temperatures have been able to predict important health issues and production traits, and can be traced back to heat loss due to thermoregulatory processes or a physiological response to a given stimuli.

2.4.3 Heat loss and thermoregulation in beef cattle

Maintenance of a constant internal body temperature is essential for homeothermic animals such as beef cattle, eliciting physiological and behavioural changes in response to changes in temperature. The thermal neutral zone (TNZ) is a range of environmental temperatures where an animal's metabolic heat production is, over the short-term, independent of ambient temperature (Webster, 1974). This range of temperatures will vary depending on animal type and performance (Hahn, 1999; NRC, 2000). The lower limit of the TNZ is known as the

lower critical temperature and represents the temperature which an animal must begin to increase its rate of metabolic heat production through cold-induced thermogenesis to maintain a constant body temperature (Young et al., 1989). Similarly, an upper critical limit exists above which heat loss mechanisms are employed to avoid heat stress with the goal of thermal homeostasis. The animal uses a complex negative feedback system via the hypothalamus to either conserve internal heat or increase heat dissipation to maintain a constant core body temperature. Heat exchange in homeotherms can be separated into heat production, non-evaporative heat loss, and evaporative heat loss (Robertshaw, 2004). Both warm and cold temperature receptors are located in the central nervous system, visceral organs, and in the skin (Cunningham, 2007) with the largest concentration being found in the skin. These receptors send temperature information to the hypothalamus, thereby allowing an animal to perceive changes in deep body or skin surface temperatures, followed by the appropriate behavioural responses (Robertshaw, 2004).

The primary source of heat in cattle within their thermal neutral zone comes from metabolism as a product of the inefficiencies experienced during maintenance and production processes (Young et al., 1989), with secondary sources such as solar radiation and conduction contributing varying amounts of heat energy (Cunningham, 2007). The heat producing processes of metabolism can be broken down into the oxidation of nutrients and synthesis of new tissues (Blaxter, 1962). The inefficiencies of maintenance processes can be described, for example, by the oxidation of one gram molecule of glucose (sourced from both ingested and stored energy), which yields 686 kcal of chemical energy. This same one gram molecule, however, only produces 39 moles of ATP, amounting to just 351 kcal of energy available for maintenance processes. Thus, the system is only 50% efficient for glucose oxidation, with the remaining energy present in the form of heat (Robertshaw, 2004). Exposure to temperatures below an

animal's lower critical limit will induce thermogenesis through two actions: shivering and non-shivering thermogenesis. Shivering thermogenesis involves the activation of antagonistic groups of limb muscles which increase heat production while producing no useful work while non-shivering thermogenesis increases the basal metabolic rate, caused especially by the oxidation of fat (brown adipose tissue in very young animals) to produce more heat (Cunningham, 2007). Variation in heat production can exist between animals of different breeds (Baker et al., 1991) and physiological states (Blaxter, 1962), as well as those fed diets which differ in composition (West, 1999). Baker et al. (1991) reported that comparisons of zero-activity heat production between breeds was significantly different for Hereford (least heat produced), Simmental, and Charolais (most heat produced) heifers. The authors suggested that a lower metabolic rate per unit of live weight$^{0.75}$ and a lower non-fat body composition in the Hereford animals may be the reason for their findings. When cattle are faced with feed restriction, heat production gradually decreases, most likely due to reduced digestion and fermentation (Blaxter, 1962). The heat increment for high-fiber feedstuffs (e.g. grass hay) is much higher than that of concentrates (e.g. barley or added fats), suggesting a decrease in heat production for cattle fed a low-fiber ration containing concentrates compared to traditional forage diets (West, 1999).

Heat loss in animals occurs through both evaporative and non-evaporative mechanisms, accompanied by small heat losses in urine and fecal waste (Cunningham, 2007). Evaporative heat loss is the process transforming sweat or other water-containing body fluids to a vapour, and is the major form of heat loss in homeotherms. This transformation requires energy input which is supplied by excess body heat or conducted or absorbed from the environment. The skin plays an essential role in homeostasis; not only does it contain a high density of thermal sensors but its temperature is regulated by peripheral vasomotor mechanisms (Young et al., 1989). Heat loss

occurs continuously by evaporation of water that is diffused through the skin and this can be amplified by increased sweat production during exposure to warm conditions. As well, evaporation of water from the respiratory tract is another mechanism used by animals to regulate heat balance. Evaporative heat loss is an important mechanism in thermoregulation as it is the only form of heat loss once the ambient temperature exceeds an animal's surface temperature (Cunningham, 2007).

Sensible heat loss is achieved through one of three modes of action: radiation, convection, and conduction (Kleiber, 1975). Almost all of the heat produced by an animal originates from deep within its core. However, body tissues are very poor conductors of heat and therefore excess heat is dissipated via blood circulation, facilitating the use of blood vessels located beneath the skin's surface (Cunningham, 2007). When thermal receptors within the body detect that the temperature has increased, signals are sent to the hypothalamus, which subsequently invokes corrective measures. Dilated skin vascular beds and the opening of arteriovenous anastomoses magnify the effectiveness of heat loss by bringing circulated blood closer to the skin's surface (Cunningham, 2007). These mechanisms of bringing heat to peripheral, non-core body tissues make non-evaporative heat loss processes possible. It has been suggested that total sensible heat loss from animals' extremities should be considered separately from heat lost from the trunk (McArthur, 1981), as the extremities play a very important role in thermoregulation (Whittow, 1962).

Heat lost (or gained) by convection involves the movement of a fluid (either air or water) passing across the animal's surface and a resulting heat exchange, dependent upon the temperature gradient that exists between the two while conduction requires the physical contact between an animal and a surface or fluid where heat transfer occurs without the movement of

molecules (Robertshaw, 2004). However, since cattle do not typically lay on cool surfaces for long periods of time conduction is not considered a primary source of heat loss (Blaxter, 1962). Heat exchange between an animal and the air immediately surrounding it is possible by radiant heat in the form of electromagnetic waves (Robertshaw, 2004). Radiation is the primary source of sensible heat loss in homeothermic animals, estimated to account for 40-65% of the total heat loss (Blaxter et al., 1959; Joyce et al., 1966; Kleiber, 1975).

2.4.4 IRT and the relationship with RFI

Heat is a byproduct of metabolism and physical work in homeothermic animals (Kleiber, 1975; Webster, 1971; Young et al., 1989); any energy lost in the form of heat (while an animal is within its thermal neutral zone) can be related to biological efficiency. Calorimetry technology has the capability to measure total heat loss and separate those losses into their respective mechanisms of dissipation (Blaxter et al., 1959; Joyce et al., 1966). However, the application of calorimetry for the purpose of selecting efficient breeding stock is limited due to labour, confinement requirements and equipment costs.

As a consequence, several researchers have attempted to find a relationship between heat production and biological efficiency as an indirect method of predicting heat losses by an animal. Richardson et al. (2001) estimated heat production in 33 Angus steers as the difference between ME consumed and retained energy in the form of body mass gained over the test. Progeny from matings between the most efficient bulls and cows and progeny from the least efficient bulls and cows were grouped into low and high RFI groups, respectively. Heat production was associated with energy expended in protein and fat synthesis, energy used for the maintenance of body tissues, energy expended during physical activity and energy lost through the heat increment of feeding. While there were no significant differences in heat production between low and high

RFI groups, a significant difference in residual heat production per unit of protein gain was reported. This implies that low RFI steers had superior efficiencies with respect to protein deposition and/or maintenance of these tissues once deposited. The authors concluded that differences in ME intake for progeny of cattle divergently selected for RFI are more likely due to variation in metabolic processes rather than to changes in body composition (Richardson et al., 2001). The very definition of heat production in this study, however, was based on energy retention in the form of body weight gained over the test. This parameter falls short of fully encompassing the biological mechanisms suspected of causing differences in biological efficiency. Nkrumah et al. (2006) utilized oxygen consumption and methane production in an indirect calorimetry chamber to predict the heat production of 27 steers separated into low, medium, and high RFI groups based on ±0.5 SD units around the mean. Steers within the high RFI group (less efficient) produced significantly more heat than steers in the medium RFI group, who produced significantly more heat than steers in the low RFI group (more efficient). The observed differences in the relationship between RFI ranking and heat production in the two studies may be attributed to differences in the methodology used to measure heat production. Heat production as measured by indirect calorimetry should be considered a separate trait from heat loss as measured by IRT as there is no adjustment for energy used for other processes, nor is there consideration for differences in factors which influence radiant heat loss from an animal's surface, which will be discussed subsequently.

One of the first studies to use IRT as a means of estimating heat exchange in animals was conducted by Clark et al. (1973) while attempting to determine the insulation resistance of sheep fleece. The authors subjected sheep to a range of radiative loads in a temperature-controlled chamber. Using an infrared camera to measure fleece surface temperatures, thermocouple probes

to measure skin temperature, and a psychrometer to measure air temperature, they were able to estimate energy balance from the total radiation experienced over the range of radiative loads. It was suggested that this method of predicting sensible heat partitioning on animals could complement energy balance studies, including metabolism and environmental factors (Clark et al., 1973).

Predicting growth efficiency in beef cattle by measuring radiant heat loss was investigated by Scott et al. (2002) using IRT. Feed intake and weight gain were recorded for 18 yearling heifers to determine feed efficiency, while indirect calorimetry and IRT methods were used to predict heat production and heat loss, respectively, in both cold and warm environmental treatments. A significant Spearman rank correlation was found between feed efficiency and heat loss measured through IRT. The results suggested that heat loss determined by IRT can be used as an index for feed efficiency in beef cattle (Scott et al., 2002).

Several experiments using the same methodology and principles followed but with different anatomical regions of interest to determine their suitability for predicting heat loss and thus biological efficiency. Schaefer et al. (2005) captured infrared scans of the dorsal area to determine radiant heat loss in 37 crossbred cows. The cows were group into low (RFI<-1), high (RFI>1) and intermediate (-1<RFI<1) RFI groups. Maximum surface temperatures for cows in the low RFI group were significantly lower than cows in the high RFI group, supporting the findings of Scott et al. (2002).

Brown (2005) analyzed dorsal, cornea, eye, forehead and nose surface temperatures determined by IRT in an RFI trial with growing and finishing steers. There were no significant correlations of body temperatures with feed efficiency, although significant negative correlations

were found between ADG and DMI with eye temperature as well as DMI with forehead temperature. Hair quality characteristics, including hair density, fiber, and curvature of hair strands measured at the start of test, were also not correlated with RFI. The author concluded that thermoregulation does not differ between low and high RFI steers, but cautions that further research is warranted (Brown, 2005).

Montanholi et al. (2008) obtained IRT measurements from the right eye and hind quarter of Angus, Piedmontese and Charolais-sired crossbred steers to predict RFI ranking. Steers in low and medium RFI groups had significantly lower eye temperatures taken at the end of the trial than steers in the high RFI group. As well, Piedmontese-sired steers had significantly lower hind quarter temperatures at the start of the feeding trial compared to Angus and Charolais steers. The difference in heat loss could be attributed to variability in maintenance energy requirements between breeds, variation in the ability of one breed to regulate heat more efficiently than another or differences in coat colour. This suggests that eye temperature measured by infrared imaging may be useful in predicting RFI ranking, however possible breed effects should be considered when evaluating potential predictors of feed efficiency (Montanholi et al. 2008).

Subsequently, Montanholi et al. (2009) assessed the relationship between IRT and ultrasound measures with the variation in feed efficiency for beef bulls. More anatomical regions were explored as possible predictors of RFI ranking, including the eye, cheek, ribs, rear area, scrotum and left and right feet. Significant correlations between RFI and rib, scrotal, or rear temperatures captured at the end of the feeding period were not observed. However, moderate correlations between eye, cheek, and back feet surface temperatures were observed, with the largest correlation of 0.43 between RFI and right foot temperatures. This supports previous research that indicates the extremities play an important role in heat dissipation (Whittow, 1962).

Montanholi et al. (2009) concluded that foot and cheek temperatures were the most promising body locations for indirectly evaluating RFI ranking. These authors also noted that additional research is required to determine the optimal time over the circadian cycle to capture images, as well as the number of thermographs required to increase the accuracy of IRT as a tool to predict RFI.

The relationship between performance traits, infrared thermography traits, feed efficiency, feeding behaviour and glucocorticoid levels and the individual contribution of each towards total variation in RFI was investigated in 91 crossbred steers (Montanholi et al., 2010). Infrared images from the eye, cheek, snout, rib, and hind areas were captured every 28 days over two 56 day periods. Feeding behaviour (visits to the feeder, meal size and eating rate), IRT traits (snout and cheek temperature) and fecal cortisol levels differed significantly between low and high RFI groups. Temperatures from the extremities (cheek and snout) were positively correlated with RFI ranking compared to those from the core body regions (rib or hind area). Although feeding behaviour, IRT and fecal cortisol metabolites were all correlated with feed efficiency, body surface temperature accounted for more than 70% of the overall variation in RFI. This implies an important application for IRT in predicting feed efficiency (Montanholi et al., 2010). Conversely, Huntington et al. (2012) recently demonstrated IRT was not correlated to RFI. Lack of significant correlation occurred despite efforts to enhance image quality by clipping the bulls. Although RFI was not correlated with any of the thermography measures, there were several correlations between surface temperature and DMI, ADG, and feed conversion, indicating that IRT could be used to assess status or progress of the rate and efficiency of gain.

2.4.5 Factors influencing body surface temperature and IRT

Observed differences in the relationship between IRT and RFI may be attenuated to both physical factors that can bias thermographs and give false surface temperature measurements, as well as certain biological responses which can cause acute increases in heat production.

In livestock, the most obvious physical characteristic affecting heat loss is the thermal resistance of pelage (hair coat). Different dynamics of a hair coat, i.e. hair density, length and pigment colour, can influence the heat retained, dissipated, or absorbed for an animal. Hair coat introduces an additional resistance between the skin's surface and the outermost layer of hair whose radiative temperature is sensed by an infrared camera (Cena and Clark, 1973). This is regarded as the surface at which the animal exchanges energy with its environment. In fact, the total thermal resistance of livestock species should include three resistances in series—the animal's skin surface, its hair coat, and the environment—with the thermal resistance of the hair coat dependent on physical factors and nearby air movement (McArthur, 1981). The physical factors that determine the insulating capabilities of a hair coat consist of hair thickness, density and length, along with the degree of piloerection, though none of these factors can be assumed to be uniform over the whole body or between individuals (Clark et al., 1973).

The presence of a hair coat alone provides increased insulation for an animal and adds another medium that heat must pass through to be radiated from the body. However, Robertshaw (2004) described how the orientation of hair can also alter its reflecting and absorbing attributes. An animal with crimped hair or hair that is arranged in many different directions will cause more reflection of radiant heat, whether that is incoming radiation or radiation reflected by the hair back towards the skin surface. Conversely, straight hair with fibers arranged in the same direction presents a flat surface for incident radiation to be absorbed (Robertshaw, 2004). It is

unclear if there is a relationship between insulation capabilities and biological efficiency. Luiting et al. (1994) reported that more efficient hens had fewer unfeathered patches for energy to be lost. They also indicated that low RFI hens tended to be better feathered. In an RFI study by Basarab et al. (2003) hair cover was measured over the rump in beef steers to determine an insulation index for each animal. However, there was no improvement was observed when the insulation index was included in a regression model used to estimate standardized feed intake (used in the calculation of RFI).

As the majority of beef animals are raised in outdoor management systems, solar radiation is undoubtedly an energy source which may impact IRT. For livestock raised outside, solar radiation is absorbed at the surface of the animal and can substitute heat produced by metabolism (Webster, 1971). When solar loading is high, the incoming radiation energy that is intercepted by an animal will often be greater than that generated by its own metabolic process (Cena and Clark, 1973). The degree of absorption will ultimately depend on behavioural and physical factors associated with individual animals. Posture, as well as the shape of the areas exposed to sunlight will have direct consequences for the energy balance since they determine the proportion of solar energy absorbed by the hair coat or skin (Cena and Clark, 1973).

Pigment colour also plays a major role in defining how much solar radiation will be absorbed by an animal. It is generally accepted that the surface temperature of darker colours will be warmer than that of lighter colours after sunlight exposure. The effect of solar radiation on surface temperatures in animals with varying hair colour measured through IRT has been examined by several researchers (Clark and Cena, 1972; Cena and Clark, 1973; Benesch and Hilsberg, 2003). Different coloured hair coats influence the solar heating effect at the surface with black hair exhibiting warmer temperatures compared to white hair. Thermographs distinctly

showed the black areas of the coat having a warmer surface temperature than the white areas when solar loading is higher with animals such as penguins, tapirs, dairy cows and zebras. In dairy cattle, the difference in temperature between the black and white regions of their coat can be as great as 8^0C in direct sunlight (Clark and Cena, 1972). However, the lasting effect of solar heating appears to be short-lived as evidence has shown an animal's surface temperature will equalized in the absence of sunlight due to either periodic clouding or shade (Cena and Clark, 1973). However, as no direct relationship has been determined to calculate the time needed for surface temperature equalization in the sun's absence, it is unclear how sunlight exposure will affect measurements in the current study, making it difficult to adjust images for solar loading.

Further to absorptive differences of the hair coat, handling procedures may result in differences of surface temperature. There are many areas whereby physical contact with cold handling equipment or the warm surface of another animal may result in conduction prior to infrared measurements, especially if contact last for a prolonged period of time. Colyn (2013) discussed several scenarios while handling beef cattle whereby surface heat could be lost to their surroundings through conduction. For example, whole body scans are not ideal for infrared thermography studies because the presence of a material that is below the animal's surface temperature (such as a chute or alley) can temporarily alter the thermal image. Although limited research is available, it is expected that heat transfer could occur between animals that are in physical contact prior to capturing the infrared image.

Apart from the physical factors affecting surface temperature measured by infrared thermography, the stimulation of certain psychological responses including stimulation of the sympathetic nervous system, or the fight or flight response which can increase heat production as well. The effect of fear exposure in animals starts with an immediate rapid-onset of the

sympathetically-mediated catecholamine response, followed by the slower-onset, longer duration cortisol response mediated by the HPA system (Mellor et al., 2002). Sympathetic activation is characterized by an increased heart rate, the release of adrenaline, and diversion of blood flow to skeletal and heart muscles in anticipation of the "fight" or "flight". Blood flow at the peripheral tissues for heat dissipation has been discussed previously. Thus, blood being diverted towards essential organs in response to fear will influence normal heat loss and impact measurements of biological efficiency. A rapid drop in eye temperature was reported immediately following disbudding in dairy calves (Stewart et al., 2008a) and fear-inducing treatments in beef bulls and heifers (Stewart et al., 2008b), likely due to vasoconstriction of the highly vascular area surround the eye. This decrease in eye temperature occurred 20-40 seconds after stimulation and remained lower until approximately 60 seconds following the stimulation whereby the eye temperature began to return to baseline levels (Stewart et al., 2008b). A similar trend in eye temperature with elapsed time after stress stimulation was observed by Stewart et al. (2008a) with temperatures reaching their initial levels no later than 5 minutes after the stimulus. This corresponds to the immediate effects expected with sympathetic nervous system activation. However, the secondary HPA activation due to fear produces a different physiological response than sympathetic activities. Cook et al. (2001) observed a correlation between maximum eye temperature and plasma and salivary cortisol levels in horses. The same relationship was described in elk and reindeer following antler removal (Cook et al., 2005). The authors suggested that the increased eye temperature may be driven by activation of the HPA axis, but the specific mechanisms involved in this relationship are not yet known.

The immediate but short-lived temperature decrease of eye temperature in the presence of a stressor is important. Stewart et al. (2008a) observed an increase in eye temperature above

their baseline levels after an initial temperature drop in dairy calves following disbudding. This suggests that studies reporting increases in eye temperatures after stresses are introduced (Cook et al., 2001; Cook et al., 2005) fail to detect the initial drop in eye temperature from sympathetic activation because sampling was too infrequent. However, the relationship between radiant heat loss measured through IRT and the timing of the measurement following a stressor has not been established. As well, habituation to the presence of human handlers will likely occur, further complicating the relationship between stress and fear on thermoregulation.

2.5 Summary

Residual feed intake is gaining increased recognition as the primary feed efficiency measure for beef cattle research and performance testing. Production traits such as ADG, WW, YW and BF are independent of RFI and therefore these traits will not be affected when selecting for feed efficient animals. As well, RFI has been shown to be positively correlated to other feed efficiency measures such as FCR and KR, and a moderate heritability makes genetic improvement possible through selection. Unfortunately, the calculation of RFI requires expensive feed intake equipment which has limited the adoption of this feed efficiency measure. There is a need to identify less expensive alternative methods to accurately predict RFI ranking in beef cattle.

Radiant heat loss experienced in beef cattle makes up a major portion of the heat lost through thermoregulation. Under steady-state conditions, energy lost as heat is a function of metabolic efficiency and in turn, heat loss can be used to predict feed efficiency. Infrared thermography has proven to be a useful and effective tool in determining radiant heat dissipated from animals by calculating the temperature of the body surface exchanging heat with the surrounding environment. As well, it has been shown in previous studies that heat loss as

measured by IRT can be used to detect poor meat quality, disease, lameness and signs of estrus in cattle. Additionally, trials have demonstrated that the surface temperature of certain anatomical regions as measured by IRT can be successfully used to predict RFI ranking in beef cattle. However, previous studies utilizing IRT to predict RFI have used high energy concentrate-based diets as the primary feed source. This does not reflect the predominantly forage-based diets being fed on Western Canadian beef operations. Further, potential changes in heat loss from different anatomical regions (eye vs. cheek) in cattle exposed to extreme cold have, to the author's knowledge, not been examined. Examining the ability of radiant heat loss as measured by IRT to predict RFI under forage-based diets would facilitate the standardization of this methodology, allowing the application in beef trials regardless of diet type. Furthermore, the effect of inclement weather conditions on the measurement of IRT traits has not been recognized in previous studies, particularly the effect of extreme cold weather that is common in Western Canada. It is conceivable that beef cattle will at some point be thermally challenged during the winter months which could ultimately affect energy utilization and the ability to maintain thermoregulation. Repeated measurements of radiant heat loss by IRT in animals fed forage-based and grain-based diets over a winter feeding period would contribute to our understanding of using infrared traits to predict RFI in a variation of environmental conditions.

Additionally, RFI is typically measured during the growing phase of a beef animal's life and is assumed to be reflective of an animal's biological efficiency throughout its entire life and under different diet treatments. Historically, performance of beef bulls has been evaluated when fed concentrate-based diets and is assumed to reflect animal performance regardless of diet composition. However, bulls and quite often their offspring are usually managed in a forage-based feeding system thereafter. Assessing the variation in metabolic efficiency for an individual

beef animal receiving a forage-based diet followed by a grain-based diet, or vice versa, would improve our understanding of RFI and benefit the beef industry.

3. Research Hypothesis and Objectives

It was hypothesized that bulls exhibiting a lower eye and cheek surface temperature are more efficient with lower RFI values. In addition, it was hypothesized that RFI ranking in yearling beef bulls determined in the first feeding period should be equal to their ranking in the second feeding period when bulls are fed grain-based diets in both periods, forage-based diets in both periods, or a grain-based diet followed by a foraged based diet, and vice versa.

The objective of this study was to explore the use of infrared thermography as a cost-effective means of predicting biological efficiency as measured by RFI in beef bulls housed in Western Canada. As well, to explore the effect of diet (forage vs grain-based rations) and other influences (i.e. environment, physiological or management factors) in successive feeding periods on RFI repeatability in growing beef bulls

4. Manuscript 1: Predicting residual feed intake in beef bulls by measuring radiated heat loss through infrared thermography

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4.1 Abstract

Residual feed intake (RFI) has been used to select metabolically efficient cattle in beef breeding programs, particularly for sire selection. Adoption of genetic selection using RFI has been limited due to the high cost and difficulty of measuring individual feed intake. An alternative method of predicting RFI is to measure radiated heat loss using infrared thermography (IRT) as previous studies have shown promise using IRT to predict metabolic efficiency in mature cows, heifers, and growing bulls. The objective of this study was to explore use of IRT to predict RFI in growing beef bulls. Sixty bulls in each of two years were fed either a forage-based or a grain-based ration as part of an RFI study. Eye (Ey) and cheek (Ck) surface temperatures were calculated using infrared images of the head collected over a total of 16 and 14 sample days in Years 1 and 2, respectively, using a FLIR S60 camera while continuous collection of infrared images using a within-pen FLIR A310 camera system occurred in Year 2. Bulls were grouped into low, medium and high classes based on ±0.5 of backfat adjusted residual feed intake (RFI_{Fat}) standard deviation; RFI_{Fat} values ranged from -2.27 to +2.61 kg day^{-1} dry matter (avg=0.0; SD=0.61). Sample day Ey and Ck temperatures were pooled and an average temperature was calculated for individual bulls. Average Ey and Ck temperatures determined using the FLIR S60 differed by just 0.03 and 0.25°C, respectively, across low, medium and high RFI groups ($P > 0.05$) while Ey and Ck values from the within-pen camera system varied by 0.49 and 1.12°C, respectively ($P > 0.05$). Temperature deviations associated with extremes in ambient temperature (placing animals outside their thermoneutral zone) and underlying subclinical health problems could bias results in IRT measurements and RFI ranking. Investigation of these factors is needed to standardize IRT collections and conditions under which RFI is determined to improve predictions.

4.2 Introduction

Beef research has traditionally focused on increasing product output (i.e. weight gain, or lean meat carcass yield), without considering the significance of inputs (i.e. feed requirements). Feed expenses account for 50% of the total operating costs in a cow-calf operation (Manitoba Agriculture Food and Rural Development, 2013), creating a challenge for producers in terms of farm profitability. Feed costs for animal maintenance has been estimated to represent approximately 60-65% of the total feed requirements for the herd, with considerable variation among individuals regardless of body size of the animal (Montaño-Burmudez et al., 1990). While the feed conversion ratio (FCR) has typically been used to evaluate feed efficiency in cattle, selection for this ratio trait (Gunsett, 1984) has led to increased body size (Koots et al., 1994), suggesting it is an ineffective method to improve biological efficiency (Archer et al., 1999; Johnson et al., 2003). Residual feed intake (RFI) has recently shown utility in assessing biological efficiency while maintaining phenotypic independence from most production traits (Arthur et al., 1997; Archer et al., 1999; Basarab et al., 2003). However, large-scale use of the RFI concept has been limited, presumably due to cost and the time necessary to calculate RFI. It is apparent that a less expensive, indirect method for determining RFI ranking would benefit the beef industry.

A significant portion of the variation in RFI can be associated with differences in energy partitioning, including but not limited to heat production (Nkrumah et al., 2006). Any excess internal heat generated by a homeothermic animal may be considered as lost energy and can be dissipated through latent (evaporation) and sensible (radiation, conduction or convection) heat loss mechanisms, with radiation accounting for 40-60% of the total sensible heat loss (Kleiber, 1975). In addition, body surface temperatures measured through infrared thermography (IRT)

have been used to predict radiant heat dissipated from homeothermic animals (Cena and Clark, 1973; Turner, 2001; McAfferty, 2007). This methodology has been successfully applied to beef cattle under the assumption that the relative biological efficiency among individuals could be predicted by measuring the radiant heat loss from specific anatomical regions, including the side of the animal (Scott et al., 2002), the dorsal region (Scott et al., 2002; Schaefer et al., 2005), the hind region (Montanholi et al., 2006), the back of the front hooves (Montanholi et al., 2009), the snout (Montanholi et al., 2010), and the eye and cheek regions (Montanholi et al., 2009, 2010; Colyn, 2013).

It is well known that peripheral tissues, especially those found on the extremities, play an important role in facilitating the transfer of heat from the body to the environment (Whittow, 1962; McArthur, 1981). In previous studies, the surface temperature of the back of the left and right hooves exhibited highly positive correlations with RFI (r=0.38 and 0.43 respectively) in beef bulls (Montanholi et al., 2009). Further, significant relationships between RFI and eye and cheek temperatures region have been reported in yearling beef bulls (Montanholi et al., 2009) and yearling beef heifers (Colyn, 2013). However, there is limited data examining the relationship between thermography and RFI on beef cattle when animals are exposed to persistently cold conditions that at times exceed their lower critical temperature (LCT). The objective of this study was to explore the use of infrared thermography as a means of predicting biological efficiency as measured by RFI in beef bulls housed in a Western Canada feedlot setting.

4.3 Materials and Methods

4.3.1 Facilities and animal management

In each of two years, sixty purebred Angus bulls representing Angus cattle from eleven pedigree lines with a mean age of 280 days (SD= 27) and 249 days (SD=22) and an average weight of 306.6 kg (SD=43) and 313.9 kg (SD=32) in Years 1 and 2 respectively, were transported to the Glenlea Research Station, University of Manitoba. Upon arrival, they were vaccinated with Vista Once (Merck Animal Health, Summit, NJ) and Vision 8 (Merck Animal Health, Summit, NJ), and treated with Noromectin (Norbrook Inc., Lenexa, KS) pour-on solution. Vitamin A and D injections were administered at the start of the trial and every 3 months thereafter. Thereafter, bulls were randomly assigned into 4 pens, each equipped with four GrowSafe® (GrowSafe Systems Ltd., Airdrie, Alberta) feed bunks and a heated watering bowl. Pens were bedded with a base of straw followed by flax shives, which was replenished as needed during the trial. Two pens were fed a forage-based (F) diet and remaining two pens were fed a grain-based (G) diet on an *ad libitum* basis in the first feeding period (FP1), as described in Table 1. Following FP1, one forage pen was switched to a grain-based diet (FG), one grain pen switched to a forage-based diet (GF), while the remaining forage (FF) and grain (GG) pens remained on their respective diets before a 14-day adaptation period was observed prior to the second feeding period (FP2).

The bulls were weighed two consecutive days at the start and end of each feeding period, where FP1 was conducted from December to March, and FP2 commenced at the end of March and ended in June each year. Biweekly weight measurements in a 76-day feeding period and weekly weight measurements in a 63-day feeding period and individual feed intake measured by the GrowSafe® feeding system provided sufficient growth and intake data needed for

determination of RFI, as outlined by Wang et al. (2006). A daily feed intake average was calculated for each animal in each feeding period.

All animals were cared for following guidelines established by the Canadian Council on Animal Care (1993).

4.3.2 Measurements

4.3.2.1 Carcass traits

An Aloka 500V diagnostic real-time ultrasound camera (Overseas Monitor Corporation Ltd., Richmond, BC) was used to measure backfat (BF), rumpfat (RF), ribeye area (REA) and intramuscular fat (IMF) at the start and end of each feeding period using procedures described by Robinson et al. (1992).

4.3.2.2 Hand-held infrared device

During scheduled weigh days, animals were moved from outdoor pens to an indoor handling facility where they were handled individually in a hydraulic squeeze chute. Radiant heaters located inside the building were turned off prior to eliminate any heat emissions which could influence image quality. Immediately after restraining the animals a FLIR S60 (FLIR Comp., Boston, MA) infrared camera located 2 meters from the head gate and positioned perpendicular to the chute, was used to capture images from the orbital and cheek regions of each animal (Figure 1). Prior to capturing the images, any dry debris located on the face of the bulls was brushed off. However, debris which created a biased thermal reading or which left a residue after removal was noted and those images were omitted from the data set. Dry-bulb ambient temperature, recorded after every third animal, was continuously adjusted within the infrared camera's parameters to reflect the current environmental conditions in order to

accurately interpret thermographs in subsequent analysis. Ambient temperature during image collection within the handling facility ranged from -5.8 to 22.8^{0}C during FP1 and FP2 which is within the thermoneutral zone (TNZ) for beef cattle (Hahn, 1999). As well, outdoor temperature data for the entire feeding trial (Figure 2) was available from the National Centre for Livestock and the Environment Weather Station located at the Glenlea Research Station.

4.3.2.3 Stationary infrared device

In addition to hand-held infrared camera, an automated stationary infrared camera system was used (Figure 3) during FP2 in Year 1 and throughout FP1 and FP2 during Year 2, to capture images of animals. A FLIR A310 (FLIR Comp., Boston, MA) infrared camera was mounted on a motorized platform 0.8 m from the watering bowl. Radio frequency identification (RFID) antennas received information from RFID tags located in the bull's ear to identify the animal. Images of the orbital region and cheek (located immediately beneath the orbital region; Figure 4) were captured while the animal was drinking from the water bowl. Ambient temperature was recorded concurrently. Image information was stored on a computer hard-drive for subsequent analysis. Images that were captured between approximately 20:00-10:00 were preferred to minimize the effects of increased surface temperatures due to radiation absorbed directly from sunlight.

4.3.3 Calculations

4.3.3.1 Residual feed intake

Residual feed intake was calculated using the methodology described by Basarab et al. (2007). The growth of each bull was modeled by using a linear regression of weight against time.

Figure 1. Illustration of the size of the anatomical areas used to determine surface temperature and the associated variability.

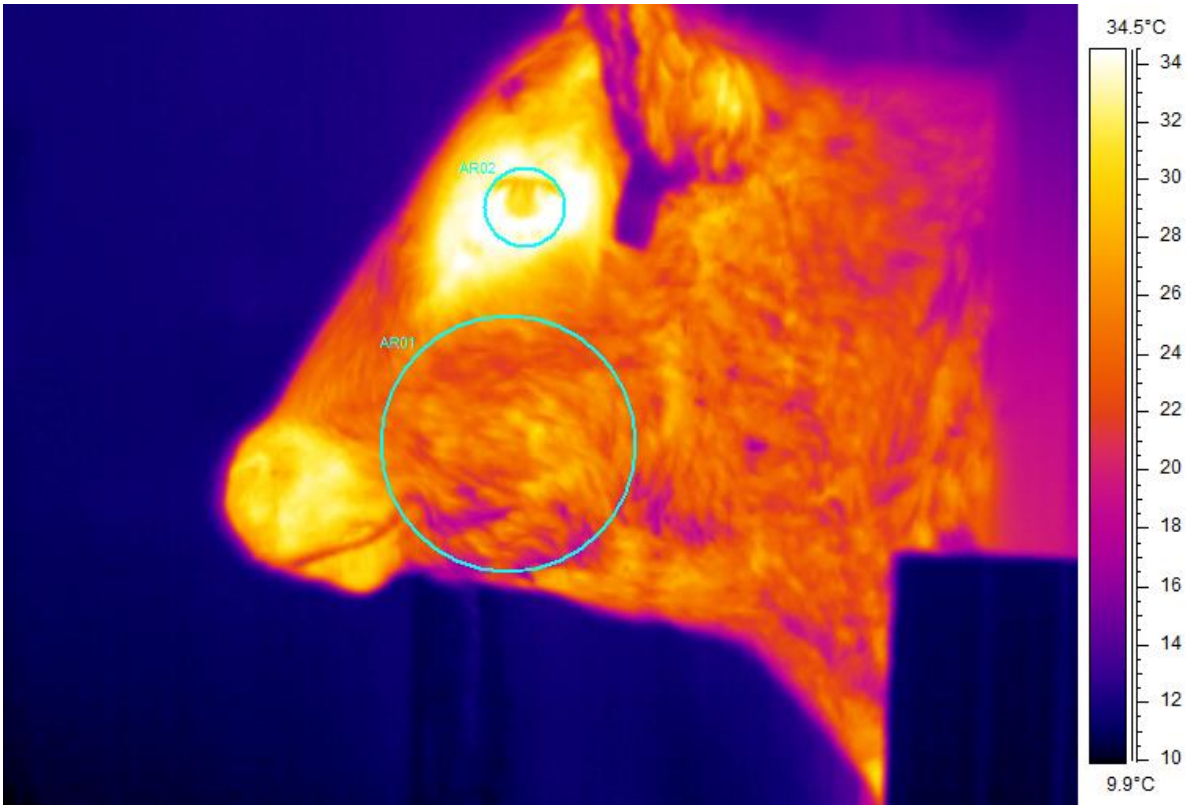


Figure 2. Average daily outside (dry-bulb) temperatures for (A) Feeding Period 1 (FP1) and (B) Feeding Period 2 (FP2) recorded at the Glenlea Research Station during Years 1 and 2 of the trial.

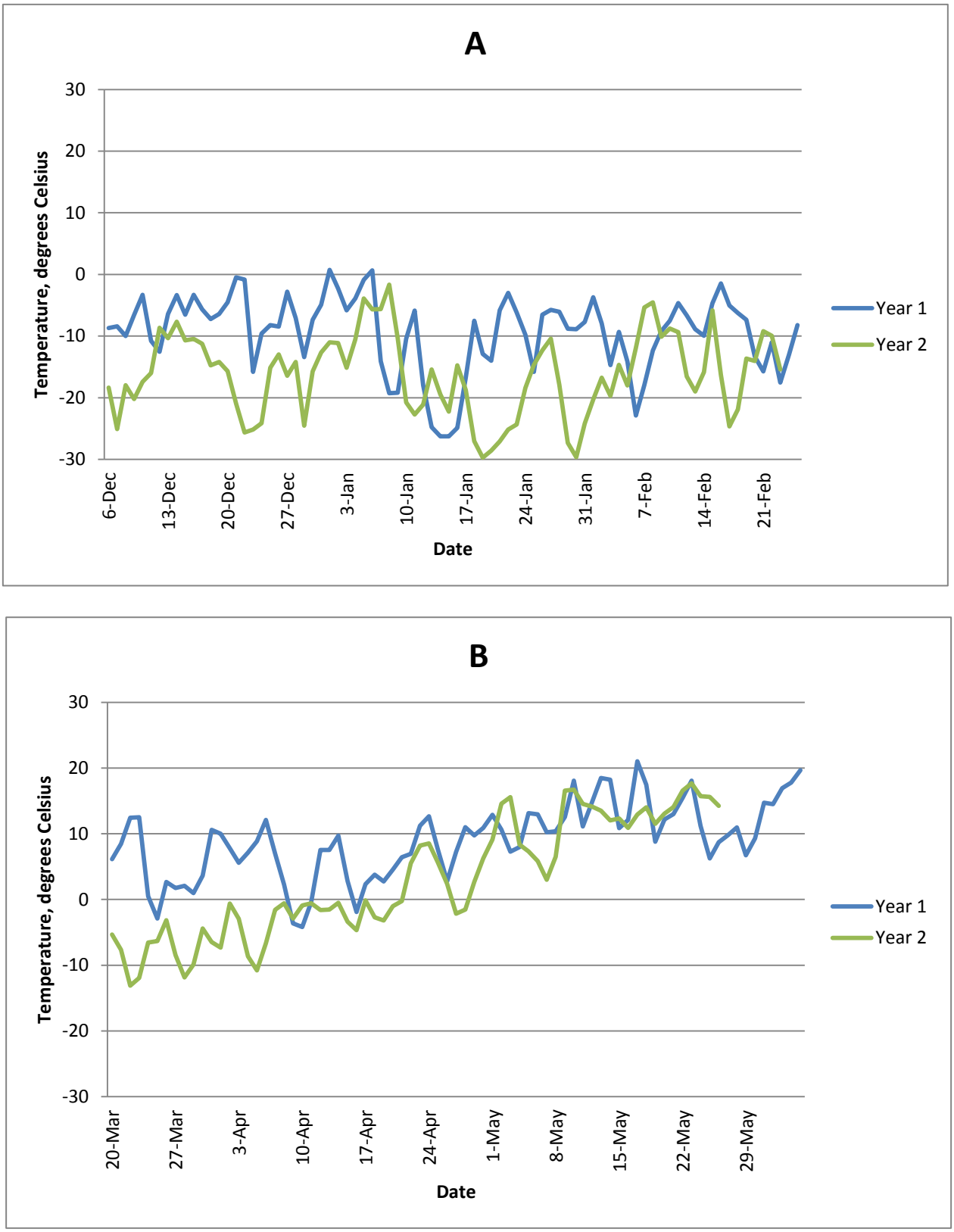


Figure 3. Stationary camera system design located at the watering bowls (a) and used to capture infrared images from bulls in pens 1 and 2. The system components include b) a unit containing necessary hardware for processing and storage of images, c) a FLIR A310 infrared camera, d) a motorized platform to monitor two different pens and e) RFID antennae to identify individuals.

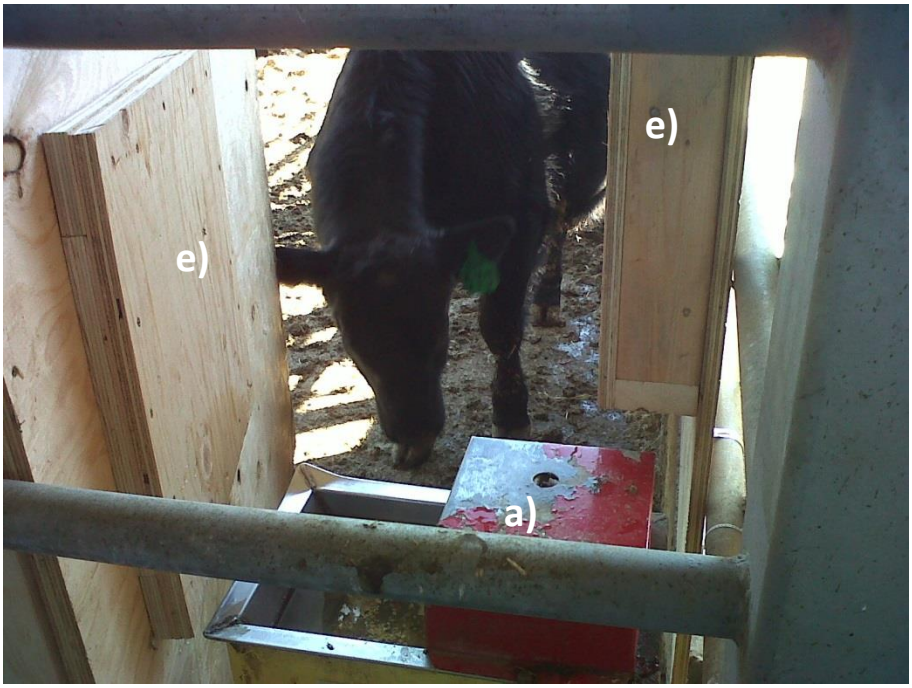
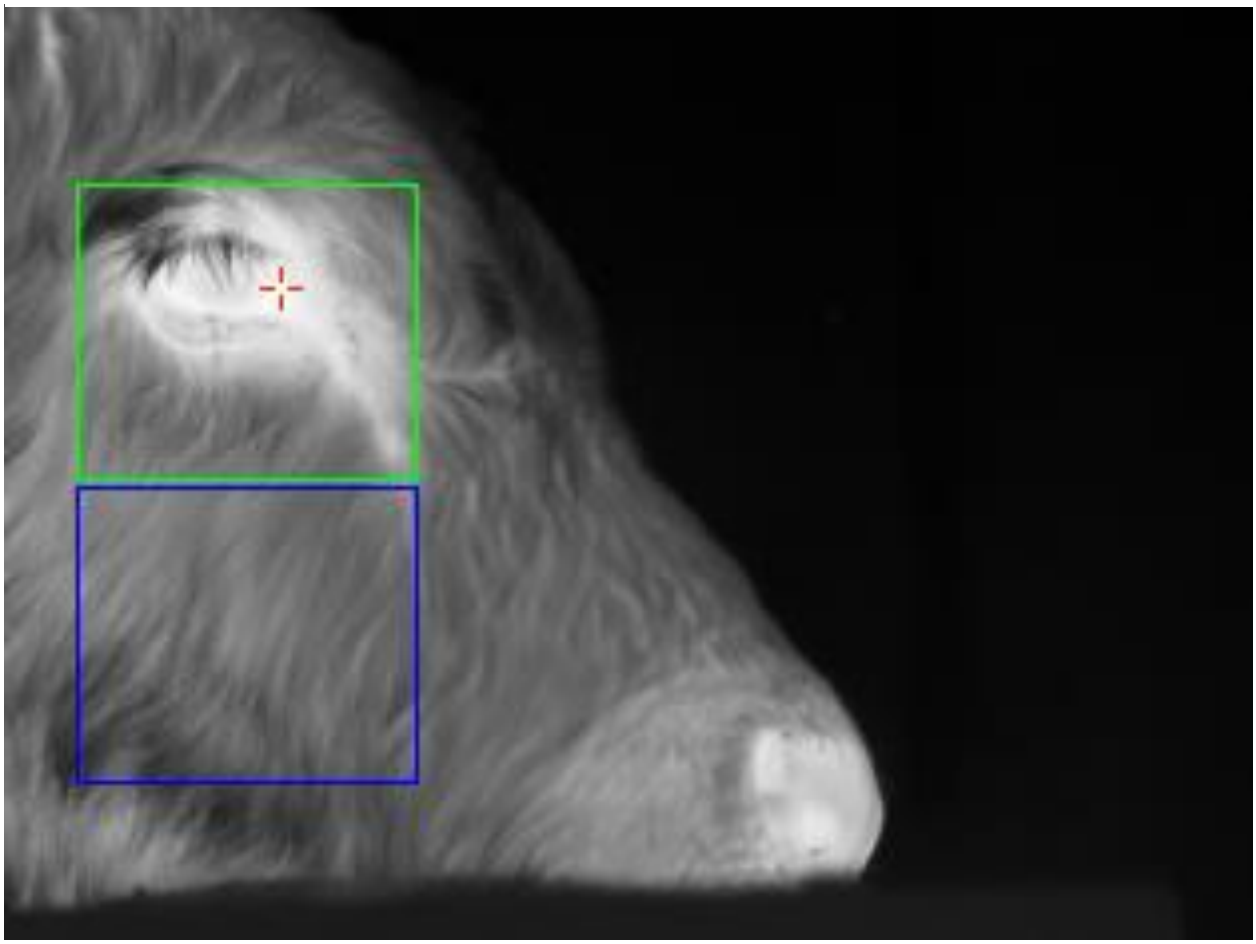


Figure 4. A sample image created by the stationary camera software which identifies eye (green) and cheek (blue) surface temperatures.



Growth curves for most bulls had a coefficient of determination (R^2) greater than 0.95 (mean=0.98) indicating that they grew normally with no hindrance from morbidity or nutritional inadequacies. Start of test (SOT) weight, mid-point weight (MWT), and average daily gain (ADG) were determined using regression coefficients from each animal's growth curve.

Total feed intake was determined by multiplying daily feed intake (calculated using the GrowSafe® feeding system) by total days on test. Dry matter (DM) and metabolizable energy (ME) values (Table 1) of the respective diets were used to calculated total dry matter intake (DMI) and total metabolizable energy intake (MEI). The total MEI was then divided by 10 MJ

ME kg^{-1} DM to standardize energy intake with previous trials (Arthur et al., 2001a; Basarab et al., 2003, Nkrumah et al., 2004). This value was divided by the DM content to convert the total standardized dry matter intake into total standardized feed intake. Finally, the total standardized feed intake was divided by the number of days on test to obtain average standardized daily feed intake (SFI, kg d^{-1}) for each bull.

Table 1. Nutrient composition of forage and grain-based diets (Years 1 and 2).

	Year 1		Year 2	
Item	Forage	Grain	Forage	Grain
Ingredient composition, %, as-fed basis				
Alfalfa Hay	26.4	-	17.9	-
Corn Silage	73.4	38.5	81.7	39
Alfalfa Silage	-	38.6	-	33.1
Corn Grain	-	22.2	-	27.5
Limestone	-	-	0.3	-
Mineral	0.1	0.1	0.1	0.1
Salt	0.1	0.1	0.1	0.1
Nutrient composition, DM basis				
Dry Matter, %	50.9	49.7	50.7	52.7
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^{-1}	9.67	10.67	11.10	12.06
Crude Protein, %	11.9	10.3	13.1	12.3
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

For prediction of expected feed intake (EFI), SFI was regressed against ADG (kg d^{-1}), metabolic MWT (MMWT, kg $^{0.75}$), and end of test BF (BFend, mm) using PROC GLM (SAS Institute Inc. 2008) and the following model:

$$Y_i=\beta_O+\beta_1 ADG_i+\beta_2 MMWT_i+\beta_3 BFend_i+e_i$$

where Y_i= SFI for animal i, β_O= regression intercept, β_1=partial regression coefficient of SFI on ADG, β_2=partial regression coefficient of SFI on MMWT, β_3=partial regression coefficient of SFI on BFend, and e_i=the residual error of SFI for the i'th animal.

Backfat adjusted residual feed intake (RFI_{Fat}) was evaluated by diet group and calculated as the difference between actual standardized feed intake and expected feed intake (RFI_{Fat}=SFI-EFI). The bulls were placed into low, medium, or high RFI groups based on ± 0.5 SD around the mean.

4.3.4 Processing infrared thermography images

4.3.4.1 Hand-held camera

Eye and cheek temperatures were calculated from the infrared images using FLIR Researcher® Software (Version 2.8, Boston, MA). Ambient temperature in the handling facility, recorded continuously during respective sampling days, was entered into the imagery software to reflect the current environmental conditions when each image was taken. A surface emissivity value was required before an accurate surface temperature can be predicted using IRT systems. The recommended emissivity value for biological tissue of 0.98 (McCafferty, 2007) was used for all images. In addition, each image was visually evaluated for acceptable focus, position, angle, clarity and lack of motion. Based on these criteria, one image for each bull was selected on a daily basis and used to determine eye or cheek temperatures. To do so, the circle tool in FLIR Researcher was utilized to trace an area over the eye to display the mean temperature and standard deviation of all of the pixels in that region. A circle was placed in such a way so as to minimize the total area being analyzed while ensuring the entire eyeball was included within this

circle. A second circular shape was traced over the cheek, bordering the lower jaw line without encroaching into the warmer muzzle or orbital regions. Both the eye and cheek circle areas were resized as needed to accommodate different head shapes and sizes. An example of the anatomical regions and how their relative size can vary based on animal type is shown in Figure 1. Mean eye and cheek temperatures were calculated for every animal on each sampling day. Mean values were used rather than minimum or maximum values because every pixel is used to derive the average, whereas maximum and minimum temperatures could potentially represent a single pixel in the area of interest.

4.3.4.2 Stationary camera system

FLIR Total2 software (FLIR Systems AB, 2003) was used to derive mean eye and cheek temperatures from stationary camera infrared pictures by using the warmest cluster of pixels (typically the eye) to locate the eye and cheek regions. As with the hand-held infrared camera, an emissivity value of 0.98 was used to calibrate the camera for all images. A thermometer probe located on the camera unit continuously monitored ambient temperature to provide accurate measurements that reflected the current environmental temperature conditions when the respective image was captured. Thereafter, images were visually inspected for proper region positioning, clarity, focus, and lack of movement, as described above. Any image that failed to meet quality requirements was not used in the statistical analysis. All images deemed suitable were used to create pooled averages for the eye and cheek within each feeding period.

4.3.5 Statistical analysis

A total of 16 and 14 repeated measures of eye and cheek temperatures were gathered in FP1 and FP2, respectively, over the two-year experiment. Descriptive measurements were evaluated by combining results from Years 1 and 2 by feeding period because bulls in each

respective feeding period, regardless of year, were at a comparable stage of growth. Additionally, bulls were considered to be at a similar stage of growth during FP1 in Years 1 and 2, and during FP2 in Years 1 and 2 so comparisons between feeding periods across years rather than between periods within a year were deemed to be more appropriate. Infrared thermography traits were analyzed using PROC MIXED (SAS Institute Inc. 2008) to determine the relationship between eye and cheek temperature and RFI group. Residual feed intake group, sampling date, year, and their interaction were fixed effects in the model with individual animals as repeated subjects. The unstructured (un) covariance structure was used as it had the lowest Akaike information criterion (AIC) value after comparing several other covariance structures. Overall significance of the main effects was determined by F-values using Type 3 tests of main effects. A simple regression of the pooled average for eye and cheek temperatures with RFI group was also performed using PROC REG (SAS Institute Inc. 2008). Mean values for eye and cheek temperature within the three RFI groups were tested using Tukey's range test.

The effects of year, period, diet treatment and RFI group were evaluated using PROC MIXED to determine their influence on growth, carcass and IRT traits; least square differences of means were tested using the PDIFF option. In this model, each trait was modeled separately as the dependent variable and year, period, diet and RFI group were used as the independent variables. Individual animals were considered a random effect. Residuals for each performance and IRT trait were calculated and used in the CORR procedure (SAS Institute Inc. 2008) to determine correlation coefficients. Infrared thermography traits were compared using pooled averages within each feeding period.

4.4 Results

Validation of feed intake and performance data is presented in Table 2. Bulls were on average 31 days older at the beginning of the feeding experiment in Year 1 compared to Year 2. The number of days excluded due to compromised data integrity ranged from five to seven days within each feeding period. However, integrity of the data collected during the experiment was exceptional; the lowest daily average feed disappearance (AFD) value observed was 99.1 % in Year 2 FP2. Pearson correlations were moderate to high between DMI and MMWT, ADG, EFI and BF, suggesting that the component data used to calculate EFI conformed well to the model used. Finally, ADG and MMWT contributed as low as 21% and as high as 82% of the variation in DMI across both feeding periods in Years 1 and 2. Improvements of the model to explain the variation in DMI ranged from 0.03 to 11% when BF was included.

The significance of year, diet, feeding period and RFI group as well as their interactions for carcass, growth and infrared traits are displayed in Table 3, while mean values are presented in Table 4. The effect of year was significant for all traits measured ($P < 0.0001$) with the exception of RFI_{Fat} ($P > 0.05$). Bulls averaged 1.74 mm, 1.56 mm and 70.8 mm^2 for RF, BF and REA in Year 1, respectively, compared to 2.56 mm, 2.27 mm, and 79.8 mm^2 in Year 2, respectively. As well, the average IMF measurement was 15% smaller ($P < 0.0001$) in Year 1 than Year 2. End of test weight, MMWT, and ADG were lower ($P < 0.0001$) in Year 1, indicating slower growing bulls with lighter body weights and smaller size compared to Year 2. Bulls consumed 8.94 ± 0.08 kg and 9.03 ± 0.09 kg for DMI and SFI, respectively, in Year 1, which was 12 and 23% lower ($P < 0.0001$) than Year 2, respectively. This resulted in a more

Table 2. Validation of feed intake and performance data during FP1 and FP2 in Years 1 and 2 for beef bulls.

Parameters	Year 1 FP1		Year 1 FP2		Year 2 FP1		Year 2 FP2	
Number of animals	60		60		59		58	
Mean age at start of feeding period	280		383		249		355	
Total days on test	83		78		82		67	
Number of days excluded	5		7		7		6	
Mean daily assigned feed disappearance (AFD), %	99.6		99.3		99.6		99.1	
Total feed station days (FSD)[1]	1328		1248		1312		1072	
Feed station days < 95% AFD	6		7		8		7	
Pearson correlations	Forage	Grain	Forage	Grain	Forage	Grain	Forage	Grain
DMI and MMWT	0.41	0.80	0.58	0.83	0.71	0.75	0.66	0.35
DMI and ADG	0.37	0.86	0.51	0.88	0.55	0.74	0.35	0.44
DMI and EFI	0.56	0.92	0.69	0.92	0.80	0.87	0.70	0.54
DMI and BF	0.20	0.50	0.22	0.57	0.37	0.24	0.32	0.24
Coefficients of determination								
Variation in SFI[2] due to ADG, MMWT	0.30	0.82	0.47	0.82	0.57	0.75	0.47	0.21
Variation in SFI[2] due to ADG, MMWT, BF	0.31	0.85	0.47	0.85	0.64	0.75	0.49	0.29

[1]Feed station days (FSD) is calculated as the product of days on test and number of feeding nodes.

[2]Standardized feed intake, adjusted for ME content of each diet and divided by 10 MJ ME kg d^{-1} to allow fair comparisons between forage and grain-based diets.

Table 3. Significance of factors and their interactions for carcass, growth and infrared thermography traits measured in beef bulls.

Parameter	Year (Y)	Diet (D)	Feeding Period (P)	RFI Group (G)	Y*D	Y*P	Y*G	D*P	D*G	P*G
Carcass traits										
Rumpfat	***	***	***	ns	ns	***	ns	ns	ns	ns
Backfat	***	***	***	ns	ns	***	ns	ns	ns	ns
Ribeye area	***	ns	***	ns	ns	*	ns	ns	ns	ns
Intramuscular fat	***	ns	***	ns	ns	**	ns	ns	ns	ns
Performance traits										
End weight	***	ns	***	ns	ns	ns	ns	ns	ns	ns
ADG	***	***	***	ns	***	***	ns	ns	ns	ns
DMI	***	***	***	***	ns	ns	ns	*	ns	ns
[1]SFI	***	***	***	***	ns	ns	ns	ns	ns	ns
FCR	***	ns	ns	***	***	***	ns	ns	ns	ns
MMWT	***	ns	***	ns	ns	**	ns	ns	ns	ns
RFI_{Fat}	ns	ns	ns	***	ns	ns	**	ns	**	***
[2]Infrared thermography traits										
Ck_{HH}	***	***	***	ns	ns	***	ns	*	*	ns
Ey_{HH}	***	**	***	ns	ns	ns	ns	ns	ns	ns
Ck_S†	N/A	ns	***	ns	N/A	N/A	N/A	ns	ns	ns
Ey_S†	N/A	ns	***	ns	N/A	N/A	N/A	ns	ns	ns

[1]Standardized feed intake, adjusted for ME content of each diet and divided by 10 MJ ME kg d^{-1} to allow fair comparisons between forage and grain-based diets.

[2]Cheek (Ck) and eye (Ey) surface temperatures were measured with the handheld (HH) and stationary (S) infrared camera systems.

† Infrared measurements captured with the stationary camera were analyzed without the year effect included in the model as stationary images were only captured in Year 2.

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

Table 4. Carcass, growth, and infrared thermography traits in relation to year, feeding period, diet and RFI group for beef bulls.

	Year			Feeding Period			Diet			RFI Group			
Parameter	1	2	SE	1	2	SE	Forage	Grain	SE	Low	Medium	High	SE
Carcass traits													
Rumpfat, mm	1.74[a]	2.56[b]	0.10	1.80[a]	2.51[b]	0.07	1.95[a]	2.36[b]	0.08	2.19	2.10	2.17	0.09
Backfat, mm	1.56[a]	2.27[b]	0.06	1.56[a]	2.27[b]	0.06	1.71[a]	2.12[b]	0.06	1.93	1.92	1.90	0.07
Ribeye area, mm^2	70.8[a]	79.8[b]	0.8	68.8[a]	81.9[b]	0.8	74.7	75.9	0.8	75.9	76.2	73.8	1.0
Intramuscular fat, %	2.95[a]	3.45[b]	0.05	3.55[a]	2.85[b]	0.05	3.17	3.23	0.05	3.10	3.21	3.29	0.06
Performance traits													
End weight, kg	478[a]	523[b]	5	421[a]	580[b]	5	478	503	5	503	501	498	6
ADG, kg d^{-1}	1.38[a]	1.70[b]	0.02	1.35[a]	1.73[b]	0.02	1.46[a]	1.61[b]	0.02	1.55	1.54	1.53	0.03
DMI, kg DM d^{-1}	8.94[a]	10.17[b]	0.08	8.52[a]	10.59[b]	0.08	9.07[a]	10.04[b]	0.08	9.02[a]	9.52[b]	10.12[c]	0.10
[1]SFI, kg DM d^{-1}	9.03[a]	11.80[b]	0.09	9.19[a]	11.64[b]	0.09	9.35[a]	11.49[b]	0.09	9.83[a]	10.39[b]	11.04[c]	0.11
FCR, kg DM kg^{-1} gain	6.67[a]	6.09[b]	0.08	6.46	6.30	0.08	6.32	6.45	0.08	5.97[a]	6.37[b]	6.80[c]	0.09
MMWT, kg	92.3[a]	99.2[b]	0.7	83.3[a]	108[b]	0.7	96.0	95.4	0.7	96.1	95.8	95.3	0.9
RFI_{Fat}, kg DM d^{-1}	0.00	0.04	0.03	-0.01	0.05	0.03	0.02	0.01	0.03	-0.63[a]	0.02[b]	0.68[c]	0.03
[2]Infrared thermography traits													
Ck_{HH}, ^0C	23.3[a]	18.2[b]	0.2	16.0[a]	25.6[b]	0.1	20.4[a]	21.1[b]	0.1	20.8	20.8	20.8	0.2
Ey_{HH}, ^0C	32.6[a]	32.0[b]	0.1	31.6[a]	33.1[b]	0.1	32.2[a]	32.4[b]	0.1	32.2	32.3	32.4	0.1
Ck_S, ^0C	-	-	-	13.4[a]	27.0[b]	0.4	20.6	19.8	0.4	19.8	20.9	19.8	0.6
Ey_S, ^0C	-	-	-	29.5[a]	32.7[b]	0.1	30.9	31.3	0.2	30.8	31.2	31.2	0.2

[1]Standardized feed intake, adjusted for ME content of each diet and divided by 10 MJ ME kg d^{-1} to allow fair comparisons between forage and grain-based diets.
[2]Cheek (Ck) and eye (Ey) surface temperatures were measured with the handheld (HH) and stationary (S) infrared camera systems.
Least square means with different superscripts within rows differ significantly ($P<0.05$); means are adjusted by Tukey's range test.

efficient ($P < 0.0001$) FCR mean in Year 2 (6.09 ± 0.08 kg DM kg^{-1} gain) compared to Year 1 (6.67 ± 0.08 kg DM kg^{-1} gain). Finally, Ck_{HH} (23.3 ± 0.2^{0}C) and Ey_{HH} (32.6 ± 0.1^{0}C) values were 0.6^{0}C warmer, and Ck_{HH} was on average 5.1^{0}C warmer in Year 1 versus Year 2 ($P<0.0001$), which corresponded to milder mean ambient outdoor temperatures in Year 1 (Figure 2).

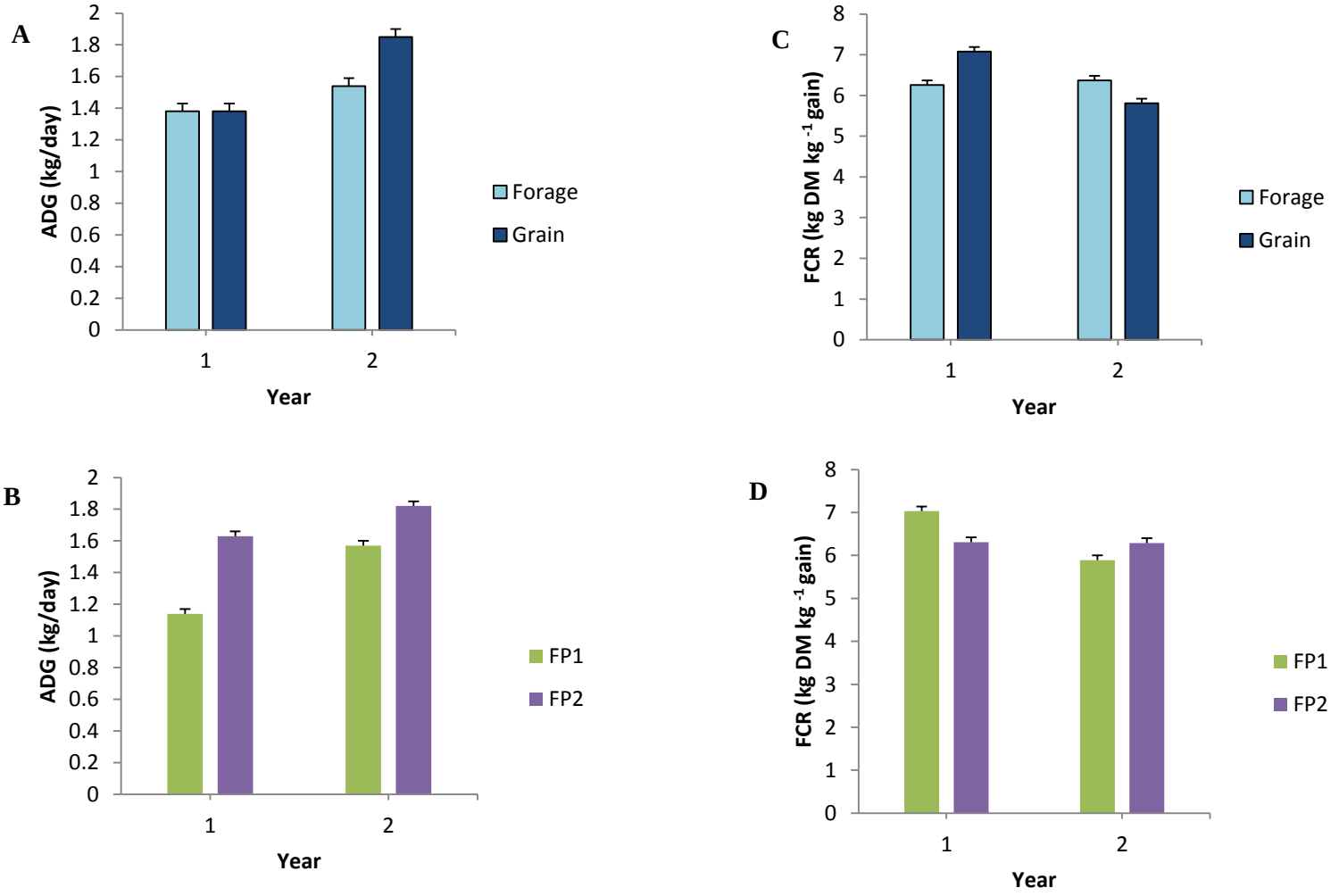
Feeding period was also a significant factor across all of the traits ($P < 0.0001$) except for FCR and RFI_{Fat} ($P > 0.05$). In FP1 bull carcass traits were significantly lower ($P < 0.0001$) than FP2, reflecting younger, more immature animals at the end of FP1. Fat deposition in FP1, measured by RF and BF, was 0.71 mm lower ($P < 0.0001$) for both measurements than in FP2. Ribeye area measured in FP1 was 13.1 mm^2 smaller than FP2 ($P < 0.0001$), while IMF was greater ($P < 0.0001$) in FP1 compared to FP2 (3.55 and 2.85 ± 0.05%, respectively). Growth performance also appeared to be greater for bulls in FP2 as bulls gained weight 28% faster and consumed 2.07 kg d^{-1} more feed in FP2 than in FP1; SFI in FP2 was also 2.45 kg DM d^{-1} higher in the second feeding period. As expected, this resulted in a heavier ($P < 0.0001$) end weight and MMWT (580 ± 5 kg and 108 ± 0.7 kg, respectively) at the end of FP2 compared to end weight and MMWT after FP1 (421 ± 5 kg and 83.3 ± 0.7 kg, respectively). Mean cheek surface temperatures determined with the stationary and hand-held cameras were 13.6 and 9.6^{0}C cooler, respectively, in FP1 than in FP2 ($P < 0.0001$). Similarly, mean eye surface temperatures were 3.2 and 1.5^{0}C cooler ($P < 0.0001$) for the stationary and hand-held cameras, respectively, in FP1. This was expected due to a warmer mean outdoor ambient temperature in FP2 compared to FP1 (Figure 2). In general, bull cheek and eye surface temperature means obtained with the handheld camera were warmer compared to mean values calculated from stationary camera images for both feeding periods.

Ribeye area, IMF, end weight, FCR, MMWT and RFI_{Fat} did not differ significantly between forage and grain diet treatments ($P > 0.05$). However, several measured traits were significantly affected by diet treatment. Rib fat and backfat were 21 and 24% greater, respectively, for bulls fed the grain diet compared to the forage diet ($P<0.0001$). Bulls in the grain diet treatment also grew 10% faster than those in the forage diet treatment ($P<0.0001$) and consumed 0.97 kg d^{-1} more feed ($P < 0.0001$). Additionally, SFI was 23% greater for bulls in the grain diet treatment versus bulls in the forage diet treatment. Finally, infrared thermography measurements differed significantly between diet treatments, where bulls in the grain treatment averaged warmer Ck_{HH} (21.1 ± 0.1^{0}C) and Ey_{HH} (32.4 ± 0.1^{0}C) values than those in the forage treatment (20.4 ± 0.1^{0}C and 32.2 ± 0.1^{0}C for Ck_{HH} and Ey_{HH}, respectively). No significant differences were observed for IRT measurements calculated from images captured with the stationary camera between diet treatments ($P > 0.05$).

The effect of RFI group on carcass and IRT traits was not significant ($P > 0.05$), but was significant for DMI, SFI, FCR, and RFI_{Fat} ($P < 0.0001$). Average DMI and SFI were greater for bulls in the medium and high RFI Groups. . Dry matter intake was at 9.02 ± 0.1 kg d^{-1} for low RFI bulls, increasing 0.5 kg d^{-1} for medium RFI bulls and 1.1 kg d^{-1} for high RFI bulls. Similarly, SFI mean values were 9.83, 10.39 and 11.04 kg DM d^{-1} for low, medium and high RFI groups, respectively. In addition, FCR improved by 6% for bulls in the medium RFI group, and by 12% for low RFI bulls compared to bulls in the least efficient (high RFI) group. As expected, RFI_{Fat} differed significantly ($P < 0.0001$) between RFI groups, averaging -0.63, 0.02 and 0.68 kg DM d^{-1} for bulls in low, medium and high RFI classifications.

As described in Table 3, interactions between Year and Diet were observed for ADG, with the faster rate of gains in Year 2 for bulls fed the grain diet treatment (Figure 5A). Year and

Figure 5. Effect of (A)Year x Diet and (B) Year x Feeding Period (FP) interaction on average daily gain (ADG) and (C)Year x Diet and (D) Year x Feeding Period (FP) for feed conversion ratio (FCR).



FP interactions were also significant; bulls in FP1 in Year 1 grew slower than all of the subsequent feeding periods (Figure 5B). Feed conversion ratios were affected by Year and Diet and Year and FP interactions as well. The most efficient bulls were observed in grain diet treatment during Year 2, while FCR values were lowest (more efficient bulls) during FP1 in Year 2 (Figure 5C, D). Figure 6 illustrates the significant interactions for RFI_{Fat} between RFI group and FP (A), Year (B) and Diet (C). Residual feed intake values for bulls in low and high RFI groups were greater in magnitude in FP2 compared to FP1 (Figure 6A). This was also the case for low and high RFI bulls in Year 2 (Figure 6B) and in the grain-fed bulls compared to the forage-fed bulls (Figure 7C). Bulls in the medium RFI group had slightly positive RFI_{Fat} values for each interaction factor but did not deviate considerably from 0.

Pearson correlation coefficients between IRT traits and growth, efficiency and carcass characteristics for FP1 are given in Table 5. Cheek and eye surface temperatures measured with the handheld infrared camera were not correlated ($P > 0.05$) with BF, RF, REA or IMF. Significant correlations were observed ($P < 0.05$) between Ck_{HH} and ADG ($r=0.29$), FCR ($r=-0.21$) and SFI ($r=0.21$) while Ck_{HH} was strongly correlated to Ck_S ($r=0.54$; $P < 0.01$). There was also a positive correlation ($P < 0.05$) between Ey_{HH} and Ey_S ($r=0.43$). Mean eye temperature measured with the stationary camera system was negatively correlated ($P < 0.05$) with REA_F ($r=-0.38$); cheek and eye temperatures calculated using stationary camera system in FP1 were also significantly correlated ($r=0.73$, $P < 0.001$). All correlations between RFI_{Fat} and IRT measurements were not significant ($P > 0.05$).

Correlation values for IRT traits with growth, carcass and efficiency performance in FP2 are displayed in Table 6. Significant correlations between Ck_{HH} and ADG ($r=0.24$; $P < 0.01$) and Ey_{HH} and SFI ($r=0.22$; $P < 0.05$) were observed. However, no other significant correlations ($P >$

Figure 6. Effect of (A) Feeding Period (FP) x RFI group, (B) Year x RFI group and (C) Diet x RFI group on RFI_{Fat}.

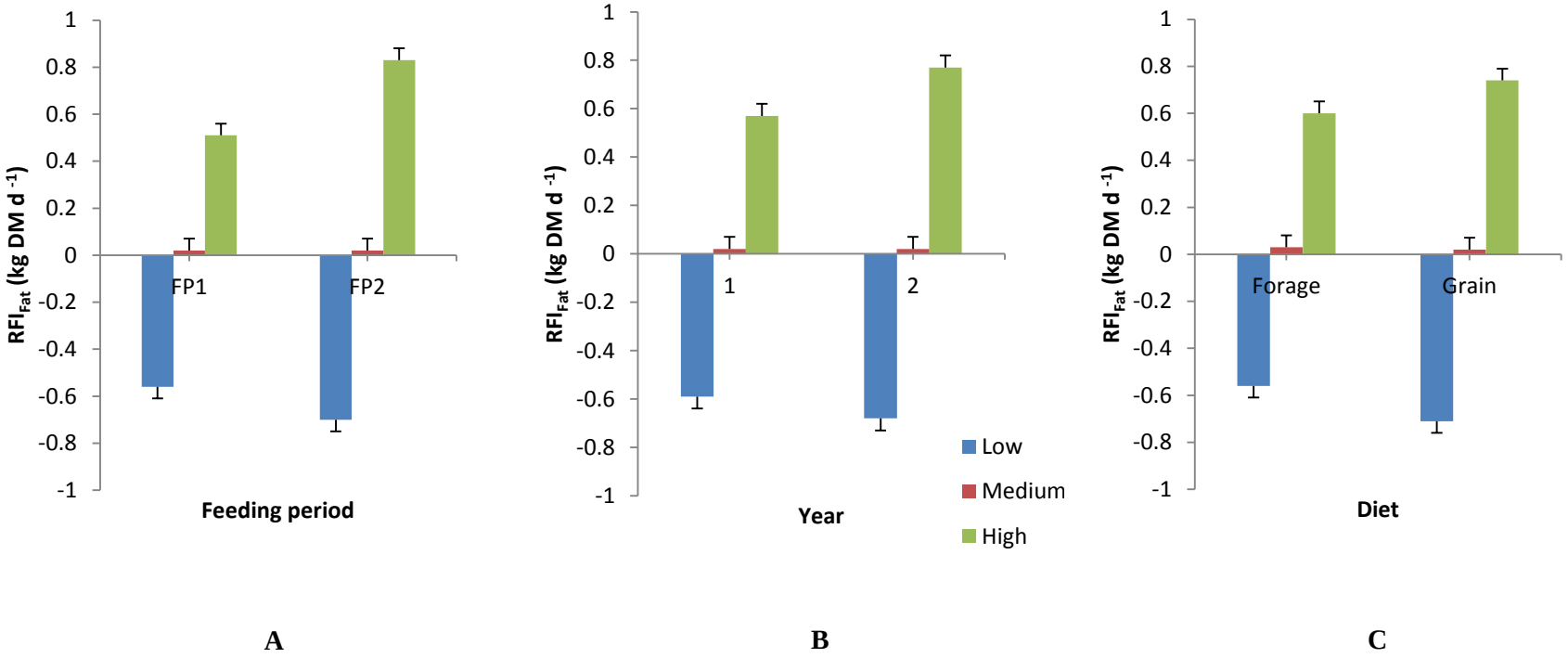


Table 5. Pearson correlation coefficients between surface temperatures (measured through infrared thermography) and growth, carcass traits and efficiency in Feeding Period 1 (FP1), Years 1 and 2, for beef bulls using residual values after correcting for year and diet effects[1].

Trait	RF_F	BF_F	REA_F	IMF_F	ADG	FCR	MMWT	SFI	Ey_{HH}	Ck_S	Ey_S	RFI_{Fat}
Ck_{HH}	-0.04	-0.14	-0.12	0.10	0.29**	-0.21*	0.03	0.21*	0.12	0.54**	0.20	0.07
Ey_{HH}	0.12	-0.04	0.04	-0.08	0.08	0.03	0.07	0.14		0.19	0.43*	0.11
Ck_S	-0.07	0.01	-0.23	0.16	0.29	-0.34	-0.01	0.04			0.73***	-0.09
Ey_S	-0.09	-0.05	-0.38*	0.10	0.13	-0.17	-0.21	0.03				0.19

*P<0.05 **P<0.01 ***P<0.001

[1] End of test rib fat (RF_F), backfat (BF_F), ribeye area (REA_F) and intramuscular fat (IMF_F) carcass traits, average daily gain (ADG), metabolic mid-test weight (MMWT), standardized feed intake (SFI) and cheek (Ck) and Eye (Ey) surface temperatures determined using handheld (HH) and stationary (S) camera systems were corrected for year and diet effects before correlations were calculated.

Table 6. Pearson correlation coefficients between surface temperatures (measured through infrared thermography) and growth, carcass traits and efficiency in Feeding Period 2 (FP2), Years 1 and 2, for beef bulls using residual values after correcting for year and diet effects[1].

Trait	RF_F	BF_F	REA_F	IMF_F	ADG	FCR	MMWT	SFI	Ey_{HH}	Ck_S	Ey_S	RFI_{Fat}
Ck_{HH}	0.05	0.05	-0.07	0.05	0.24**	-0.09	0.15	0.22	0.06	0.31	-0.29	0.01
Ey_{HH}	0.15	0.17	0.08	-0.17	0.02	0.11	0.16	0.22*		-0.14	0.48**	0.16
Ck_S	-0.14	-0.06	0.21	0.26	0.36	-0.18	0.28	0.21			0.41*	0.02
Ey_S	-0.33	0.10	-0.17	0.11	0.02	-0.02	-0.23	0.08				0.16

*P<0.05 **P<0.01 ***P<0.001

[1] End of test rib fat (RF_F), backfat (BF_F), ribeye area (REA_F) and intramuscular fat (IMF_F) carcass traits, average daily gain (ADG), metabolic mid-test weight (MMWT), standardized feed intake (SFI) and cheek (Ck) and Eye (Ey) surface temperatures determined using handheld (HH) and stationary (S) camera systems were corrected for year and diet effects before correlations were calculated.

0.05) were present for IRT traits derived from the handheld camera data with growth, intake or carcass traits. In addition, there were no significant correlations ($P > 0.05$) between Ck_S or Ey_S with any of the reported performance traits. Eye surface temperature measurements derived using the handheld and stationary cameras in FP2 were significantly correlated ($r=0.48$, $P < 0.01$); cheek and eye temperatures measured using the stationary camera system were also positively correlated ($r=0.41$, $P < 0.05$). Backfat-adjusted RFI was not correlated ($P > 0.05$) with any of the IRT traits measured.

4.5 Discussion

4.5.1 GrowSafe data integrity

The strength of the feed intake data is important as it is used not only to calculate individual average daily feed intake, but also serves as the basis for regression analysis to predict expected feed intake and ultimately RFI. GrowSafe® data collected during the present study was of very high quality with AFD values > 99% for each feeding period in both years. These values are similar to those reported by Durunna et al. (2011), Basarab et al. (2011) and Colyn (2013). Feed intake data on days where AFD values failed to reach 95% was excluded, and these days were usually associated with weather conditions (strong winds), power outages or mechanical failures. The number of days excluded ranged from five to seven days for each feeding period in the current study. Durunna et al. (2011) had up to 28 days in a single feeding period that were excluded due to feed intake data integrity while Basarab et al. (2011) did not include 14, 13 and 2 days in years 1, 2 and 3 of their feeding trial, respectively. Feed intake data was included from scheduled weigh days as it was determined the time away from the feed bunks did not cause a significant difference in bull feeding behaviour or individual intake compared to days where the bulls were not handled (data not shown). This is in contrast to some other RFI trials (Basarab et

al., 2003; Colyn, 2013) where feed intake data was excluded on days where test animals were weighed.

Pearson correlations of DMI with MMWT, ADG, EFI and BF were calculated to evaluate the feed intake and performance data for known relationships among different variables, particularly those used in the calculation of RFI_{Fat} (Table 2). Correlations observed in the present study were as expected, and agree with findings reported by Durunna et al. (2011) and Basarab et al. (2011) where correlation values ranged from r=0.12 to 0.86 and r=0.23 to 0.84, respectively. Overall, the authors of the current study are confident in the integrity of feed intake data collected.

4.5.2 RFI and growth traits

Residual feed intake was calculated and used as a measure of individual biological efficiency, serving as a means to evaluate relationships with other traits. Calculation of RFI relies on strong data integrity for its component traits. Feeding periods of 76 and 63 days in length (corresponding to biweekly and weekly weight measurements, respectively) were sufficient for accurate data collection to determine ADG and average daily feed intake for yearling bulls on test (Wang et al., 2006; BIF, 2010). A shorter 63 day feeding period was observed in FP2 for both years to ensure feed supplies were not depleted before the end of the trial.

Bulls were 228 days (SD=29) of age upon delivery and fell within the suggested range to ensure linearity of growth during postweaning performance testing (BIF, 2010). Regression analysis of body weight on time revealed linear growth (R^2=0.98) on average among bulls. The coefficients of determination ranged from 0.996 to 0.842 for individual bulls with 7.9% of the growth curves having R^2<0.95. However, values below 95% generally corresponded to animals

that were treated for respiratory illness and as such growth was expected to be non-linear during the treatment period. The total variation in DMI explained by the EFI regression models differed considerably between the diet, feeding period and year for which it was determined (Table 2). In general, bulls receiving the grain-based diet had a greater proportion of the variation in feed intake explained by the regression model than the forage-based diet. The lowest R^2 value (0.29) was observed in year 2 FP2 for the grain diet and the largest R^2 (0.85) occurred with the grain diet in year 1 FP1. With the exception of two RFI calculations (Year 1 FP1 forage diet and year 2 FP2 grain diet) the R^2 values fell within the range reported by Koch et al., 1963 (0.48 and 0.60), Arthur et al., 2003 (0.70), Basarab et al., 2003 (0.71 and 0.82), and Lancaster et al., 2009 (0.62). Finally, the EFI model's ability to explain variation in DMI improved only slightly in the current experiment when BF measurements were included. Similar slight improvements were experienced by Durunna et al. (2011) and Basarab et al. (2011). The variation in feed intake that could not be explained by the RFI model differed for each feeding period. Regardless of year or feeding period, the unexplained variation in feed intake can be attributed to unknown factors and may include thermoregulation.

Different models have been used to predict expected feed intake in the calculation of RFI. The base model developed by Koch et al. (1963) completes a regression of SFI on ADG and MMWT to estimate feed intake. Arthur et al. (2003) explored possible improvements to the RFI model by making adjustments for body composition with ultrasound measurements. However, the authors did not observe a difference of sufficient magnitude when calculating RFI and including body composition traits. Contrary to these findings, Basarab et al. (2003) reported that 6.8% of the variation in RFI was explained by gain in backfat during the trial. Similarly,

including the end of test backfat measurement in the RFI regression model accounted for an additional 0.8-3.8% of the variation in DMI ($P < 0.05$) for beef heifers (Basarab et al., 2010).

Average DMI within the grain-based diet treatment in both feeding periods for Year 1 and 2 was similar to trials where bulls were fed high moisture corn diets (Lancaster et al., 2005; Montanholi et al., 2010; Huntington et al., 2012). Bulls within the forage diet treatment consumed 6-18% less feed than bulls in the grain diet treatment which was expected due to a higher fiber content of the forage diet (Table 1). Average daily gain observed during both feeding periods in each year for bulls in the grain diet treatment was similar to previous trials where beef bulls were fed a high moisture diet containing corn grain and/or corn silage (Lancaster et al., 2005; Montanholi et al., 2010; Huntington et al., 2012) but FCR was also greater, representing less efficient animals. A lack of literature limits further comparisons of DMI, growth or carcass traits for bulls on forage-based diets. Fat content of the bulls as measured by RF in both diet treatments for the current study was considerably lower compared to other trials involving young beef bulls (Lancaster et al., 2005; Montanholi et al., 2009). The forage diet in the present study contained a lower energy density compared to both Montanholi et al. (2009) (mean TDN= 68.78% versus 85.56%) and Lancaster et al. (2005) (mean ME= 10.39 MJ/kg versus 11.63 MJ/kg) Additionally, the grain-based diet contained both alfalfa and corn silage with corn grain constituting less than 50% of the ration while Lancaster et al. (2005) and Montanholi et al. (2009) were both feeding diets containing greater than 50% corn grain (DM basis). However, ADG in the current study was comparable with previous studies evaluating young bulls (Devitt and Wilton, 2001; Lancaster et al., 2005; Montanholi et al., 2009).

Significant interactions between factors are illustrated in Figures 1 and 2. Bulls in both forage and grain diet treatments in Year 2 gained faster compared to those in Year 1. This

relationship reflects the ME content of the diet (Table 1) with Year 1 bulls fed the forage diet having the slowest rate of gain (lowest diet energy density) and Year 2 bulls in the grain diet treatment growing the fastest (greatest diet energy density). Greater ADG values in FP2 compared to FP1 for both years are likely representative of a higher diet energy density for both diets in FP2 (data not shown). In addition, the year by feeding period and year by diet interactions significantly affected FCR values, though no patterns were observed (Figure 5C, D). Lastly, there were significant interaction effects for RFI group with feeding period, year and diet (Figure 6). Residual feed intake values were more variable for bulls in FP2 (-1.41 to +0.97) compared to FP1 (-2.27 to +2.61), Year 2 (-2.27 to +2.61) compared to Year 1 (-1.16 to +1.45) and the grain diet treatment (-2.27 to +2.61) compared to the forage diet treatment (-1.25 to +1.40). Increased variability is most likely linked to increased feed intake, due to either larger animals, diet type or increased nutrient requirements associated with colder temperatures. For example, bulls in FP2 were 38% heavier at the end of the feeding period and consumed 24% more feed than bulls in FP1. As well, bulls in Year 2 were 9% heavier and ate 13% more than bulls in Year 1. There was a significant increase ($P < 0.0001$) in DMI between the grain diet treatment (10.04 kg DM d^{-1}) and the forage diet treatment (9.07 kg DM $^{-1}$). This was presumably due to faster rates of passage associated with grain-based diets allowing bulls to consume more feed, as well as a higher fiber content of the forage diet that would result in the rumen reaching capacity more rapidly.

Durunna et al. (2011) observed a feeding period effect on RFI and other feed efficiency measures. One proposed reason for this interaction is potential differences among cattle to utilize greater metabolizable energy at a younger age, which implies that some individuals may have different efficiency performance in one feeding period compared to another. The significant

effect of diet on RFI may have been driving by differences in gut-fill and subsequently DMI between treatments (Durunna et al., 2011). However, other studies evaluating RFI in consecutive feeding periods (Kelly et al., 2010; Durunna et al., 2012) did not report such interactions.

4.5.3 Infrared thermography traits

Previous IRT trials have measured the radiant heat emitted from various anatomical locations of beef cattle in an attempt to predict heat loss. The number of collection dates or number of images used to calculate an average heat loss value is generally not reported (Brown, 2005; Montanholi et al., 2008; Montanholi et al., 2009; Montanholi et al., 2010). Schaefer et al. (2005) captured infrared images on three separate collection days, although the number of images used to calculate the reported average is unknown. In a recent IRT study, Colyn (2013) recorded real-time video on individual beef heifers during three collection dates and determined average surface temperature of the eye and cheek regions using still images from the video clip. The number of still images used to calculate a single surface temperature from one anatomical region ranged from 10 to 558. Because RFI is calculated using feed intake and weight measurements collected over the entire feeding period, it is perhaps more applicable to evaluate surface temperature averages that are derived from multiple collection dates throughout the same feeding period. In the current trial, infrared images were collected using the handheld camera on eight collection days in each feeding period, with the exception of Year 2, FP2 where six collection dates were used. Image collection from the stationary infrared camera system was continuous and thus the number of images used to calculate average eye and cheek surface temperature differed (n=23 to 369).

Eye and cheek temperatures reported in the current study were similar to temperatures reported in previous postweaning IRT studies completed in Canada (Montanholi et al., 2009;

Montanholi et al., 2010; Colyn, 2013). However, there was less variation for Ey_{HH} (SD=0.66 and 0.52 for FP1 and FP2, respectively) in the present study compared to values reported by Montanholi et al. (2009; SD=1.43), Montanholi et al. (2010; SD=1.27) and Colyn (2013; SD=1.12 to 1.65). Conversely, Ck_{HH} temperatures exhibited more variability between individuals in the current study (SD=3.39 and 2.50 in FP1 and FP2, respectively) compared to previous IRT studies (SD=1.88 and SD=1.31 to 1.50 for Montanholi et al., 2010 and Colyn, 2013, respectively). The variation in cheek surface temperature described by Montanholi et al. (2009) for yearling beef bulls was comparable to the current study. There is limited literature using stationary infrared camera systems, and therefore comparison between studies is difficult. Schaefer et al. (2012) observed an average eye temperature of $34.91 \pm 0.22^{0}C$ using an automated stationary infrared camera, which is warmer than the average Ey_s of $29.58 \pm 1.08^{0}C$ in FP1 and $32.67 \pm 0.48^{0}C$ in FP2 observed in the current study.

The stationary infrared camera system positioned near a watering bowl was effective in capturing images from the bulls as they were not subjected to possible stressors such as handling or human presence. Nor did collection of infrared images from the handheld camera appear to provoke any visually apparent fear-related responses. The operator approached the head gate slowly and stopped at what was perceived to be a non-threatening distance of two meters from each animal. While image collection was not invasive, processing activities (e.g. blood collection, vaccination) were likely associated with previous handling and could have increased hypothalamic-pituitary-adrenal axis activity. The resulting increased catecholamine and cortisol production, as well as any potential corresponding blood flow responses, may produce changes in heat production and heat loss from an animal (Schaefer et al., 2002). In addition, physical activity due to movement to and from the processing facility may have also increased metabolic

activity and therefore heat production prior to image collection. However, significant correlations ($P < 0.05$) were found between Ey_{HH} and Ey_S in both FP1 ($r=0.43$) and FP2 ($r=0.48$) suggesting that the two systems are comparable. As well, there were significant correlations between Ck_{HH} and Ck_S in FP1 ($r=0.54$; $P < 0.01$). This suggests that over the duration of the trial, stress of handling and increased locomotion associated with sampling procedures did not cause any significant changes in body surface temperatures. Alternatively, there may have been a change in heat production due to handling activities but that effect proved to be similar across the entire population. To the author's knowledge, such a comparison using images collected from animals while restrained to images collected while in a steady state under pen conditions has not been investigated. Thus, IRT appears to serve as an accurate, non-invasive strategy for collection of biometric data with potential for future studies using bio-surveillance information, particularly with the use of automated camera systems within a feedlot pen, and supports findings by Schaefer et al. (2012).

As depicted in Tables 5 and 6, there were no significant correlations ($P > 0.05$) between end of test RF, BF, REA or IMF and either handheld or stationary eye and cheek surface temperatures. Montanholi et al. (2009) found positively significant correlations between cheek surface temperature and ultrasound measurements (REA, BF and IMF) ranging from 0.24 to 0.36 ($P < 0.05$) which suggest that bulls with higher radiant heat loss as measured by cheek surface temperature deposited more fat than bulls with cooler cheek surface temperatures. The lack of relationship between IRT and ultrasound traits in the current study may be due to differences in image collection protocols or environmental conditions in each of the studies. Montanholi et al. (2009) collected infrared images on a single day at the conclusion of the feeding experiment and observed average ambient temperatures ranging from -3.8 to 12.5^0C throughout the study. As

many as eight image collection days occurred in a single feeding period and mean ambient temperatures ranged from approximately -30 to 23^{0}C for the present study.

No significant differences were observed for Ey_{HH}, Ey_s, Ck_{HH}, or Ck_S between bulls in the low, medium and high RFI groups in the current study. The relationship between heat production and RFI has also previously been investigated. Basarab et al. (2003) observed that less efficient (high RFI) steers produced 9% more heat than more efficient (low RFI) steers as using calculated heat production values. Similarly, Nkrumah et al. (2006) reported a significant correlation ($r=0.68$, $P < 0.05$) between heat production (measured using indirect calorimetry) and RFI in growing steers. Subsequent beef trials have found significant differences in the surface temperatures of extremities (specifically the eye and cheek regions) between different RFI groups for steers (Montanholi et al., 2010), heifers (Colyn, 2013; (cheek only)) and bulls (Montanholi et al., 2009).

These results are contrary to those reported by Montanholi et al. (2009) who reported average eye temperatures that were 0.86^{0}C lower for low RFI bulls compared to high RFI bulls ($P < 0.05$) and average cheek temperatures that were 2.09^{0}C lower for low RFI bulls than high RFI bulls ($P < 0.001$). Similarly, Montanholi et al. (2010) reported that low RFI steers had an average cheek temperature 1.1^{0}C cooler than high RFI steers ($P < 0.05$). However, no significant differences existed for average eye temperature between RFI groups. Finally, Colyn (2013) also described cheek surface temperature differences between RFI classes; low RFI heifers were 1.41^{0}C cooler than high RFI heifers ($P < 0.05$). A lack of relationship between RFI_{Fat} and the surface temperature of the eye in the present study may be attributed to changes in blood flow as the small areas around the medial posterior palpebral border of the lower eyelid and the lacrimal caruncle are highly innervated and respond to blood flow changes associated with the

sympathetic nervous system. As such, IRT of the eye has proven successful for measuring temperature changes in response to pain (Stewart et al., 2008a) and stress of handling (Stewart et al., 2008b), as well as early disease detection (Schaefer et al., 2004-2012). Because the entire eye and parts of the surrounding skin tissue were included in the image analysis for the present study, it is expected that the presence of any subclinical disease, inflicted pain, or stress would influence radiant heat loss from this area. Although Montanholi et al. (2009) reported significant correlations between eye surface temperature and RFI group for bulls, the eye region may not be a suitable area for measuring surface temperature to predict biological efficiency. Previous studies evaluating beef steers (Montanholi et al., 2010) and beef heifers (Colyn, 2013) also did not observe significant correlations between eye surface temperature and RFI ranking, and the authors share the same reservations for predicting RFI based on individual animal variation of eye temperature.

Observed differences between the results in the current trial and that of other studies may also be attributed to differences in the number of collection days used to determine the average eye and cheek temperature Montanholi et al. (2009) captured infrared images on a single day at the end of the feeding period, while Montanholi et al. (2010) collected images were collected every 28 days during the 114-day feeding period, which coincided with weigh days. However, the total number of collection days is not clear as it is not known whether images were also collected at the start and end of the trial. As well, Colyn (2013) collected infrared data on three different collection dates, and used multiple frames of live video recording to calculate average eye and cheek temperatures. Utilizing multiple frame shots to derive an average temperature may account for any warming or cooling effects during collection. The number of samples that were pooled to estimate average individual heat loss in previous studies is comparatively small

compared to the current study. While the conditions present between collection days will vary, increasing the number of collection days should produce a trial average that is more accurate as it accounts for these conditions.

Observed differences between studies may also be attributed to ambient temperatures (dry-bulb) which are described for FP1 and FP2 in Figure 2. This figure depicts average daily temperatures throughout each feeding period, however, values recorded every half hour over the same time frame depict a wide range of conditions where extreme cold temperatures were experienced, particularly during FP1 (data not shown). Livestock must produce heat to maintain homeothermy if they are exposed to temperatures below their lower critical temperature (LCT), resulting in greater energy expenditure through the activation of acute physiological mechanisms and behavioural responses related to thermogenesis. Webster et al. (1970) showed that both cold temperatures and wind velocity can contribute to increased nutrient requirements and depressed performance in beef cattle that are attempting to maintain a constant core body temperature. In addition, previous thermal conditions and cold acclimation will determine the severity to which livestock are affected by the cold (Young, 1975).

Thermoneutral zones (TNZ), defined as the range of environmental temperatures where an animal's metabolic heat production is independent of ambient temperature (Webster, 1974), vary significantly based on conditions pertaining to animal type, age, diet energy density, or stage of production (NRC, 2000). Lower critical temperatures can be estimated from an animal's thermoneutral rate of heat production and thermal insulation, and can be as low as -35^{0}C for yearling cattle consuming an energy-dense diet. Historical records from both commercial and research feedlots, however, tend to reflect seasonal effects on cattle performance at much warmer temperatures than predicted LCT values (Young, 1981). While it is difficult to predict a

TNZ for the bulls in the current study, the often sudden onset and frequency of extreme cold temperatures would lead the authors to believe that cold stress was evident at least to some degree. During FP1 the wind chill-corrected ambient temperature fell below -20^{0}C on 37% and 86% of the days in Years 1 and 2, respectively. Such a high incidence of cold temperatures, particularly in Year 2, presumably results in bulls which are expending more energy on thermoregulation than growth or production and may not reflect an accurate biological efficiency as measured by RFI. Further, the environmental conditions experienced in the present study are representative of those commonly experienced in Western Canadian bull test facilities and therefore the effect of cold stress should be considered when evaluating animal performance. It should be noted that acclimation (an improved thermogenesis response to better cope with incidence of extreme cold temperatures) of bulls in the present study, while difficult to quantify, may have occurred to some degree.

While cold stress is a concern during the winter months in Western Canada, heat stress should also be considered, especially during the transition from winter to spring months. For example, over a 24 hour period at the beginning of FP2 in Year 1 the temperature ranged from -5.7 to 16.9^{0}C. The almost 23^{0}C temperature spread may have induced thermal stress as bulls tried to dissipate heat during a sudden elevation in temperature, and represents a common issue for beef producers, particularly concerning calf health in the spring and fall which correspond to seasonal climate patterns.

The reasons described above suggest that the evaluation of biological efficiency as measured by RFI may be affected by thermoregulatory activity. It is likely that animals under thermal stress attempting to maintain a constant core body temperature allocate energy differently than when they are in their TNZ. While this may be difficult to quantify, it is possible

that a high frequency of extremely cold days or days with extreme fluctuations in temperature could confound the measurement of RFI. This may be one explanation why significant correlations were not found between eye or cheek temperatures and RFI, contrary to previous IRT trials (Montanholi et al., 2009; Montanholi et al., 2010; Colyn, 2013) where environmental temperatures may have been more moderate. However, environmental temperature data was either not reported or not recorded for the entire feeding period in past RFI experiments utilizing IRT. Montanholi et al. (2009) observed average ambient temperatures ranging from -3.8 to 12.5^{0}C, while Colyn (2013) reported similar outdoor temperatures of -5 to 10^{0}C on days where images were captured. Outdoor temperatures on collection days in the current study were substantially colder than each of the previous trials with values ranging from -34.0 to 7.1^{0}C in FP1 and 12.9 to 26.1^{0}C in FP2 (data not shown).

There were no significant correlations between IRT traits and RFI_{Fat} during FP2 in the absence of cold stress. However, year was a significant effect for Ey_{HH} and Ck_{HH} measurements ($P < 0.0001$), presumably because Year 2 was 6.8 and 2.7^{0}C cooler than Year 1 in FP1 and FP2, respectively (Figure 6). Due to the nature of conducting two successive RFI feeding periods, the bulls were on average 370 days of age (SD=28) at the start of FP2, which is older than bulls in previous RFI trials (Lancaster et al., 2009; Montanholi et al., 2009; Awda et al., 2013) and outside the recommended age range for postweaning performance testing (BIF, 2010). While it is required that postweaning cattle are achieving linear growth during RFI testing, it is possible that some of the bulls were approaching or starting the growth stage where protein deposition slows and fat deposition increases. This could have led to discrepancies in the determination of individual ADG, the amount of fat being deposited relative to lean tissue and ultimately the calculation of RFI. Additionally, some bulls were likely to have already reached or would be

expected to have reached puberty in FP2 due to the length of trial associated with two feeding periods. Pubescent bulls will begin to exhibit sexual activity characterized by higher energy demands; additional energy will also be to be used towards the development of their reproductive systems. These extra energy requirements for earlier maturing bulls negatively influence the RFI phenotype (Awda et al., 2013) and without the consideration of bull maturity the ability of RFI to reflect true biological efficiency might also have been affected.

4.6 Conclusion

While RFI has broadly been accepted as an accurate method for evaluating biological efficiency in beef cattle, widespread adoption of this measure and subsequent genetic improvement through selection has been limited due to high labour requirements and expensive equipment necessary for its calculation. The present study investigated radiant surface temperatures of the eye and cheek regions as measured through IRT to predict RFI ranking in young beef bulls. There were no significant correlations observed between eye or cheek surface temperatures and RFI_{Fat}. The results contradict research conducted elsewhere. Due to the variation in environmental conditions as well as differences in the frequency of image collection, it is apparent that procedures must be standardized in order to compare data between future IRT studies. Increased energy requirements for beef cattle associated with maintaining a constant body temperature in cold temperatures should be considered when evaluating RFI. In particular, feed intake during a sudden drop in temperature will not reflect normal eating habits, nor should the same response be assumed equal for every individual. Results from the current study suggest more research is needed into standardizing IRT procedures before infrared camera systems can confidently be used to predict biological efficiency. Moreover, the current study has identified

that the variation in environmental conditions during a measurement period can have significant effects on measuring metabolic efficiency irrespective of the method used.

5. Manuscript 2: Repeated measures of residual feed intake in growing beef bulls fed forage and grain-based diets

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5.1 Abstract

Residual feed intake (RFI) has been used to select metabolically efficient cattle in beef breeding programs. Cattle are traditionally performance tested on concentrate-based diets, and this is assumed to reflect performance regardless of diet composition. The objective of this experiment was to determine if beef bulls change their RFI ranking when fed a forage-based as compared to a grain-based diet. Sixty purebred Angus bulls were used in each of two years (n=120) during the feeding study with a mean age of 280 days (SD= 27) and 249 days (SD=22) and an average weight of 306.6 kg (SD=43) and 313.9 kg (SD=32) in Years 1 and 2 respectively. Bulls were randomly assigned into four pens, with two pens receiving the forage diet treatment and two pens receiving grain diet during feeding period 1 (FP1; 76 d). Thereafter, diets were switched for one of the forage and one of the grain pens, while the remaining two pens continued their original diet treatment during feeding period 2 (FP2; 63 d). Bulls in each diet treatment were grouped as either low, medium or high RFI based on ±0.5 of backfat adjusted RFI (RFI_{Fat}) standard deviation. RFI_{Fat} values ranged from -1.41 to +0.97 kg d^{-1} dry matter (SD=0.48) and -2.27 to +2.61 kg d^{-1} dry matter (SD=0.73) for FP1 and FP2, respectively. Reranking was observed across all treatments; approximately 59, 53 and 53% of bulls in the diet switch, forage and grain diet treatments, respectively, changed their RFI group from FP1 to FP2. Rank correlations for RFI_{Fat} between FP1 and FP2 were found to be low in the diet switch treatment ($r=0.24$; $P > 0.05$) but high in the forage ($r=0.58$; $P < 0.01$) and grain treatments ($r=0.64$; $P < 0.001$). The data reveals the inherent variability of individual measurements of RFI, suggesting many factors, including diet, animal age and environmental conditions, may account for the observed variability.

5.2 Introduction

Improving feed efficiency in beef cattle through the selection of efficient breeding stock has the potential to significantly reduce on-farm expenditures. Feed expenses account for 50% of the total operating costs in a cow-calf operation (Manitoba Agriculture Food and Rural Development, 2013) while feed costs for maintenance has been estimated to represent approximately 60-65% of the total feed requirements for the herd, with considerable variation among individuals independent of body size (Montaño-Burmudez et al., 1990). Residual feed intake (RFI) has recently shown utility in assessing biological efficiency while maintaining phenotypic independence from most production traits (Arthur et al., 1997; Archer et al., 1999; Basarab et al., 2003). Common to most performance traits, RFI is typically measured during the growing phase of a beef animal's life and is assumed to be reflective of an animal's biological efficiency throughout its entire life and under different diet treatments in repeated testing. Previous research has investigated the repeatability of RFI in various beef production systems. Kelly et al. (2010) observed moderate to high repeatability (R=0.62) comparing within- animal RFI rankings for beef heifers evaluated during the growing and then finishing phases. In contrast, Durunna et al. (2011) stated that over half of the steers in both the control and feed swap (grower to finisher diet) groups changed RFI by at least 0.5 standard deviation units in successive feeding periods, suggesting that diet type and feeding period may each affect RFI ranking. As well, Durunna et al. (2012) reported that 51% of beef heifers fed the same diet in successive feeding periods changed RFI class (RFI classes were low, medium, and high based on ±0.5 standard deviation around the mean). It is apparent that further investigation exploring the repeatability of RFI in beef cattle is warranted.

Beef cattle performance has historically been measured on concentrate-based diets and is assumed to reflect animal performance regardless of diet composition. Typically, central test stations have evaluated bull performance, including RFI, when fed high-energy diets. However, bulls and most often their offspring will spend the rest of their lives in a forage-based feeding system. Assessing the variation in biological efficiency for an individual beef animal receiving a forage-based diet followed by a grain-based diet, or vice versa, would improve our understanding of RFI and the effectiveness of selecting more efficient animals to increase the future profitability in cow-calf operations. The objective of this study was to calculate RFI for young beef bulls fed forage and grain-based rations in successive feeding periods to determine repeatability and the effect of diet type or animal age on biological efficiency.

5.3 Materials and Methods

5.3.1 Facilities and animal management

Sixty purebred Angus bulls were used in each of two years (n=120) during the feeding study with a mean age of 280 days (SD= 27) and 249 days (SD=22) and an average weight of 306.6 kg (SD=43) and 313.9 kg (SD=32) in Years 1 and 2 respectively. As described in Manuscript 1, bulls were vaccinated with Vista Once (Merck Animal Health, Summit, NJ) and Vision 8 (Merck Animal Health, Summit, NJ) and treated with Noromectin (Norbrook Inc., Lenexa, KS) pour-on solution. Vitamin A and D injections were administered at the start of the trial and every 3 months thereafter. Bulls were randomly assigned to four pens, each equipped with four GrowSafe® (GrowSafe Systems Ltd., Airdrie, Alberta) feed bunks; two pens were fed a forage-based (F) diet and remaining two pens were fed a grain-based (G) diet on an *ad libitum* basis in the first feeding period (FP1), as described in Table 1. Following FP1, one forage pen was switched to a grain-based diet (FG), one grain pen switched to a forage-based diet (GF),

while the remaining forage (FF) and grain (GG) pens remained on their respective diets before a 14-day adaptation period was observed prior to the second feeding period (FP2). A base of straw was provided in each pen for bedding followed by flax shives (replenished as needed) during the trial.

5.3.2 Measurements

Body weight was recorded during two consecutive days at the start and end of each feeding period; FP1 commenced in December and ended in March while FP2 began at the end of March and finished in June each year. Thereafter, weight measurements were recorded biweekly in a 76-day FP1 while weekly weight measurements were utilized in a 63-day FP2. Individual feed intake measured by the GrowSafe® feeding system and a daily feed intake average was calculated for each animal in each feeding period. The weighing and feed monitoring protocol provided sufficient growth and intake data needed for determination of RFI, as outlined by Wang et al. (2006).

5.3.3 Calculations

5.3.3.1 Residual feed intake

Residual feed intake was calculated using the methodology described by Basarab et al. (2007). Individual bull growth was modeled by using a linear regression of weight against time. The majority of bulls had individual growth curves with a coefficient of determination (R^2) greater than 0.95 (mean=0.98) indicating that the animals grew normally without negative effects associated with morbidity or nutritional inadequacies. Start of test (SOT) weight, mid-point weight (MWT), and average daily gain (ADG) were determined using regression coefficients from each animal's growth curve.

Feed intake for the entire feeding period was determined by multiplying daily feed intake by total days on test; total dry matter intake (DMI) and total metabolizable energy intake (MEI) was calculated using dry matter (DM) and metabolizable energy (ME) values (Table 1) of the respective diets. In order to standardize energy intake with previous RFI trials (Arthur et al., 2001a; Basarab et al., 2003, Nkrumah et al., 2004) the total MEI was divided by 10 MJ ME kg^{-1} DM, which was then further divided by the DM content to convert the total standardized dry matter intake into total standardized feed intake. Finally, the total standardized feed intake was divided by the number of days on test to obtain average standardized daily feed intake (SFI, kg d^{-1}) for each bull.

Expected feed intake (EFI) was estimated by regressing SFI against ADG (kg d^{-1}), metabolic MWT (MMWT, kg $^{0.75}$), and end of test BF (BFend, mm) using PROC GLM (SAS Institute Inc. 2008) and the following model:

$$Y_i=\beta_O+\beta_1 ADG_i+\beta_2 MMWT_i+\beta_3 BFend_i+e_i$$

where Y_i= SFI for animal i, β_O= regression intercept, β_1=partial regression coefficient of SFI on ADG, β_2=partial regression coefficient of SFI on MMWT, β_3=partial regression coefficient of SFI on BFend, and e_i=the residual error of SFI for the i'th animal.

Evaluating bulls within each diet treatment, RFI_{Fat} was calculated as the difference between actual standardized feed intake and expected feed intake (RFI_{Fat} =SFI-EFI). Bulls were then placed into low, medium, or high RFI groups based on ± 0.5 SD around the mean.

5.3.4 Statistical Analysis

Data records for FP1 and FP2 from both years were combined for analysis. The proportion of bulls that changed RFI group from FP1 to FP2 was compared to those who maintained their RFI group using a chi-square of the FREQ procedure (SAS Institute Inc. 2008) where the null hypothesis stated that RFI ranking in FP1 is independent of RFI ranking in FP2. Bulls were also placed into low, medium or high ADG groups in each feeding period by using ±0.5 SD around the feeding period mean, consistent with the methods used for RFI group determination. Similar to RFI reranking analysis, the proportion of bulls which switched ADG group was compared to those who maintained their ADG group from FP1 to FP2; the null hypothesis was that ADG ranking in FP1 is independent of ranking in FP2.

Growth and feed efficiency traits measured in each feeding period were corrected for year and diet treatment effects using PROC GLM (SAS Institute Inc. 2008) by modeling each trait separately as the dependent variable and year and diet as the independent variable; individual animals were considered a random effect. Residual values from this model were used to determine Spearman's rank correlations between traits. Finally Spearman's rank correlations were calculated between traits measured in each feeding period to determine reranking within each diet treatment.

5.4 Results

Least square means for feed intake and end of test carcass and performance traits are summarized by year, feeding period, diet and RFI group effects and displayed in Table 4 (as discussed in Section 3.3).

The proportion of bulls which maintained and changed RFI group between FP1 and FP2 are reported in Table 7. All diet treatment groups exhibited a similar degree of reranking; 41.4%

of bulls in the diet switch group maintained their previous RFI group in FP2, compared to 46.7% of bulls in both the forage and grain diet treatments. The average absolute change in RFI rank, determined within diet treatments, was 4.1 for bulls that changed diets after FP1. This value was comparable between diet treatments (average rank change was 3.5 and 3.0 for the forage and grain diet treatment, respectively; $P > 0.05$).

Table 7. Percentage of bulls that changed or maintained RFI group from FP1 to FP2, and average change in rank (± SE) within diet treatments.

	Diet treatment		
	Diet Switch	Forage	Grain
Maintained RFI group[1]			
n	24	14	14
%	41.4	46.7	46.7
Changed RFI group			
n	34	16	16
%	58.6	53.3	53.3
P value	0.6294	0.1440	0.0837
Mean rank change[2]	4.1 ± 0.36	3.5 ± 0.50	3.0 ± 0.50

[1]Within each diet treatment, the null hypothesis for the Chi-square test that FP1 RFI rank is independent of FP2 RFI rank is accepted, $P > 0.05$ for each treatment.

[2]Mean rank change is the absolute difference in RFI rank determined within individual pens between FP1 and FP2; treatment means did not differ ($P > 0.05$).

Table 8 displays the proportion of bulls that maintained and changed ADG groups between FP1 and FP2. Three groups were created by ranking bulls within their respective pens based on ADG calculated during each feeding period and allocating the top third, middle third and bottom third of each pen into high, medium and low ADG groups, respectively. The diet switch group showed the highest frequency of reranking with just 41.4% of bulls with the same ranking between the two feeding periods while the forage diet treatment was slightly higher with

46.7% of bulls with the same value from FP1 to FP2. The grain diet treatment had the greatest number of animals (66.7%; $P < 0.05$) with the same ranking. However, bulls reranked in a comparable way when determined by mean rank change as ADG was 4.3, 3.7 and 2.9 ($P > 0.05$) for the diet switch, forage and grain diet treatments, respectively.

Table 8. Percentage of bulls that changed or maintained ADG group from FP1 to FP2, and average change in rank (± SE) within diet treatments.

	Diet treatment		
	Diet Switch	Forage	Grain
Maintained ADG group[1]			
n	24	14	20
%	41.4	46.7	66.7
Changed ADG group			
n	34	16	10
%	58.6	53.3	33.3
P value	0.3244	0.5578	0.0007
Mean rank change[2]	4.3 ± 0.37	3.7 ± 0.51	2.9 ± 0.51

[1]Within each diet treatment, the null hypothesis for the Chi-square test that FP1 ADG rank is independent of FP2 ADG rank is accepted for diet switch and forage diet treatments ($P > 0.05$) but not for the grain diet treatment ($P < 0.05$).

[2]Mean rank change is the absolute difference in ADG rank determined within individual pens between FP1 and FP2; treatment means did not differ ($P > 0.05$).

Spearman correlation coefficients between growth and feed efficiency traits for bulls which switched diets from one period to another, were fed the grain-based diet in both feeding periods, or fed the forage-based diet in both feeding periods are presented in Table 9, 10 and 11, respectively. Repeatability values were calculated as the correlation coefficient between the same traits measured consecutively in FP1 and FP2. Average daily gain in FP1 (ADG1) for bulls in the diet switch treatment (Table 9) was significantly correlated with FCR in FP1 (FCR1) and Kleiber ratio (KR) in FP1 (KR1) ($P < 0.001$). There were significant correlations between ADG2 and FCR2 and KR2 ($P < 0.001$). Feed conversion ratio measured in FP1 was correlated with KR1 (P

< 0.001) and RFI_{Fat} in FP1 (RFI1) (P < 0.01) and FCR2 was correlated with KR2 (P < 0.001) and RFI_{Fat} in FP2 (RFI2) (P < 0.01). Repeatability estimates for bulls in the diet switch treatment were not significantly different (P > 0.05) for any of the measured growth and efficiency traits, as indicated by the bolded values in Table 9.

Table 9. Spearman correlation coefficients between growth and efficiency traits measured in FP1 and FP2 for beef bulls in the diet switch treatment

Trait	ADG2	FCR1	FCR2	KR1	KR2	RFI1	RFI2
ADG1	**0.21**	-0.73***	0.12	0.73***	-0.06	-0.06	0.20
ADG2		-0.16	-0.73***	0.15	0.85***	-0.01	-0.03
FCR1			**-0.02**	-0.83***	-0.10	0.43**	-0.15
FCR2				0.02	-0.80***	0.10	0.54***
KR1					**-0.16**	-0.04	0.24
KR2						0.00	-0.11
RFI1							**0.24**

Diagonal correlation coefficients in bold represent repeatability estimates between traits measured in FP1 and FP2.
*P<0.05 **P<0.01 ***P<0.001

For bulls fed the forage diet in both FP1 and FP2 (Table 10), significant correlations (P < 0.001) were observed for ADG with FCR and KR values measured in the same feeding period, while ADG2 was also correlated with FCR1 (P < 0.05). There were significant correlations between FCR1 and FRC2 (P < 0.05), KR1 (P < 0.001), and RFI1 (P < 0.01), while FCR2 was correlated with KR2 (P < 0.001) and RFI2 (P < 0.05). Repeatability estimates for bulls in the forage diet treatment were much greater compared to the diet switch treatment; significant estimates were evident for ADG and FCR (P < 0.05), as well as RFI_{Fat} (P < 0.01), as indicated by the bolded values in Table 10.

Table 10. Spearman correlation coefficients between growth and efficiency traits measured in FP1 and FP2 for beef bulls in the forage diet treatment

Trait	ADG2	FCR1	FCR2	KR1	KR2	RFI1	RFI2
ADG1	**0.41***	-0.77***	-0.17	0.82***	0.21	-0.09	-0.10
ADG2		-0.41*	-0.80***	0.27	0.91***	-0.06	-0.01
FCR1			**0.38***	-0.82***	-0.36	0.55**	0.31
FCR2				-0.20	-0.81***	0.15	0.43*
KR1					**0.25**	-0.16	-0.02
KR2						-0.06	0.04
RFI1							**0.58****

Diagonal correlation coefficients in bold represent repeatability estimates between traits measured in FP1 and FP2.
*P<0.05 **P<0.01 ***P<0.001

Spearman correlations for bulls fed the grain-based diet in FP1 and FP2 can be found in Table 11. Coefficients for ADG1 were significantly correlated to FCR1 and KR1 ($P < 0.001$), as well as FCR2 ($P < 0.05$), while ADG2 was significantly correlated with FCR2 and KR2 ($P < 0.001$). Further, FCR1 was significantly correlated with KR1 ($P < 0.001$), RFI1 ($P < 0.01$) and RFI2 ($P < 0.05$). Finally, FCR2 was significantly correlated with KR2 ($P < 0.001$), RFI1 ($P < 0.05$) and RFI2 ($P < 0.01$). Similar to the forage diet treatment, repeatability estimates were strong for bulls in the grain diet treatment. Repeatability values above 0.60 were calculated for ADG and RFI_{Fat} ($P < 0.001$) while the estimate for FCR was also significant ($P < 0.01$), as indicated by the bolded values in Table 11.

Table 11. Spearman correlation coefficients between growth and efficiency traits measured in FP1 and FP2 for beef bulls in the grain diet treatment

Trait	ADG2	FCR1	FCR2	KR1	KR2	RFI1	RFI2
ADG1	**0.67*****	-0.59**	-0.43*	0.79***	0.45*	0.11	0.03
ADG2		-0.34	-0.73***	0.32	0.87***	-0.04	-0.06
FCR1			**0.53****	-0.69***	-0.35	0.48**	0.46*
FCR2				-0.30	-0.82***	0.38*	0.55**
KR1					**0.32**	0.21	-0.06
KR2						-0.07	-0.21
RFI1							**0.64*****

Diagonal correlation coefficients in bold represent repeatability estimates between traits measured in FP1 and FP2.
*P<0.05 **P<0.01 ***P<0.001

5.5 Discussion

Mean values for growth, feed intake and feed efficiency parameters were consistent with other Canadian trials evaluating yearling bulls (Schenkel et al., 2004; Montanholi et al. 2009; Awda et al., 2013). However, fat deposition as measured by BF was noticeably less in the current study which may be due to lower energy densities of the diets as a result of diet composition. Reranking was observed in all three diet treatments; 53.3% of bulls changed their RFI group in both the grain and forage treatments while 58.6% of bulls in the diet switch treatment did not maintain RFI group between FP1 and FP2. Similar RFI studies with successive feeding periods involving growing beef bulls have not been conducted and therefore there is no basis for comparison to other studies. As well, there have been limited studies evaluating differences in feed efficiency for animals fed forage-based and grain-based diets in successive periods. Christopher and Marston (2007, unpublished) reported non-significant correlations ($P > 0.80$) between RFI calculated in two successive feeding periods where beef heifers were fed a forage-based ration in one period followed by a grain-based ration in the second period. The low correlations were attributed to a small sample size (n=26). Durunna et al. (2011) investigated RFI reranking in beef steers on diets which differed in energy density, although both diets were grain-based. They observed 50.7%, 51.1% and 54.7% of steers in finisher-fed, grower-fed and feed swap (grower then finisher) groups changed RFI group from one feeding period to another. The feed swap group exhibited the greatest proportion of reranking, similar to the present study, however the differences between treatment means were not significant ($P > 0.05$) for either study. The authors of that study suggest that reranking between the first and second feeding periods may be due to differences in both animal maturity and diet composition.

The degree of reranking within each treatment group was also measured by determining the average absolute change in rank (Table 7). This measurement provides an indication of reranking within individual pens (n=15); mean rank change was greatest in the feed switch diet treatment, followed by the forage and then grain diet treatments. The mean rank changes are in agreement with the change in RFI group results above, illustrating significant reranking between successive feeding periods regardless of whether or not diet treatment changed. For comparison, a reranking analysis was also completed on ADG among bulls in each diet treatment to evaluate the effect of age during the testing period. Similar to RFI, reranking was observed in each of the diet treatments for ADG. Growth rate was more consistent in the grain treatment compared to the diet switch and forage treatments, however, just 66.7% of these individuals stayed in the same ADG group in FP2. In commercial beef cattle performance tests, ADG is the standard performance measurement. The current data suggests that ADG ranking would likely change depending on the age of the animal at the start of a test period, even though bulls may be within the linear portion of their growth phase, and that testing guidelines such as those recommended by the Beef Improvement Federation (2010) should be followed. The results also imply that similar guidelines with respect to animal age at the start of test should be investigated and standardized for RFI determination.

As expected, ADG was significantly correlated with FCR and KR in the respective periods during which they were calculated across all three diet treatments ($P < 0.01$). There were also a strong relationship between FCR and KR calculated within the same feeding period, although KR and RFI did not exhibit significant correlations ($P < 0.05$) in any diet treatment. However, FCR was positively correlated ($P < 0.05$) with RFI_{Fat} calculated in the same feeding period in each diet treatment which suggests that selection for low RFI livestock would create an

indirect response of improving FCR without the observed increase in cow size that is normally associated with direct selection on FCR (Herd and Bishop, 2000). In general, the relationships between growth and efficiency traits were similar across each of the three diet treatments, while observed correlations between feed efficiency traits were consistent with other RFI reranking studies (Kelly et al., 2010; Durunna et al., 2011; Durunna et al., 2012).

Spearman rank correlation coefficients between the same trait measured in FP1 and subsequently in FP2 were used to predict repeatability. Repeatability estimates for ADG, FCR, KR or RFI_{Fat} were not significant ($P > 0.05$) for bulls in the diet switch treatment. However, animals in both the forage and grain diet treatment groups showed moderate to high correlation coefficients ($P < 0.05$) for ADG, FCR and RFI_{Fat} measured in consecutive feeding periods. Repeatability values for ADG (r=0.67), FCR (r=0.53) and RFI (r=0.64) were greatest for bulls in the grain diet treatment. These results indicate that diet had a significant effect on how an individual bull performed in FP2 relative to their performance in FP1. Performance of cattle being fed a forage-based diet may not be reflective of their performance when fed grain-based diets and vice versa. The data also implies that repeated performance measurements are likely to be more consistent between successive feeding periods when bulls are fed a grain-based diet, perhaps due to increased variability of nutrient quality in forage ingredients compared to concentrates.

Other RFI studies have conducted successive feeding periods and maintained similar diets to explore the effect of maturity on RFI repeatability. Beef heifers that were divergently selected for low and high RFI at 11 months of age were evaluated again at 16 months of age after grazing on pasture during the summer months (Kelly et al., 2010). Spearman rank correlations were used to calculate repeatability values between both feeding periods; values for ADG and

KR were 0.11 and 0.14, respectively ($P > 0.05$) while values of 0.37 and 0.62 were observed for FCR and RFI, respectively ($P < 0.0001$). Durunna et al. (2012) investigated 190 crossbred heifers over three years to determine repeatability of RFI measured in consecutive feeding periods with the same diets. Repeatability estimates for RFI_{Fat}, though moderate, were the greatest among all feed efficiency measures ($r=0.50$; $P < 0.001$), while lower but significant values were observed for KR and G:F ($r=0.33$ and 0.37, respectively; $P < 0.001$). Repeatability values for KR, FCR and RFI observed by Durunna et al. (2012) and Kelly et al. (2010) were consistent with the values obtained for the forage and grain diet treatments in the current study.

Reranking in consecutive feeding periods may be associated with several factors, including differences physiological status and diet composition that may exist between test periods. Pre-pubescent cattle, both male and female, expend less energy as they do not exhibiting sexual activity or development of the reproductive system which favours the RFI phenotype while on trial (Awda et al., 2013). The age at which Angus beef bulls reach puberty is approximately 295 days of age (Lunstra and Echternkamp, 1982). Based on mean bull age during each feeding period, this increase in activity associated with puberty would not be present until FP2, although it may not be observed for some bulls at all. Since up to 9% of the underlying variation in feed efficiency has been attributed to physiological mechanisms caused by differences in physical activity (Arthur and Herd, 2008), it is conceivable that increased sexual activity in pubescent bulls would influence their biological efficiency differently in FP2 compared to FP1. Because bulls were not evaluated for breeding soundness it is likely that individuals reached puberty at different ages and may have influenced energy expenditure during one or both feeding periods, thus affecting RFI.

The efficiency of bulls may differ depending upon the composition of the diet for which they are being fed. Guan et al. (2008) stated that rumen microbial profiles were related to cattle feed efficiency, implying that individual feed efficiency may differ dependent upon diet composition. Therefore it is possible that changes in diet composition from one feeding period to another could result in changes to feed efficiency as illustrated by RFI reranking. These changes may be attributed to different primary carbohydrate sources in each of the two diets; forage-based diets are associated with fibrolytic bacteria in the rumen while grain-based diets will favour the proliferation of amylolytic bacteria. In the current study, average starch content across both years was 27.4% for the grain-based diet, almost twice that of the forage-based diet (15.1%). Carberry et al. (2012) observed that the chemical composition of high and low forage diets influenced rumen bacterial diversity, potentially allowing diet type to control the effect of RFI phenotype from the abundance of specific rumen microbes. Similarities in diet treatment and RFI reranking to Carberry et al. (2012) suggest that changes in RFI may be a result of chemical differences between the forage and diet treatments in the current study.

The occurrence of RFI reranking between feeding periods may also be a result of variation in DMI caused by differences in the physical properties of each diet. The forage-based diet treatment consisted of corn silage and hay whereas the grain-based diet treatment was composed of almost 50% corn grain on a DM-basis. It has been shown that the physical nature of rations have been identified to influence efficiency of microbial protein synthesis in the rumen more so than the chemical composition of the ration (Rode et al., 1985). Faster rates of passage for high concentrate diets will increase the turnover of ruminal solids and increase the nutrient flow and absorption to the small intestine, resulting in improved efficiency of animal performance (Varga and Harpster, 1994).

Finally, observed changes in RFI between feeding periods may be attributed to environmental conditions during the study and individual variability in response to changes in ambient temperature which were drastically different; characterized by extreme cold temperatures during FP1 and a broad temperature range throughout FP2. Heat production is essential for homeothermic animals when exposed to temperatures below their lower critical temperature (LCT) and is accompanied by increased energy expenditure through the activation of physiological and behavioural responses related to thermogenesis. Increased nutrient requirements and depressed performance were associated with cold temperatures and wind velocity for beef cattle attempting to maintain a constant core body temperature (Webster et al., 1970). Furthermore, previous thermal conditions and cold acclimation will determine the severity to which livestock are affected by the cold (Young, 1975). Environmental data from the present study illustrates the magnitude for which temperature can fluctuate in a short period of time. Over a 24 hour period during FP2 in Year 1 the ambient temperature rose to 16.9^{0}C in late afternoon following the early morning low of -5.7^{0}C. A 23^{0}C change in temperature over the course of one day may have induced acute thermal stress as bulls tried to dissipate heat during a sudden elevation in temperature and is indicative of a common challenge that beef producers face. Therefore, sudden changes in temperature should be monitored so that performance measures, such as feed intake, can be corrected for accordingly for climate acclimation to provide the most accurate RFI value.

Thermoneutral zones (TNZ), defined as the range of environmental temperatures where an animal's metabolic heat production is independent of ambient temperature (Webster, 1974), will vary based on animal type, age, diet energy density, or stage of production (NRC, 1996). Thus, it is difficult to predict a TNZ for the bulls in the current study, although the often sudden

onset and frequency of extreme cold temperatures would lead the authors to believe that cold stress was evident at least to some degree. During FP1 temperatures below -20^{0}C were observed on 37 and 87% of the days in Years 1 and 2, respectively. The frequent occurrence of extremely cold days may have confounded feed intake and growth measurements that do not reflect performance when bulls are within their TNZ, ultimately affecting the calculation of RFI during FP1 when compared to FP2 (where it is assumed bulls were within their TNZ). Since the environmental conditions experienced in the present study are commonly observed in Western Canadian bull test facilities the effect of cold stress should be considered when evaluating animal performance. This suggests that biological efficiency may have been influenced by thermoregulatory activity as it is likely that regular energy partitioning was affected by increased energy requirements necessary for regulating body temperature. It should be noted that acclimation (an improved thermogenesis response to better cope with incidence of extreme cold temperatures) of bulls in the present study, while difficult to quantify, may have occurred to some degree.

5.6 Conclusion

Repeated individual feed efficiency measurements in consecutive feeding periods with two diet treatments provided an opportunity to investigate the effect of diet and age on RFI. Evidence of RFI reranking in the feed switch treatment, as well as the diet treatments which were consistent between feeding periods, suggests that diet composition alone might not be the only factor affecting RFI repeatability. While a greater proportion of bulls changed their RFI group from FP1 to FP2 in the diet switch treatment, over 50% of the forage and grain control diet treatments differed in RFI ranking between feeding periods. This implies that feeding period played a significant role in the determination of RFI. However, it is not known whether animal

age or different environmental conditions between feeding periods were associated with the observed reranking. As well, the diet treatment may also have been associated with reranking due to different physical and chemical properties of forage and grain-based rations.

These results provide further evidence for the need to standardize testing procedures when evaluating yearling bull performance. Specifically, bull age during the testing period and diet composition should be standardized to be able to fairly compare results between studies. Environmental conditions should also be monitored for days where bulls may be thermally stressed and daily feed intake studied during those periods to determine the influence on individual bulls. Finally, further studies evaluating the changes in energy requirements due to thermal stress and the corresponding effect on RFI determination should be investigated to ensure that energy consumption due to thermoregulation processes is accounted for and correction efforts are implemented. While the current study suggests that yearling beef bulls will change RFI rank in consecutive feeding periods, regardless of diet, the influence of other factors such as environment and bull age should be further investigated to determine their effect on RFI determination.

6.0 General Discussion

There is a growing interest in use of RFI in the beef industry as a means of identifying animals with greater growth efficiency. However, a better understanding of this efficiency trait is required, particularly when measured in different environmental conditions and under various production systems. Further, an indirect, less expensive and more rapid method of determining RFI within a contemporary group would be of great utility for the beef producers. The current study was designed to determine if biological efficiency in growing beef bulls could be predicted by measuring heat loss from the surface of the eye and cheek regions using two different infrared camera systems. It was hypothesized that bulls with a cooler surface temperature as measured by IRT are more efficient (lower RFI value). However, in the present study mean surface temperature of the eye and cheek regions as measured by IRT using handheld and stationary camera systems did not differ significantly between low, medium and high RFI groups. In addition, correlation coefficients were insignificant ($P > 0.05$) for RFI_{Fat} with Ey_{HH}, Ck_{HH}, Ey_S and Ck_S.

A second objective of the RFI study was to evaluate the incidence of reranking between consecutive feeding periods. Rations which differed in physical composition were utilized to study the effect of diet type on RFI repeatability when measured in successive feeding periods, with the hypothesis that bulls will rank differently when fed a forage-based diet compared to a grain-based diet, and vice versa. Reranking among bulls from one feeding period to another was observed in the diet switch treatment, but also in both treatments where diets were maintained through the trial. Repeatability was estimated using Spearman correlation coefficients for RFI measured in both feeding periods. The diet switch treatment showed a low, insignificant RFI repeatability while values for the grain and forage control treatments exhibited moderate to high

repeatabilities. Further, bulls in the grain diet treatment displayed the highest repeatability for RFI.

6.1 Suitability of measuring eye and cheek temperature to estimate surface temperature

In the current study surface temperature was measured from both the eye and cheek locations. These anatomical regions were selected as they are considered extremities on a beef animal, free of any excessive fat cover, which serve as a means to efficiently dissipate heat during homeotherm thermoregulation (Whittow, 1962; McArthur, 1981). Utilizing the eye and cheek regions also helped to facilitate a safe, non-invasive collection process by being able to focus on the head region from a two meter distance. In addition, previous IRT studies have captured infrared images from these locations and demonstrated a significant positive relationship between the eye (Montanholi et al., 2009) and cheek (Montanholi et al., 2010; Colyn, 2013) temperatures with RFI.

However, bulls in the present study did not exhibit significant correlations between eye temperatures measured with either the handheld or stationary camera systems. Other researchers (Montanholi et al., 2010; Colyn, 2013) have observed non-significant relationships between the eye temperature and RFI. The canthus and area around the lachrymal gland is known to be quite vascularized and innervated. As such it is expected that the vascular nature of tissues immediately around and behind the eye may influence surface temperature due to other physiological responses. Differences in surface temperature around the eye may be attributed to changes in blood flow associated with the sympathetic nervous system. Stewart et al. (2008a) used IRT to detect eye temperature changes in response to pain for Holstein Friesen heifer calves, while differences in eye temperature were linked to handling stress in yearling beef heifers and bulls (Stewart et al., 2008b). The temperature of the eye and its surrounding tissues

has also been utilized for early disease detection (Schaefer et al., 2004; 2012). It is possible that this highly innervated region was being influenced by factors other than thermoregulation, such as the presence of subclinical disease, pain or stress of handling, resulting in surface temperatures that did not solely reflect thermoregulatory heat loss.

6.2 Image collection protocol and analysis

The observed lack of relationship between cheek and eye heat loss and biological efficiency may be explained by differences in image collection protocol. Mean eye and cheek temperatures from images collected with the handheld camera system were calculated in each feeding period as the average surface temperature value determined across all collection days. The number of collection days ranged from six to eight in a single feeding period. Image collection with the stationary camera system was continuous, and therefore a larger number of images (n=23 to 269) were used to derive an average temperature value. Regardless, the number of image collection days utilized to calculate each feeding period mean was substantially greater than Montanholi et al. (2009) and Colyn (2013). In the latter study, multiple frames of live video recording were analyzed to calculate mean eye and cheek temperatures, accounting for any warming or cooling effects observed while the animal was restrained during collection. This approach would presumably allow the operator analyzing such images to detect any warming or cooling effects that may occur on the eye's surface. The present study collected images more frequently than previous IRT studies; expected variability between collection days associated with individual or environmental effects should be reduced by increasing the number of days that images are taken. The frequency of image collection in the current study was presumed to adequately account for the expected individual and environmental variability throughout a 76-

day feeding period, while providing a convenient opportunity to collect images on days which coincided with scheduled weigh days.

6.3 Influence of stress of handling on IRT measurements

The stationary camera system was effective for continuously capturing images of bulls while they were presumably in a "steady-state" and not being subjected to possible stressors. Collection of images with the handheld camera system was not expected to induce any fear-related responses. To explore potential differences in stress or heat production due to activity, a simple method was used to compare mean cheek and eye temperatures for both camera systems (within-pen conditions compared to being restrained in a squeeze chute). Coincidental activities that took place during scheduled weigh days (e.g. blood collection, vaccination) were probably associated with entering the chute and could have increased hypothalamic-pituitary-adrenal axis activity, resulting in the production of stress hormones or a corresponding blood flow response that may affect thermoregulatory mechanisms (Schaefer et al., 2002). Further, heat production due to the physical activity associated with moving bulls from their pens to the handling facility would also presumably affect surface temperature values measured using IRT. Moderate to high significant correlations ($P < 0.05$) were observed between Ey_{HH} and Ey_S in FP1($r=0.43$) and FP2 (r-0.48) while Ck_{HH} and Ck_S were also significantly correlated ($P < 0.01$) in FP1 ($r=0.54$). This would suggest that both stress and increased activity during weigh days did not result in a corresponding response to heat loss, as measured by IRT. If this effect was present during collection days then it proved to be similar for the entire population of bulls. Effectiveness of the stationary camera to accurately measure eye and cheek surface temperature, along with the increased capacity for image collection when compared to the handheld camera, suggests that within-pen image collection is a suitable method for collecting IRT data in a feedlot setting.

6.4 Effect of cold stress on IRT measurements and RFI determination

Energy requirements of beef cattle related to thermoregulation can vary substantially depending on the environmental conditions. Both the severity of inclement weather and the opportunity for acclimation will affect a cow's energy demands. Cold temperatures, either alone or in combination with wind velocity, can result in increased nutrient requirements and reduced performance in beef cattle while attempting to maintain a constant body temperature (NRC, 1996). The previous thermal conditions experienced by livestock, along with the frequency of occurrence and the ability, or lack thereof, to acclimatize to such conditions will determine the degree to which animals are affected (Young, 1975). In general, temperatures were much cooler in FP1 than FP2 due to the normal seasonal climate conditions, and as such the incidence of cold stress would be more likely to occur in FP1. However, sudden increases in ambient temperature during the transition from winter to spring may present conditions in which bulls experienced heat stress. For example, the temperature ranged from -5.7 to 16.9^{0}C over a 24 hour period of time in FP2 of Year 1, representing a range of almost 23^{0}C. It is likely that bulls were expending additional energy to lose heat compared to retaining heat at this unexpectedly warm temperature due to a lack of acclimation. The fluctuation in temperatures during spring months is a common occurrence in Western Canada. Hence, environmental temperatures should be monitored during bull performance testing and any sudden changes in temperature should be noted so that attempts to correct performance measures, such as feed intake, for climate acclimation can be investigated to provide the most accurate RFI value.

In addition to temperature fluctuations, the presence of extreme cold during the present study could potentially impact RFI and IRT measurements when compared to animals in a thermoneutral environment. Establishing a TNZ for yearling beef bulls is difficult; estimated

lower critical temperatures published by NRC (1996) do not account for unexpected temperature drops and the corresponding increase in feed intake or additional energy required for thermoregulatory responses. It is possible that the sporadic incidence of extreme cold temperatures throughout the winter months affects normal energy utilization and physiological mechanisms in such a way that heat loss, feed intake and growth measurements would be influenced, ultimately producing biased IRT and RFI values. Similarly, individual animal variation for the ability to cope with cold stress might favour some bulls over others under cold-stress conditions compared to thermal neutrality. As mentioned previously, thermoregulation processes have been identified as causing underlying variation in RFI yet no estimates or attempts to quantify this source of variation have been given (Herd et al., 2004; Richardson and Herd, 2004). Therefore, the magnitude of the response in previous studies had not been quantified at any temperature, including those experienced throughout the winter season in Western Canada. During FP1 37% and 87% of the days in Years 1 and 2, respectively, reached temperatures below -20^{0}C. Such an occurrence of extremely cold days may have confounded component measurements (feed intake, body weight gain) used to calculate RFI and produced a value that does not reflect biological efficiency when bulls are within their TNZ. This suggests that biological efficiency may have been influenced by thermoregulatory activity as it is likely that regular energy partitioning was affected by increased energy requirements necessary for regulating body temperature. A lack of relationship between IRT traits and RFI, and well as RFI reranking observed between feeding periods, may be attributed to thermally challenged bulls during FP1 and FP2. As such, it would be beneficial to further study the acute effects of cold and heat stress on measurements associated with IRT and RFI determination in order to develop standard operating procedures when undertaking future trials.

6.5 Potential effects of bull age on the determination of RFI

The age of the animals at the end of the test was also identified as a possible influence on RFI reranking. Two consecutive feeding periods of 63 and 76 days with weekly and biweekly weigh days, respectively, were necessary in order to gather sufficient growth and intake information to determine RFI. In total (including between-period adaptation periods) the entire experiment lasted 178 days in Year 1 and 174 days in Year 2. This is up to 66 days longer than a standard 112 day commercial bull test and almost three times the suggested feeding period duration to accurately determine feed intake and growth (BIF, 2010). In the current study bulls were on average 370 days of age at the beginning of FP2, considerably older than bulls in previous RFI trials (Lancaster et al., 2009; Montanholi et al., 2009; Awda et al., 2013) and outside of the suggested start-of-test age range for central bull tests (BIF, 2010). It is be possible that even though bulls were still maintaining linear growth during FP2, other factors such as puberty, seasonal climate conditions and unknown physiological influences related to bull age caused discrepancies in growth and feed intake measurements. This could be a reason for poor correlations between IRT traits and RFI, as well as a possible factor associated with RFI reranking.

Onset of puberty is another factor which may have impacted energy utilization in the bulls and therefore impacted RFI ranking. A reduced amount of energy will be expended in pre-pubescent cattle due to exhibiting less sexual behaviour and having later development of the reproductive systems, which favours the RFI phenotype (Awda et al., 2013). Similarly, increased activity would presumably be associated with the expression of sexual activity in bulls. Since bulls were already 370 days of age at the beginning of FP2, approximately 75 days older than the suggested age of puberty in Angus bulls (Lunstra and Echternkamp, 1982) it is expected that

they had already reached puberty or would reach puberty during the second feeding period. Up to 9% of the underlying variation in feed efficiency due to physiological mechanisms has been attributed to physical activity (Arthur and Herd, 2008) and thus it is possible that discrepancies exist between RFI determined in FP1 compared to FP2 for bulls that had reached puberty in FP2. Basarab et al. (2011) evaluated the effect of puberty on RFI in young heifers and reported that prepubescent animals consumed 4.7% less feed ($P < 0.001$) and had a 7.4% improvement in FCR ($P < 0.001$) compared to animals that had already reached puberty, given equal ADG, body size and BF. The authors suggest that adjusting RFI for feeding activity, in addition to BF, will help to remove effects associated with puberty on feed intake in growing heifers. This would allow for the selection of efficient (low RFI) heifers without any indirect negative effects on reproduction. A similar approach should be investigated for RFI studies evaluating beef bulls and using concurrent breeding soundness exams to aid in determining whether bulls have achieved puberty.

6.6 The impact of diet composition on RFI determination

As described in Section 4.4, RFI reranking was observed in all diet groups, regardless of whether or not diets switched between feeding periods. However, the effect was greatest for the diet switch treatment. The procedure of changing diets which differed in primary carbohydrate source may have affected the individual's ability to utilize that feed. Rumen microbe population structures will shift from amylolytic to fibrolytic species when forages replace starch as the primary energy source (Goad et al., 1998; Fernando et al., 2010), and it has been shown that rumen microbial profiles are related to cattle feed efficiency (Guan et al., 2008). This implies that feed efficiency may differ relative to the diet composition being offered to beef cattle. Mean starch values of the grain-based diet in the present study were much greater than levels in the

forage-based diet, suggesting that a shift in rumen microbe populations would have occurred. Differences in the chemical composition of high and low forage diets have also been reported to affect the RFI phenotype in cattle by influencing rumen bacterial diversity as Carberry et al. (2012) proposed that diet type may in fact control the effect of RFI through the abundance or lack of certain rumen microbes.

In addition to variability in the chemical composition between both diets, the physical characteristics may also have contributed to RFI reranking. The physical density of the forage-based diet could have limited dry matter intake due to animals reaching gut-fill sooner. The physical nature of rations has also been reported to influence the efficiency of microbial protein synthesis in the rumen, even more so than the chemical composition (Rode et al., 1985). This may be related to faster rates of passage for high concentrate diets which increase the ruminal solids turnover rate and subsequently the nutrient flow and absorption to the small intestine, improving the efficiency of animal performance (Varga and Harpster, 1994). For these reasons, it is conceivable that RFI could be affected by offering diets which differ in composition, such as those utilized in the present study.

6.7 Conclusions and future research

Utilizing IRT technologies to predict biological efficiency in beef cattle has shown promise as an alternative method for RFI determination. However, results from the current study suggest that the influence of environmental conditions on surface temperature measurements and energy partitioning related to thermoregulation requires further investigation in an effort to standardize IRT collection and RFI determination protocols. In addition to environmental conditions, management practices such as diet type and bull age should also be considered while attempting to standardize RFI calculation procedures.

Conditions during the collection procedure for IRT images with the handheld camera system were controlled as best as possible. Radiant heaters within the handling facility were turned off prior to image collection to minimize the effect of external radiant heat on bull eye and cheek temperature. However, several possibilities for factors to influence IRT measurements were beyond control. Unfortunately, it was not possible to eliminate the presence of solar radiation from incoming sunlight prior to the bulls entering the facility. Clark and Cena (1972) reported up to 8°C difference in hair coat temperature when under direct sunlight, depending on the pigment of the hair. Therefore, it is likely that there was some effect of solar load on collection days without cloud cover. Further, the potential for additional heat production due to increased locomotion or handling stress would most likely have occurred. In terms of image analysis, both IRT images and real time video have strengths and weaknesses associated with them; collecting chute-side images is less time consuming and allows the operator to quickly confirm image quality prior to releasing the animal whereas real time video theoretically detects warming or cooling effects during the time spent in the chute. Lastly, the frequency of IRT collection has varied significantly among previous studies. More frequent image collection days would presumably account for some of the expected variation over a 76- day feeding period, providing a more accurate IRT value. One solution that addresses each of the aforementioned issues is utilizing a within-pen IRT system. The stationary camera system used in the present study successfully captured continuous images of bulls and was significantly correlated ($P < 0.05$) to measurements made with the handheld camera system. Image collection made while the animals are in a steady-state condition would remove incidence of stress and any influence from increased locomotion while permitting data to be collected during the evening without the presence of radiant heat sources (sunlight or radiant heaters). Continuous collection of images

throughout the entire feeding period would provide a robust sample of data to determine mean eye and cheek temperatures. In the present study, a software program was designed to identify the eye and cheek regions automatically, producing a mean temperature for each anatomical location and removing the chance of operator error or inconsistency when analyzing individual images. Adopting this technology would provide a unique opportunity for accurate, non-invasive collection of biometric data that could serve a wide range of studies requiring bio-surveillance information and supports findings by Schaefer et al. (2012).

As discussed above, the combination of environment, bull physiological status and diet composition influence the component measurements (growth and feed intake) for calculating RFI. It is not uncommon for extreme cold temperatures to be experienced in beef operations with considerable variation across Western Canadian. To the author's knowledge previous RFI studies have not been conducted in extreme cold conditions. Cold stress is often viewed as a potential issue affecting feed intake and partitioning energy demands from production to thermoregulation. As indicated, 37% and 87% of the days in FP1 of Years 1 and 2, respectively, had wind chill corrected temperatures below -20°C (data not shown). As well, fluctuations in temperature of almost 23°C in a single day during FP2 could have resulted in bulls becoming heat stressed. Energy utilization in situations where livestock are using more energy to maintain a constant core body temperature is not reflective of the utilization when within their TNZ, although knowing which bulls perform better under cold stress conditions may be of interest. Considerations for the thermal stresses that bulls are subjected to, cold or heat, should be made when measuring RFI, beginning with the continuous monitoring of environmental conditions during an RFI feed period. With this data, it would be possible to omit feed intake data during periods of time where bulls are likely to have experienced extreme temperature conditions. In

addition, feed intake patterns during periods of thermal stress could be evaluated to determine the deviation from intake when animals are assumed to be within their TNZ, with possible adjustment methods applied thereafter.

A suggested age range for determining RFI in classes of beef cattle should also be formulated. Several studies (Durunna et al., 2011; Kelly et al., 2010; Durunna et al., 2012) have reported RFI reranking in beef cattle when measured at different stages of production, and suggests that RFI values calculated at different ages should be considered separate traits. A comparison with ADG reranking was made in the current study and animals were observed to change rank at almost the same degree to RFI. Developing a recommended range of ages for postweaning, yearling and mature livestock classes would be a beneficial step for standardizing RFI determination.

It is evident that further studies are needed to determine changes in biological efficiency when different diets are offered. A higher proportion of bulls changed rank in the diet switch treatment compared to the forage and grain control treatments, while non-significant correlations between RFI measured in each feeding period were also observed for these bulls. Diet formulations for growing bulls can vary in energy content and ingredient composition between RFI studies. Additional experiments evaluating RFI and rumen microbial populations on forage and grain-based diets would provide valuable information on the effect of diet type. However, with this approach it may be difficult to separate the individual diet effect from the age-of-bull effect due to the time required for consecutive feeding periods. Currently the Beef Improvement Federation recommends a minimum dietary energy value of 2.4 Mcal ME kg^{-1} DM for growing bulls when testing performance, however, there is no mention of ingredient composition or using forage versus grain-based diets. The rate of passage and previously described associated effects

on feed intake (and subsequently RFI determination) could be evaluated by conducting RFI reranking studies with different lengths of forage fiber. If reranking is not observed similar to the current study, the significant effect of diet would be attributed to differences in chemical composition of grain diets compared to forage diets, rather than differences in physical form. As well, the inclusion level of forage compared to grain can be measured using starch analysis; establishing a range of starch levels in which results can be compared fairly between studies may be the best immediate approach to standardizing diets for RFI determination.

Finally, testing young bulls in consecutive feeding periods during an RFI reranking trial presents challenges related to an extended length of time on test, such as bulls reaching puberty before or during the second feeding period, or vast differences in the environmental conditions experienced by the animals. A substantially shorter test period that would allow accurate RFI determination would have broad applications in beef efficiency studies. Of interest in this regard are the findings of Schaefer et al. (2014a) with heifers and (2014b) with bulls that demonstrate a thermal induction process conducted over a short time period which enables the prediction of efficient and non-efficient animals using IRT. The methodology used in these studies would avoid some of the aforementioned problems and prove efficacious in using IRT to rank metabolic efficiency.

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