The assessment of Replacement Heifer Production Efficiencies through Residual Feed Intake and Key Hormone Profiles

By

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ABSTRACT

THE ASSESSMENT OF REPLACEMENT HEIFER PRODUCTION EFFICIENCIES THROUGH RESIDUAL FEED INTAKE AND KEY HORMONE PROFILES

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University of Guelph, 2012
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Biological factors regulating feed efficiency were investigated in replacement beef heifers to establish factors that differ between efficient and less efficient animals. Feed efficiency, measured as residual feed intake (RFI) adjusted for body ultrasound measurements, was determined in forty-seven cross-bred heifers. Reproductive differences between efficient (low RFI) and less efficient (high RFI) heifers were examined. Low RFI heifers had an earlier age at both sexual maturity (P=0.08) and conception (P=0.08), and delivered heavier calves (P=0.006). The potential of fecal progesterone metabolites (FP₄M) as an indicator of sexual maturity was examined. Measurements of FP₄M present a promising non-invasive alternative technique for determining the onset of sexual maturity. A subset of 36 heifers was used to determine if plasma triiodothyronine (T₃) concentrations could be used to predict feed efficiency. Triiodothyronine concentrations a correlation of 0.58 (P=0.001) to those from a quadratic prediction model of RFI in heifers sampled as yearlings.

Keywords

Beef cattle, cow-calf, production efficiency, puberty, reproductive efficiency, thyroid hormones
Advisory Committee:  Dr. Stephen P. Miller (Advisor)

Dr. Kendall C. Swanson (Co-Advisor)

Dr. John P. Cant
DEDICATION

I would like to dedicate this dissertation to the dearly beloved Rose-Anne McNichol.

I would not be in the present situation without your perseverance in modeling me into the man I have become. You have been, and will forever continue to be an important part of my life. I am deeply grateful for all of the wonders you brought to my life. You may be gone in body now, but the many thoughts and memories of you will live on forever.

I love you—Rosie!
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<td>A</td>
<td>Average</td>
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<tr>
<td>BD</td>
<td>Birth date</td>
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<td>BIC</td>
<td>Bayesian information criterion</td>
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<td>BFT</td>
<td>Back fat</td>
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<td>BW</td>
<td>Body weight</td>
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<td>cm</td>
<td>Centimeter</td>
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<td>d</td>
<td>Day</td>
</tr>
<tr>
<td>DG</td>
<td>Daily gain</td>
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<tr>
<td>DIG</td>
<td>Days in gestation</td>
</tr>
<tr>
<td>DNA</td>
<td>Deoxyribonucleic acid</td>
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<tr>
<td>°C</td>
<td>Degrees Celsius</td>
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<tr>
<td>Δ</td>
<td>Delta</td>
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<tr>
<td>DM</td>
<td>Dry matter</td>
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<tr>
<td>DMI</td>
<td>Dry matter intake</td>
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<tr>
<td>EIA</td>
<td>Enzyme immunoassay</td>
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<td>FI</td>
<td>Feed intake</td>
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<td>FP₄M</td>
<td>Fecal progesterone metabolites</td>
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<td>g</td>
<td>Gram</td>
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<td>G</td>
<td>Gain</td>
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<tr>
<td>GA</td>
<td>Gauge</td>
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<tr>
<td>GLM</td>
<td>General linear model</td>
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<tr>
<td>h</td>
<td>Hour</td>
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<tr>
<td>IFT</td>
<td>Intramuscular fat</td>
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<tr>
<td>kg</td>
<td>Kilogram</td>
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<td>lb</td>
<td>Pound</td>
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<td>Metre</td>
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<td>Miligram</td>
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<td>ng</td>
<td>Nanogram</td>
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<td>NE</td>
<td>Net energy</td>
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<td>mL</td>
<td>Millilitre</td>
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<td>mm</td>
<td>Millimetre</td>
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<tr>
<td>P₄</td>
<td>Progesterone</td>
</tr>
<tr>
<td>P₄</td>
<td>Probability (P-value)</td>
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<td>PP₄</td>
<td>Plasma progesterone</td>
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<td>PT</td>
<td>Pre-feed trial</td>
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<td>QTL</td>
<td>Quantitative trait loci</td>
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<td>R²</td>
<td>Coefficient of determination</td>
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<tr>
<td>REA</td>
<td>Rib eye area</td>
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<td>Residual feed intake</td>
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<td>Rump fat</td>
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<td>Description</td>
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<tr>
<td>RIA</td>
<td>Radioimmunoassay</td>
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<tr>
<td>rpm</td>
<td>Revolutions per minute</td>
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<td>rT3</td>
<td>Reverse triiodothyronine</td>
</tr>
<tr>
<td>S</td>
<td>Second</td>
</tr>
<tr>
<td>S.D</td>
<td>Standard Deviation</td>
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<td>SNP</td>
<td>Single-nucleotide polymorphism</td>
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Chapter 1

INTRODUCTION

1.1 General introduction

Replacement beef heifers are a vital component of the cow-calf sector. These animals represent the introduction of new genetics and contribute to the future productivity of the herd. Significant money is invested in these animals without having any return on investment until the sale of a successfully weaned calf. To reduce investment requirements, a producer needs to lower costs such as feed expenses associated with development of these animals, improve efficiency, and ensure breeding animals become pregnant in a timely manner.

Efficiency can be described as obtaining the greatest quantity of output from minimal inputs. From an animal production standpoint, efficiency is the ability to obtain the greatest amount of output in terms of meat or milk, for example, from the consumption of the least amount of animal feed and other inputs. In the cow-calf sector, it can therefore be described as the consumption of the least amount of fodder required for maintenance and growth (in heifers), in conjunction with the successful rearing of at least one calf annually. A great variation exists in animal efficiencies (Arthur et al., 2004); the limitation to determining this variation resides in the requirement of individual animal feed intake and body weight measurements over a relatively lengthy period of time (Tatham et al., 2000). Wide scale adoption of efficiency measurement is prohibited by the costs associated with measuring individual animal feed intake and body weights, along with the required facilities to do so. As a result, there is a need to determine alternatives for assessing feed efficiency that are reliable and affordable.

In the current research, feed intake data was collected from puberty to calving to determine the relationships between feed efficiency ranking and other characterizable traits and measures.
such as those related to heifer growth, development, and pregnancy. Residual feed intake (RFI) was used to classify the relative feed efficiency of each research heifer (Koch et al., 1963) used in this study. Residual feed intake calculates the difference between actual daily feed intake and expected intake for the maintenance of body weight and growth calculated from biweekly body weight measurements. Animals with less-than-expected actual feed intakes are classified as efficient (-RFI), and those with intakes of greater-than-expected values are classified as inefficient (+RFI).

Numerous unknown factors may influence feed efficiency. The components influencing feed efficiency covered in this study include potential relationships between feed efficiency and the onset of sexual maturity, as well as circulating thyroid hormone levels as a potential indicator of efficiency. Sexual maturity needs to occur in heifers by 12 to 15 months of age in order for them to conceive and calve at two years of age for greatest return on investment (Patterson et al., 1992). Measurements of age at sexual maturity were determined by measuring plasma progesterone concentrations from blood samples collected over time (Wehrman et al., 1996). Fecal samples were collected simultaneously with blood sampling to determine the usefulness of using a progesterone derivative within this alternative body matrix source as an indicator of sexual maturity (Schwarzenberger et al., 1996). Triiodothyronine (T₃) levels in the blood were examined to identify their usefulness as a biological indicator of feed efficiency. Blood samples were harvested over a 24 h period to determine the variability in plasma T₃. Variations in circadian hormonal cyclic profiles that shadow differences in RFI will alleviate some of the perplexities contributing to observed differences in feed efficiency. If the thyroid hormones were found to significantly affect efficiency ranking, they could be utilized as an easily measurable indicator trait of efficiency. This would enable ranking of animals according to efficiency, without requiring the collection of feed intake and body weight measurements.
Results from this study will further our knowledge of animal efficiency and contribute to understanding of the interactions that may exist. Volatility of cattle markets, rising feed prices, surging land and input costs, and decreasing farm profit margins make it imperative to raise efficient animals that have improved feed conversion ratios. This result will increase competitiveness in the meat market, and decrease opportunity costs associated with feeding cattle compared to other livestock species. The industry needs to know this information in order to aid in the process of selecting for heifers that are not only efficient, but also reproductively sound and genetically superior. A reduction in production costs through an increase in feed efficiency will make producers more profitable, make the industry more competitive, and ensure sustainable beef production. Greater efficiency in the beef industry will support an essential component of the Canadian economy.
1.2 Overall objectives

The goal of this thesis is to investigate and evaluate feed efficiency in Angus-Simmental composite breed replacement heifers to determine if differences exist between efficient and inefficient animals in regards to reproductive performance including age at puberty, as well as blood triiodothyronine (T3) concentrations.

Objectives of the study are the following:

- Determine if age of sexual maturity is associated with feed efficiency in beef heifers
- Determine the usefulness of fecal progesterone as an indicator of sexual maturity in beef cattle
- Examine whether circulating concentrations of triiodothyronine (T3) is an indicator of feed efficiency
- Determine how triiodothyronine (T3) relates to feed efficiency, age, maturity, and pregnancy.
Chapter 2

LITERATURE REVIEW

2.1 The Canadian beef industry

The Canadian beef industry is an extremely important sector of Canada’s economy and food supply. This sector is shaped by and is highly dependent on export sales and global demand. It comprises 4.2 million beef cows and 554,300 replacement heifers as of January 2012 (Statistics Canada, 2012). Although responsible for only 1.2 percent of the world’s cattle supplies, Canada boasts itself as the fifth largest cattle exporting country at 7.3 percent of world exports (Canfax, 2012b). In 2010 alone, Canada’s exported beef and cattle was valued at 1.42 billion dollars (AAFC, 2011; FCC, 2011).

Canada’s beef herd inventory has been in decline since 2006. Ontario’s cow numbers, now at seven percent of the nation’s total, have also followed this downward trend over the last six years (Canfax, 2011a). There has been a drop in Ontario cow inventory from 389,000 in 2006 to the present number of 316,000, largely due to increased culling (Statistics Canada, 2012; Canfax, 2012b). Replacement heifer inventory has also declined from 58,500 head in 2006 to the current count of 46,000 (Statistics Canada, 2012; Canfax, 2012b). This reduced supply is supporting higher cattle prices (Canfax, 2011b) and gives producers additional incentive to increase culling rates.

Producers are beginning to move toward replacing older animals, as shown through a 6.7 percent increase in Canadian replacement heifer retention from 2011 levels (Canfax 2011c; CCA, 2011). Replacement heifers have the ability to stay in the herd for extended periods of time, and their introduction can be seen as the addition of new, young genetic lines selected for superiority of certain traits and characteristics (Canfax, 2011c). Heifer numbers are not, however, concrete
values, as some never carry a calf to term and are marketed for beef (Canadian Cattlemen, 2011). The progeny from the heifers that raise a calf will not be added to the herd numbers until after a successful wean the following year.

The lower cattle inventory in Canada has recently been reflected through higher cattle prices; however, these higher prices have not led to an expansion of cattle numbers. Expansion of the Ontario cattle herd has been non-existent as profitability in the cow-calf sector is what determines expansion rather than cattle prices alone (Canfax, 2011a). Costs associated with cattle rearing, especially those related to feed, have been eroding profit margins in the cattle industry for some time, and have kept expansion from occurring (CCA, 2011). Corn prices alone more than doubled in the course of a year, increasing from 150 dollars per tonne in 2010 to 330 dollars per tonne at the end of 2011 (CCA, 2011). Other crops have mirrored the increase in corn price, and the combination has pushed land values to unforeseen levels. Increased crop prices put greater pressure on cattle numbers, as opportunity costs are weighted in the calculations, and land is removed from cattle production and converted to crop production to obtain greater returns from less labour and risk (Canfax, 2011c; FCC, 2011). Food prices in general have all been rising, being pushed upward by underlying commodity prices; the same results are occurring in the feed sector (Canfax 2011b).

The price of beef has been increasing steadily, but it continues to be a preferred protein product. In 2011, beef captured 42 percent of the Canadian domestic income expenditure on protein products at a value of $6.32 billion (Canfax, 2011b). This trend shows consumer’s willingness to pay for beef products. Canadian beef consumption, however, follows the trend of total meat consumption, and has been in decline since 2007, falling to its current level of 33.6 percent of meat consumption; a per capita value of 20.2 kg out of a total of 73.7 kg (Canfax, 2011b). Regardless of a decreased Canadian consumption of beef products as a result of increased
prices, overall demand for beef still remains quite high with prospects of global demand set to increase.

The demand for beef is expected to increase, with the rise in global economies such as those of China, North Africa, and the Middle East (Canfax, 2011a; FAO, 2011). A growing world population is estimated to increase beef consumption from its current levels by an additional 50 percent by 2050 (FAO, 2011). More important than the increase in the demand for beef from population growth are the increases in the expectations of a global economy and disposable household incomes (FAO, 2011). A greater number of families with higher incomes will have money to spend on a desired high-protein diet containing greater quantities of beef.

Further investigations into factors related to feed efficiency in the cow-calf sector are required in order to sustain beef production in Ontario and Canada, as well as to meet the future demand for beef products. It is unlikely that the growth in the future supply of beef will occur from a drastic increase in the number of cattle on feed (FAO, 2011). The challenge of meeting the future demand for beef will have to be met though improved efficiencies in resource utilization and the maximization of beef production from the minimal quantity of arable land (FAO 2011).

2.2 Feed efficiency

2.2.1 Categorizing efficiency

Efficiency can be described as the lowest quantity of input required to produce a certain quantity of output. In regard to beef production, a key way in which to look at efficiency entails the quantity of feed consumed for a given amount of animal production (Taylor, 1994; Okine et al., 2004; Carstens and Tedeschi, 2006). Feed efficiency cannot be measured directly (Koch et al., 1963), therefore its determination requires the quantification of both feed intake and weight gain (Taylor, 1994). These measurements can be difficult and costly to obtain (Arthur et al., 2004;
Okine et al., 2004; Tedeschi et al, 2006), but form the underlying driver for alternative economically feasible indicators of feed efficiency (Arthur and Herd, 2008).

There are numerous methods of categorizing feed efficiency. Each method has its own benefit depending upon circumstances and desired outcomes. Detailed descriptions of the various feed efficiency measures can be found in the publications by Swanson and Miller (2008), Arthur and Herd (2008), and Carstens and Tedeschi (2006). The main divergence between measures of feed efficiency stem from those which attempt to segregate gross energy consumption or requirements into two categories of maintenance and growth (Okine et al., 2004; Carstens and Tedeschi, 2006).

2.2.2 Residual feed intake as a measure of feed efficiency

First introduced by Koch et al. in 1963, the concept of residual feed intake (RFI), also referred to as net feed intake, involves estimates of both maintenance and production. Residual feed intake adjusts energy intake for differences in bodyweight gain and animal size, with the remainder of intake reflecting differences in maintenance energy costs beyond those expected due to size alone (Koch et al., 1963). The difference between the observed energy intake and the expected energy intake calculated from a regression using body weight and intake measurement during the test (Arthur and Herd, 2008), produces the residual feed portion (Koch et al., 1963). Animals with intake less than expected for growth and maintenance will have a negative RFI corresponding to a greater feed efficiency, while those that deviate in the other direction, having a greater than expected intake, will have a positive RFI value. This latter indicates a less feed efficient animal (Koch et al., 1963; Okine et al., 2004; Carstens and Tedeschi, 2006; Arthur and Herd, 2008). The concept of RFI adjusts an animal’s intake for the variation in feed intake due to body mass and gain, while the remainder of its intake is considered representative of background energy requirements (Carstens and Tedeschi, 2006; Nkrumah et al., 2006).
There are many benefits to the use of RFI as a measure of feed efficiency. Accounting for energy intake for both growth and background energy requirements are key factors (Koch et al., 1963). In particular, the total cost of feed for maintenance requirements alone have been determined to be upwards of 65 percent, as reported by Montano-Bermudez et al., (1990). Ferrell and Jenkins, (1985) reported similar values of energy requirements for maintenance in a cow herd with values of 70 to 75 percent of total requirements. Improvements in maintenance energy requirements can decrease the amount of feed required in a cow herd, thereby reducing costs associated with feed and increasing profitability (Swanson and Miller, 2008; Arthur and Herd, 2008).

Other advantages of the use of RFI evolve from it having less dependence on production and growth factors (Arthur and Herd, 2008), which allows for improved points of comparison between animals (Carstens and Tedeschi, 2006). Residual feed intake may also parallel metabolic processes (Swanson and Miller, 2008), making it useful for investigations of mechanisms and processes that are responsible for differences in efficiency (Arthur and Herd, 2008).

2.2.3 Contributions to the variance in residual feed intake

The overall biological mechanisms known to control variation of residual feed intake have not been completely elucidated, and are not well understood (Nkrumah et al., 2006). Numerous sources, processes, or combinations of the two have been shown to contribute to the variation in residual feed intake. Others have categorized these processes into seven main factors which include the following: feed intake, feed digestion, metabolism, physical activity, thermoregulation, stress (Herd et al., 2004; Richardson and Herd, 2004; Herd and Arthur, 2008 ), and body composition (DiCostanzo et al., 1991; Johnson et al., 2003; Herd et al., 2004; Basarab et al., 2004). Of these, two main areas emerge as highly influential factors – heat production, and body composition.
Inefficiencies in the conversion of energy from a nutrient source to adenosine triphosphate, chemical energy usable by the body, results in the production of heat (Ferrannini, 1988). This heat production acts as a source of energy loss from an animal. Determining this extent of energy loss requires calculating the amount of heat produced through chemical stoichiometric equations of the complete oxidation of the energy sources (Nienaber and Maddy, 1985). Complete oxidation results in the production of carbon dioxide, water, and heat (Ferrell and Oltjen, 2008). Calorimetry is used to measure the energy lost as heat during this process.

Measuring direct energy source oxidation in the animal is extremely difficult due to the intricacy of the processes involved. To do so, indirect measures have been devised. Indirect calorimetry measures metabolic rate and heat production though the measurements of individual oxygen consumption, and carbon dioxide production (Ferrannini, 1988; Brosh, 2007). This method holds true because oxygen gas reservoirs in the body are non-existent except for the negligible amount found in the blood (Jequier, 1985). Therefore, nutrient oxidation can be reflected through oxygen consumption of the species (Ferrannini, 1988). The efficiency of this oxidization is reflected through oxygen consumption by the animal. This process is most likely the underlying determinant for the associations between RFI, calorimetry and heat production (Nkrumah et al., 2006) as well as the reason why heat production estimates may explain a large portion of the variation in RFI (Basarab et al., 2003; Arthur and Herd, 2008).

In combination with heat production, body composition also plays an important role in the variation in RFI. The importance of the effect of body composition on RFI variation must be taken into consideration (Swanson and Miller, 2008). Energy costs associated with the deposition and maintenance of bodily tissues are determined by fat and lean makeup of an animal’s tissues (Herd et al., 2004). Research in this area has found a small positive correlation between RFI and body fatness, indicating that a leaner growing animal is more efficient (Richardson et al., 2001; Basarab et al., 2004). Compensation for bodily makeup can be done by adjusting the RFI calculation to
include ultrasonic bodily measures such as back-fat thickness, rump-fat thickness and intramuscular fat percentage (Basarab et al., 2003). This adjustment allows for the fair assessment of animals for efficiency without favouring certain body composition characteristics (Basarab et al., 2004). Even though adjustments can be made to reduce body composition effects on the RFI computation, their importance in the contribution to variance of residual feed intake cannot be overlooked. Body composition and associated energetic costs have been shown to be associated with five to nine percent of the variation in RFI (Herd and Arthur, 2008; Lancaster et al., 2009). Combined with heat production, these factors explain a large portion of the variation of RFI.

Other sources have been found to play minor roles in the variation in RFI in the majority of circumstances; however, their importance to overall animal efficiency cannot be overlooked. These include digestion, physical activity, and stress. The inefficiency from digestion begins with a greater quantity of intake which requires more energy for processing, but also results in larger digestive organs to do so. These larger organs require an increased amount of energy in order to function (Herd et al., 2004). Greater intakes therefore mean increased heat increments of feeding and digestive fermentation (Richardson and Herd, 2004). Variation in RFI from the heat increment attributed to feeding has been reported to be nine percent (Herd and Arthur, 2008). Lower overall digestibility has also been correlated to increased intakes (Herd et al., 2004).

Energy losses due to digestive inefficiency are cumulative and extend to those contained within feces (Johnson et al., 2003), urine and methane gas (Reynolds et al., 2011). Efficient animals have been shown to produce less methane than inefficient animals, as reported in a positive correlation of enteric methane emissions with RFI (Nkrumah et al., 2006; Hegarty et al., 2007). The energy losses in the conversion of food to substrates results in a large variance in RFI. Overall, the cumulative effect of these digestive constituents contribute ten to 14 percent of the variation in RFI (Richardson and Herd, 2004; Herd and Arthur, 2008).
Physical activity and feeding behaviours such as meal size, eating rate, and meal frequency have been found to contribute to variance in RFI (Montanholi et al., 2009). Richardson and Herd (2004) found feeding patterns to contribute only two percent to variations seen in RFI. Others have found, however, that feeding behaviours contribute to a larger portion of the variation in RFI, with values extending from three and a half percent (Lancaster et al., 2009), up to 18 (Montanholi et al., 2009) and 20 percent (Kelly et al., 2010). Activity, in addition to feeding behaviour, accounts for approximately five to ten percent of the variation in RFI (Richardson and Herd, 2004).

Stress also contributes to energy expenditure factors. Although difficult to measure objectively, stress appears to alter energy requirements of an animal. Richardson et al., (2004) hypothesized that high RFI steers are more susceptible to stress, while Colditz (2004) introduced the relationship between a reduction in stress and an improvement in energy utilization. However, Montanholi et al. (2009) have objectively related stress levels measured through fecal glucocorticoid levels, with evidence of efficient animals having higher baseline cortisol levels. Stress along with heat production, body composition, digestion, and physical activity forms the main factors that have been determined to help explain the variation seen within RFI.

2.2.4 Indicators of feed efficiency

Biological indicators of efficiency such as major metabolites and hormones may have the ability to aid in the selection of efficient cattle. Indicators of efficiency that have been shown to be correlated with RFI include insulin-like growth factor-1 (IGF-1) (Bishop et al., 1989; Stick et al., 1998), uncoupling proteins, leptin (Bottje and Carstens, 2009), fecal cortisol metabolites (Montanholi et al., 2009), non-esterified fatty acids (NEFA) and beta-hydroxybutyrate (BHBA) (Kelly et al., 2010). The main restriction on the adoption of indicator traits in the selection of efficient animals results from inconsistent findings in studies showing little to no correlation to identical indicator traits (Lancaster et al., 2008). Inconsistency of results across studies may be due
to an inadequate number of samples, infrequent intervals between samplings, or the effect of varying environmental conditions on the indicator trait. The accuracy of any biological indicator of efficiency is based on the extent of an indicator’s correlation to the RFI rating along with the repeatability of this measure (Moore et al., 2009). Animals with high levels of efficiency are assessed with increased accuracy when biological indicators of efficiency can be matched with corresponding molecular genetic techniques.

2.2.5 Genetics of residual feed intake

Phenotypic variance in RFI can ultimately be observed as an outcome from a combination of genetic and environmental interactions. Three main factors are of critical value when assessing the genetics of RFI—genetic variation, determination of genes responsible for this existing variation, and the expression of these genes in the following generation. Genetic variation in RFI exists within cattle (Arthur et al., 2004), and enables genetic selection for improvements in efficiency. One method of selection has been through the use of quantitative trait loci (QTL) markers, which correspond to specific deoxyribonucleic acid (DNA) sequences that are linked to particular genes of interest (Miller, 2002; Sherman et al., 2009). Five QTL’s have been identified in cattle as having an effect on feed intake and efficiency (Pitchford et al., 2002). The genes responsible for RFI can further be identified through the use of single-nucleotide polymorphisms (SNPs), to identify differences in nucleotides within the DNA strand. Mujibi et al. (2011) analyzed 100 SNPs as a method of selection for RFI, and found them to have low predictability of efficiency ranking. The main reason for this low predictability of the SNPs on RFI lies most likely in the limitation of the number of animals having both documented genetic information and feed intake data (Hill and Azain, 2009).

Residual feed intake and its associated genes have been shown to be moderately heritable (Arthur et al., 2004). Response to selection shows that dams divergently selected for RFI produced
calves that had similar efficiency ratings (Basarab et al., 2007; Arthur and Herd, 2008). Heritability values for RFI have been reported to range from 0.26 to 0.58 (Crews, 2005; Moore et al., 2009), with the majority reported to be near 0.45 (Crowley et al., 2010; Rolfe et al., 2011).

Unfortunately, selection for efficiency has the tendency to select indirectly for undesirable side effects (Rauw et al., 1998). Studies determining genetic relationships or correlations of various traits with RFI have shown a relationship between a higher efficiency and a delayed first calving (Basarab et al., 2007; Crowley et al., 2011a). Similarly, selection for RFI has resulted in leaner animals with fewer fat stores, suggesting an animal’s potential inability to deposit extra energy stores, as well as being unable to meet quality carcass grades (Lines et al., 2009; Crowley et al., 2011b). Efficient heifers have also been shown to possess less longissimus muscle area, a main component of carcass value (Shaffer et al., 2011). Fortunately, negative relationships have not been established between RFI and beef quality (Baker et al., 2006). A greater understanding of the undesirable side effects associated with RFI will assist in breeding programs that seek to minimize negative associated effects while reaping the benefits of efficient animals. The accuracy of any correlation with RFI, however, is ultimately dependent upon the precision of measurements included in the RFI calculation.

2.2.6 Accuracy of residual feed intake measurement

Daily feed intakes along with interval body weight measurements are required for the accurate determination of RFI ranking. The number of daily measurements required for the accurate measurement of RFI in beef bulls—also called “test length”—was originally set at 140 days (Beef Improvement Federation, 1986). Longer test lengths tend to average out fluctuations observed in individual animal growth and reduce measurement error such as gut fill effect at measurement, however, a greater number of days of measurements drastically increases the cost associated with measuring RFI (Liu and Makarechian, 1993). A test length of 70 to 84 days is
required for accurate measurement of RFI with the optimal length falling at 112 days (Archer and Bergh, 2000). During the test, animals should have their body weights recorded every other week (Archer et al., 1997), with more frequent weights allowing for a shorter test length (Kearney et al., 2004). In combination with animal weights over the test period, accurate feed intake measurements affect the precision of the RFI determination.

Precise quantification of feed intake for RFI determination requires the minimization of errors that exist with intake measurements using individual access controlled feed bunks such as Calan gates (van der Werf, 2004; American Calan Inc., Northwood New Hampshire). Errors are additive, and include, but are not limited to, the following: spillage, denied access or open access to all, precision of delivery and weigh-back scales, feed moisture content gained or loss, uniformity of delivered ration, spoilage, and finally underfeeding. Of these errors, providing ad libitum access to feed is of greatest importance, as RFI is independent from growth only under unrestricted feed access (Arthur and Herd, 2008). This is reinforced by findings that restricted access to feed positively alters efficiency of energy utilization (Roberts et al., 2007; Tovar-Luna et al., 2010).

Missing data due to inaccurate record keeping of intakes has also been found to affect intake estimations, especially those of growing, young animals (Hebart et al., 2004). After ensuring the precision of intake measurements and animal weights over the test period, the question then arises as to whether this animal efficiency measure of RFI is repeatable within the animal over time.

The repeatability of RFI will determine whether an animal with a known efficiency, measured by a feeding test, will continue in this manner throughout various life stages. Post-weaning RFI measurements in the heifer have been shown to be associated with efficiency later on pasture (Herd et al., 1998). However, Durunna et al. (2012) observed a re-ranking in RFI, with heifers fed the same diet over consecutive test measurement periods, particularly in the animals with the greatest or least RFI. RFI has been shown to be repeatable in heifers between the growing and finishing stages of production (Kelly et al., 2010). However, others have found diet alterations
between these two stages to change RFI ranking in steers (Durunna et al., 2011). Further studies are required to elucidate the within-animal repeatability of RFI measurement over time during various stages of production, as well as to determine the effects of environmental factors, such as diet, have on RFI. These results would provide a better understanding of the biological, physiological, and molecular basis of RFI that ultimately contribute to the successful selection of efficient animals.

2.3 Puberty and reproduction

Replacement heifers, a vital component of the cow-calf sector, have a significant impact on the economics of the breeding herd. Greater economic pressure has driven the desire to have heifers calve at two years of age because significant monetary value is invested in the development of these animals without any economic return until the sale of the first successfully weaned calf (Short et al., 1994; Warnick, 1994; Engelken, 2008). Reduction of the duration of time to return on investment, compared to calving at an alternatively later age therefore seems highly desirable.

Heifers are required to conceive successfully by 15 months of age in order to calve by the time they are 24 months old (Bellow and Short, 1994). The age at puberty therefore impacts the ability of a heifer to become pregnant at an early age (Ferrell, 1982; Patterson et al., 1992; Bellows and Staigmiller, 1994). Fertility and conception rate have been shown to be lower in heifers bred at pubertal estrus, as compared to the two subsequent estruses (Byerley et al., 1987; Kinder et al., 1994). Thus, puberty will ideally occur at 12 to 14 months of age in order for conception in a timely manner (Short et al., 1994; Brinks, 1994). Breeding replacement heifers to calve early in the season compared to the rest of the herd aids in lengthening both the postpartum recovery period and the second breeding season (Patterson et al., 2002; Funston and Deutscher, 2004). Heifers that
conceive early in the season have been shown to continue this trend in subsequent breeding seasons, leading to greater production through increased longevity (Lesmeister et al., 1973).

Puberty occurs at a predetermined stage unique to each animal; for this reason, individual animal size plays a key role in the timing of initiation of puberty (Taylor and Fitzhugh, 1971). This size, equal to the point of inflection on growth rate, is related to physiological maturation and development of the reproductive tract and axis (Moran et al., 1989), and suggests a need for having a pre-breeding target weight of 60-65 percent of an animal’s expected mature weight (Patterson et al., 2002; Engelken, 2008). Care in selection and development of replacement heifers is required to ensure a timely puberty and a greater chance of reproductive success (Engelken, 2008). Puberty can be positively influenced through managerial practices, as it is a result of the function of both genetic and environmental factors and interactions between the two (Patterson et al., 2002).

Age at puberty is moderately heritable (Laster et al., 1979; Martin et al., 1992; Morris et al., 2000; Snelling et al., 2012) and therefore can be selected for in breeding programs. Age at puberty is somewhat restrictive in selection, however, due to the difficulty of measurement of this trait (Brinks, 1994). Measures of puberty include blood progesterone profiles from the collection of, usually, weekly plasma or serum samples (Gonzalez-Padilla et al., 1975), the use of a teaser bull or estradiol-treated steer (Dodson et al., 1988), reproductive tract palpation and scoring (Anderson et al., 1991), as well as other estrus detection tools and combinations. Individual techniques for measuring puberty each have specific benefits of use which depend on the production setup and available resources. There are numerous and long-lasting benefits and outcomes from the selection for age at puberty, all of which are independent of how puberty is objectively measured (Lesmeister et al., 1973).

Selection based on an alternative trait such as residual feed intake brings rise to the notion of positive or negative associations that may exist between efficiency and fertility traits. Selection for feed efficiency has resulted in lower litter sizes in swine (Kerr and Cameron, 1995), as well as
mice (Nielsen et al., 1997). It results in lower ovulation rates for these litter-bearing species (Nielsen et al., 1997), but may not appear in cattle since cows are not normally multiparous animals. Nevertheless, efficient cows have been shown to calve an average of seven days later in the calving season than their inefficient herd mates (Arthur et al., 2005b; Basarab et al., 2007; Donoghue et al., 2011). The possible reason for delayed calving in efficient animals is thought to be due to a delayed age at puberty (Basarab et al., 2011). A delayed age at puberty in efficient heifers has been found (Basarab et al., 2011), although the relationship tends to be small (Shaffer et al., 2011). The relation between heifer efficiency ranking, conception rates, number of times bred, and other reproductive measurements have been found to be inconsistent between the studies.

Post-weaning feed intake measurements used for the calculation of feed efficiency include animals of varying sexual maturation (Wang et al., 2012). This varying sexual maturity over the measurement period is thought to impact fertility negatively, by favouring animals that reach puberty at a later date (Arthur et al., 2005). Reaching puberty later in the trial period does not require the energy demands of sexual development and activity over the trial to the same degree as for those that are sexually mature by the start of measurement (Basarab et al., 2011; Wang et al., 2012). Thus, further research is required to determine the relation between age at puberty and RFI using animals that are post-pubertal at the start of measurements.

Current literature on the selection for RFI and its effects on other traits, such as reproduction, is limited (Donoghue et al., 2011). The large range of variation in age at puberty as well as RFI provides opportunities for the successful selection of animals that are efficient and reach puberty at a timely age (Shaffer et al., 2011). Further research is required to elucidate associative effects of selection for RFI to ensure that biological and reproductive efficiency can occur simultaneously.
2.4 Thyroid hormones

Hormones are molecules secreted by specific tissues and transported to other areas of the body where they exert substantial effects (Cunningham, 2002). The thyroid hormones are unique among them in that they are the only hormones that contain a halide—iodine (Klimienè, et al., 2008). The thyroid hormones that exert biological activity are found in decreasing biological concentrations throughout the circulatory system—including 3’’,5’’,3,5-L-tetraiodothyronine (T4); 3’’,5,3-L-triiodothyronine (T3); 3’’,5’’,3-L-triiodothyronine (rT3) and 3,5,3-L-diiodothyronine (3,5-T2) (Hulbert, 2000). Triiodothyronine and T4 are secreted directly from the thyroid gland; T4 dominates, however, representing greater than ninety percent of all thyroidal secretions. The vast majority of T3 found in circulation originates from the deiodination of T4 (Bitman et al., 1994).

The effects of thyroid hormones are extensive, but general consensus points to their association with energy expenditure and basal metabolism (Kunde, 1927; Freake and Oppenheimer, 1995; Goglia et al., 1999; de Lange et al., 2001). Metabolic rate was shown to decrease and reach equilibrium at low levels after thyroidectomy in rabbits (Fleishmann et al., 1940). Metabolic rate, measured by oxygen consumption and carbon dioxide production, was re-established in thyroidectomised mice through injections of T3 (Wang et al., 2000). Thyroid disorders and the effect they have on basal metabolic rate and oxygen consumption confirm these findings (Silva, 1995).

Triiodothyronine and T4 levels are independently regulated, meaning that associated patterns and variations within each hormone need to be interpreted independently (Hulbert, 2000). Concentrations of each have been shown to follow circadian rhythms, with T3 levels having greater divergence from its mean value (Bitman et al., 1994). This greater variation within T3 values presents the opportunity to observe significant differences between animals at distinguishable times of the day. Tetraiodothyronine follows roughly the same pattern.
Triiodothyronine and T4 can be found in the makeup of cell membranes of all animals (Nixon et al., 1988). As membrane constituents, these thyroid hormones play a key role in the sensitivity of bodily tissues to their activity, and have considerable impact on the overall function of each cell (Hulbert, 2000). Their multiple modes of action create some difficulty in determining their exact role at the cellular level, however, and their effectiveness has not been fully understood (de Lange et al., 2001).

Triiodothyronine has been shown to have greater biological effectiveness compared to T4, even though its circulating concentration is much lower (Gross, 1993). Increases in effectiveness results from a greater attraction of nuclear receptors for T3 (de Lange et al., 2001). Triiodothyronine’s effects are a function of concentration (Hulbert, 2000), as hormone receptors far outnumber the amount of hormone present in circulation (Cunningham, 2002). Triiodothyronine increases energy expenditure by reducing metabolic efficiency through the inactivation of the mitochondrial oxidative phosphorylation pathway (de Lange et al., 2001). This inactivation, referred to as “uncoupling”, interferes with the electron gradient of the inner mitochondrial membrane resulting in an exothermic condition (Lebon et al., 2001). Triiodothyronine promotes this uncoupled process, favouring heat production instead of the production of the energy carrier adenosine triphosphate (Lebon et al., 2001). Thyroid hormones affect thermogenesis and the amount of energy lost from the animal in the form of heat (Hulbert, 2000). In general, thyroid hormones stimulate oxidative metabolism, coupled or uncoupled, resulting in an increase metabolic rate (Scheele et al., 1992; Wang et al., 2000).

Numerous factors have been shown to have an effect on thyroid hormone levels. Although season has been demonstrated to have an effect on thyroid hormone levels (Vanjonack and Johnson, 1975), no differences have been observed between spring and fall T3 levels (Nixon et al., 1988). Pregnancy has been reported to raise T3 levels significantly for both women (Rahman et al., 2007) and cattle (Paulíková et al., 2011), and the stage of gestation in cattle was also shown to
have considerable effect on thyroid hormone levels during pregnancy (Vanjonack and Johnson, 1975; Paulíková et al., 2011). Additional factors that have been found to have an effect on thyroid hormone levels include breed (O’Kelly and Spiers, 1994), dietary restriction and level of feed intake (Christopherson et al., 1979; Pethes et al., 1985; Cavallo et al., 1990), sex (Johansson et al., 1987), and stage of lactation (Nixon et al., 1988; Oberkotter and Rasmãœssen, 1991). The prevention or control of the factors that affect thyroid hormone concentrations can aid in the reduction of experimental error and undesirable results, which may combine with inadequate sampling frequencies to yield conflicting data (Bitman et al., 1994).

Greater substrate utilization results from thyroid hormones increasing energy expenditure (Hulbert, 2000). The energy for this processing is obtained through the animal’s diet. Differences in RFI reflect differences in feed intake caused by underlying metabolic processes (Koch et al., 1963). Since thyroid hormones are associated with energy expenditure and metabolic rate, and superior feed efficiency was associated with a decrease in metabolic rate measured by oxygen consumption (Rauw et al., 1998; Dunnington and Siegel, 1996), associations between RFI and thyroid hormone levels become plausible. Thyroid hormones therefore offer potential as biological indicators of feed efficiency in the replacement beef heifer if an association can be established.

Triiodothyronine levels in pullets from efficient and inefficient lines have been found to be significantly different at 17 weeks of age (Bordas and Minvielle, 1999; Van Eerden et al., 2006). The literature in existence on the associations of RFI and thyroid hormone levels in cattle is sparse, and obtaining knowledge will require increased numbers of sampling per animal in order to clarify and evaluate the relation between feed efficiency and the many factors influencing it.
FEED EFFICIENCY, SEXUAL MATURITY, AND REPRODUCTIVE PERFORMANCE IN REPLACEMENT BEEF HEIFERS

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Short title

Sexual maturity, reproductive performance and feed efficiency in replacement beef heifers.
Summary

Age at the onset of sexual maturity has great implications on the lifetime reproductive efficiency of replacement beef heifers, while feed efficiency can drastically impact economic efficiency of production. An alternative method of measuring the onset of sexual maturity through fecal matter in addition to the connections between reproductive performance traits, including the onset of sexual maturity, with feed efficiency were examined in this study. The aim of this research was to verify differences in reproductive characteristics between efficient and inefficient animals so that management factors can be utilized to avoid possible undesirable outcomes.

ABSTRACT. Research on associations between residual feed intake (RFI), sexual maturity, and other reproductive traits can be used to determine consequences on important production traits that may occur with increased selection intensity for feed efficiency. Because age at sexual maturity is an important trait in heifers, the study investigated the relationship between RFI and sexual maturity. The use of fecal progesterone metabolites (FP₄M) as an indicator of sexual maturity was also investigated. Age at sexual maturity was established for a population of 47 cross-bred replacement beef heifers, based on weekly plasma progesterone concentrations with fecal samples collected simultaneously during the sampling procedure. The initiation of feed intake measurements occurred after the onset of sexual maturity (n = 42) and within four days of onset (n = 2); while three heifers were not found to have reached sexual maturity by the end of sample collection. Residual feed intake, calculated from daily individual feed intake and bi-weekly body weight records, was adjusted for body composition through ultrasound images captured every 28 days. Sexual maturity was found to occur at an average age and body weight of 384 ± 42 days and 387 ± 45 kg (mean ± standard deviation), respectively. A FP₄M concentration threshold of 250 ng/g was found to properly indicate sexual maturity in 95% of the heifers. Residual feed intake
differed significantly between the low and high RFI groups (P < 0.001), with an earlier age of sexual maturity by 22 days (P = 0.08) and age at conception by 14 days (P = 0.08) observed in the low RFI heifers. Low RFI heifers also gave birth to significantly heavier calves (P = 0.006). No differences were observed between low and high RFI heifers in age and ultrasound measurements at sexual onset, age at first service, conception rate, and gestation length. Fecal progesterone metabolite concentrations can be used successfully to determine the onset of sexual maturity. Associations were found among RFI adjusted for body composition and age at sexual maturity, age at first conception, and offspring birth weight in replacement beef heifers.

**Key words**

Beef cattle, cow-calf, cyclicity, puberty

**INTRODUCTION**

Lowering production costs through gains in feed efficiency in combination with promoting successful reproduction and the consequent sale of viable calves can aid in financial success within the cow-calf sector. Replacement heifers require a greater duration of time as a net expense before providing any monetary returns compared to other female breeding members of the herd; however, these animals are a vital component in the introduction of new genetics into a herd and add prospects for great longevity.

Feed costs comprise the greatest portion of variable costs in a beef production system, with reports at approximately 70 percent of annual costs (Taylor, 1994; Arthur et al., 2004). Maintenance energy expenditures alone represent 65-75 percent of all intake energy (Ferrell and Jenkins, 1985; Montano-Bermudez et al., 1990). Thus, both great potential and extensive pressure
exists for improvements in feed utilization and efficiency in bovines to lower costs of production, particularly in the cow-calf sector. Efficient feed utilization is of even greater importance in times when crop prices are at record highs, and fodder supplies are in short supply. Greater efficiency requires fewer resources to produce similar product outputs, resulting in reduced costs of production, decreased land and resource use, and less environmental impact (Capper, 2011). Greater feed efficiency in cattle would also make them more competitive with other farmed livestock species that utilize similar inputs at superior feed conversion ratios.

Selection pressure for feed efficiency is increasing due to a greater capacity for measuring feed intake in bulls and increasing the use of bulls with superior feed efficiency as herd sires (Herd et al., 2003; Basarab et al., 2011). Residual feed intake (RFI) has been a preferred measure of feed efficiency due to its relative independence from other production traits (Richardson et al., 2001; Carstens and Tedeschi, 2006). Residual feed intake was first introduced for cattle by Koch et al. (1963) and can be defined as the difference between observed dry matter intake and expected intake for the maintenance of body weight along with a given level of production (Archer et al., 1999). Residual feed intake has been under scrutiny recently for having possible ties to reproductive factors; however, there remains a paucity of studies in the literature on RFI and reproductive characteristics in beef cattle.

Age at puberty is an important trait in replacement heifers that signifies the initiation of reproductive life. Greater economic pressures have provided the initiative to have heifers reach puberty at an earlier age in order to become pregnant in a timely manner for the delivery of their first calf at two years of age (Short et al., 1994). The earlier a heifer reaches puberty, the greater the chance it has at becoming pregnant earlier in the breeding season. Heifers that calve early in the calving season have also been shown to carry this trend into future successive calving seasons, resulting in increased longevity within the herd (Lesmeister et al., 1973). Many benefits result from
the early onset of puberty; however, this trait remains difficult to measure and define (Brinks, 1994).

Cattle selected for RFI may have some negative associations, as a trend of inferior sperm motility has been observed in low RFI bulls (Wang et al., 2012). Basarab et al. (2005) first reported the trend between RFI and reproductive characteristics through the findings of low RFI cows calving later in the calving season. More recent studies have found this later calving in low RFI cows to be significant (Basarab et al., 2007; Donoghue at al., 2011), indicative of a delayed conception date. This delayed conception date was not due to pregnancy rate, as this was observed to be similar between low and high RFI heifers (Donoghue et al., 2011, Shaffer et al., 2011). The question arises as to whether age at puberty plays a significant role in the differences observed in date of conception, and hence calving date relative to RFI. Possible associative effects that occur with the selection for RFI need to be recognized in order to strategize accordingly, and minimize any undesirable outcomes.

Trends between feed efficiency, measured by RFI, and age at puberty have been reported with feed efficient heifers displaying an increased age at puberty (Donoghue et al., 2011, Shaffer et al., 2011), although differences were not significant. Puberty, regardless of efficiency ranking, has been shown to occur earlier in heifers that had greater quantities of back fat (Donoghue et al., 2011). Thus, differences in body fat could be responsible for delayed age at puberty and not specifically RFI. Ultrasound measurements of body composition can be included in the RFI calculation to make them independent from RFI, and thus, remove confounding effects that these measurements and RFI may have on age at puberty.

Common practices for defining puberty include, but are not limited to, blood progesterone concentrations (Gonzalez-Padilla et al., 1975), ultrasonography of ovarian structure (Rosenkrans and Hardin, 2003), and the detection of estrous behavior (Hansel and Convey, 1983). The possibility of utilizing fecal progesterone metabolite measurements as a non-invasive option for
determining pubertal onset also exists. Although studies have determined the presence of progesterone metabolites in the feces of cattle (Estergreen et al., 1977; Schwarzenberger et al., 1996b), none have determined whether or not fecal progesterone metabolites could be successfully used as an indicator of reproductive maturity.

This study was conducted using replacement beef heifers with the objectives to 1) establish the usefulness of measuring fecal progesterone derivatives in the determination of the onset of sexual maturity; and to 2) determine the relationship between reproductive measures and feed efficiency measured through RFI.

MATERIALS AND METHODS

Animals

This study used 48 spring-born, crossbred replacement heifers from the Elora Beef Research Centre, University of Guelph, Ontario, Canada. One heifer was removed from the study due to health problems. The average breed composition of the 47 heifers used in the study was predominantly Angus (61.5 %) and Simmental (25.7 %). Other minor breeds, each representing an inclusion rate of 3.2 percent or less in the average heifer breed composition were Piedmontese, Gelbvieh, Charolais, Hereford, and Maine-Anjou. All heifers were managed and cared for to meet or exceed the recommendations specified by the Canadian Council of Animal Care (1993), and the experiment was approved by the University of Guelph’s Animal Care Committee.
Sample collection and management for the determination of sexual maturity

After weaning at an average age and weight of 192 ± 16 days and 246 ± 41 kg (mean ± standard deviation), respectively, heifers were fed for *ad libitum* consumption a total mixed ration composed of corn silage, haylage, salt and minerals (Table 3.1). Heifers, in groups of four, were housed in semi-sheltered pens during puberty assessment. Each pen measured 9.14 m in length, 3.05 m in width and had a sheltered area of 9.30 m². This covered area was bedded with straw, which was added to the pens as often as required to keep the animals comfortable and dry, usually occurring at frequencies of once a week or more.

Sample collection occurred on a weekly basis between 09:00 and 12:30 h. Sample collection for the determination of sexual maturity was initiated 83 days after weaning, corresponding to an average age and weight of 275 ± 16 days and 301 ± 50 kg, respectively. Collection continued for the duration of 182 days, equivalent to 26 weekly samplings. Each sampling involved the recording of body weights, in combination with the simultaneous harvest of both blood and fecal samples. Animals were moved from their pens into a building containing a corral and restrained in a hydraulic squeeze chute equipped with a head restraint bar (Silencer® Hydraulic Squeeze Chute; Moly Manufacturing Inc., Lorraine, KS, USA).

Blood samples were collected from the right jugular vein using a vacuum-tube containing sodium heparin mounted on a holder equipped with a needle (BD Vacutainer® holder, tube, and 20 GA x 25.4mm BD Vacutainer® Needle; BD Inc., Franklin Lakes, NJ, USA). The blood sample was inverted three times to ensure adequate mixing of tube contents, and immediately placed on ice in a cooler until sampling was complete. Blood samples were centrifuged (Sorvall® Legend® RT; Thermo Fisher Scientific Inc., Waltham, MA, USA) at 3750 rpm for 20 minutes at 4°C within four hours from the initiation of sampling. Plasma was withdrawn and placed in 1.5 mL micro-centrifuge tubes (Thermo Fisher Scientific Inc., Waltham, MA, USA) and stored in a -30°C freezer for 24 hours, before being moved into a -80°C freezer until further analysis was performed.
Fecal collection entailed the placing of a plastic bag (10 LB Polybag®; Alpha Polybag Corporation, Brampton, Ontario, Canada) over one hand and arm of the person obtaining the sample, and using stimulation of the heifer’s inter-anal sphincter to trigger defecation. All fecal samples were placed into a -20°C freezer within four hours from the initiation of sampling and held at this temperature until further processing.

**Measuring blood plasma progesterone and fecal progesterone metabolites**

Plasma progesterone was measured with a radioimmunoassay kit (Coat-A-Count, Diagnostics Products Co-operations, Los Angeles, CA, USA). All contents in the kit had identical lot and batch codes. Standards, from the kit contents, used in producing the standard curve included the progesterone (P₄) concentrations of 0.08 ng/mL, 0.49 ng/mL, 0.94 ng/mL, 1.88 ng/mL, 9.80 ng/mL, and 19.60 ng/mL. Steer plasma stripped of progesterone, and pregnant cow plasma containing high concentrations of progesterone observed in the normal physiological range, were used as controls throughout the analysis.

Plasma samples were removed from the -80°C freezer and placed in a refrigerator to thaw for 12 hours. The plasma and the kit contents were brought to room temperature over two hours before the initiation of incubations. Plasma samples and radioactive tracer were incubated for 24 hours at room temperature prior to aspiration. After incubation and aspiration, one mL of a phosphate buffered saline solution containing gelatin was added to each tube to remove any unbound tracer and plasma from the inner tube surface and the tube contents were aspirated once again. The tubes were read on a Wallac 1274 RIA Gamma Counter (Perkin Elmer, Inc., Boston, MA, USA) within four hours from the initial aspiration of the plasma and radioactive tracer. Intra- and inter-assay coefficients of variation were 7.5 and 9.3%, respectively. Heifers were considered to have reached sexual maturity on the first sample of two consecutive sample concentrations of
progesterone each greater than 1.00 ng/mL, or one concentration was greater than 2.00 ng/mL followed by continued cyclic profiles (Wehrman et al., 1996).

Progesterone steroid metabolites were extracted from fecal samples following procedures outlined by Möstl and Palme (2005). Fecal samples were allowed to thaw slowly for 48 hours at 4°C. The thawed fecal samples were processed in the laboratory within four hours from their removal from the cooler. A 0.5251 ± 0.0136 g fecal sample weighed into a 15 mL centrifuge tube (Thermo Fisher Scientific Inc., Waltham, MA, USA) with the use of an analytical balance (AE 50; Mettler-Toledo International Inc, Columbus, OH, USA). Five mL of an 80 percent methanol solution (Thermo Fisher Scientific Inc., Waltham, MA, USA) was added to each fecal sample within the 15 mL centrifuge tube and homogenized for one minute using a vortex (Vortex-Genie® 2; Scientific Industries, Inc., Bohemia, NY, USA). Tubes were centrifuged (Sorvall® Legend® RT; Thermo Fisher Scientific Inc., Waltham, MA, USA) at 2500 g for 15 minutes at 22°C. After centrifugation, one mL of supernatant was removed and placed into a five mL plastic tube (Fisherbrand®; Thermo Fisher Scientific Inc., Waltham, MA, USA) to dry. A 70°C heat block (Isotemp Dry Bath Incubator®; Thermo Fisher Scientific Inc., Waltham, MA, USA) was used to evaporate the methanol. Once drying was complete, the tubes containing the fecal steroid extracts were sealed with a cap until further progesterone metabolite analysis of 20-oxo-pregnane-C3 conjugates using an enzyme immunoassay (EIA) was performed. This EIA has been validated for use with bovine fecal samples (Schwarzenberger et al., 1996). The intra- and inter-assay coefficients of variation were 10.3 and 12.4 percent, respectively.

Management in juxtaposition to production measures

Heifers, in groups of six, were moved into new pens to enable the measurement of individual feed intake. Each pen measured 10.8 m in length, 5.4 m in width and had a sheltered area of 29.2 m² over a bedded-pack. The bedded-pack and addition of bedding was consistent with
previous pen management practices. Six Calan gates® (American Calan Inc., Northwood, NH, USA) mounted on tombstone headboards in each pen were used to control access to individual feed bunks. Each heifer was equipped with a unique electronic neck tag that would only allow access into one of the six feed bunks within the pen. Heifers were trained and accustomed to the Calan gates for a two week period prior to the start of individual feed intake assessment.

Individual animal feed intake measurement was initiated at an average age and weight of 424 ± 16 days and 420 ± 53 kg, respectively. Feed intake test duration of 114 days, and the range in animal ages and weights were well within recommended guidelines (BIF, 2010). The conclusion of intake measurements corresponded to an average age and weight of 542 ± 16 days and 514 ± 59 kg, respectively. The total mixed ration (Table 3.1) was offered to each animal in the morning on a daily basis and the amount offered was recorded. Animals were fed for ad libitum intake at a rate of 105 to 110 percent of intake and with offered amounts adjusted according to intake. Feed refusals were weighed and removed from the bunks once or twice a week, in order to avoid spoilage, keep the bunks fresh, and encourage ad libitum consumption. Daily feed samples were compiled into weekly samples used for diet dry matter determination. Feed sample dry matter, determined by drying samples in a 65°C oven for 96 hours were used to determine dry matter intake for each animal.

Body weights were recorded throughout the feed trial on a bi-weekly basis. Ultrasound images were also taken every 28 days by a trained technician. Ultrasound images were used to measure rib fat (mm), rib eye area (cm²), rump fat (mm), and intramuscular fat score. An Aloka SSD-500, with a 3.5 MHz probe (Corometrics Medical Systems, Wallingford, CT, USA) was used to capture the images into the Auskey program (Animal Ultrasound Services, Ithaca, NY, USA). The procedure was similar to that used in the study by Bergen et al. (2005).

All heifers were bred by artificial insemination. A teaser bull was introduced into each pen of heifers each morning. Heifers that were observed in standing heat were bred by a certified
technician (EastGen; Guelph, Ontario, Canada) later that same day. Animals were checked for pregnancy using blood samples collected 30 days after the cessation of the breeding season (BioPRYN®; BioTracking, LLC, Moscow, ID, USA) as well as by rectal palpation by a veterinarian 60 days after the end of the breeding season. In situations where discrepancies were found between the two tests, rectal palpation was considered the authoritative measure. Replacement heifer weight at calving, calf weight, and calf sex were measured and recorded within 24 hours after parturition.

**Residual feed intake calculation**

Twice a week feed refusal measurements were averaged over each week, subtracted from weekly offered amounts, and divided by seven to determine individual daily feed intake. Compromised feed intake data due to malfunctioning head gates represented 4.8 percent of the feed data, and were excluded from the analysis. Feed intake data were summarized for each animal over the intake measurement period to determine the average daily dry matter intake (DMI).

Residual feed intake was calculated using the general linear model (GLM) procedure of SAS (Statistical Analysis Software, 2008; SAS Institute Inc., Cary, NC, USA). Data from two periods, corresponding to a pre-feed trial period and a feed trial period, were used in the models. The pre-feed trial (PT) period included 22 weight observations per animal, and six ultrasound observations per animal. Data from the trial (T) period included 10 weight observations per animal, and five ultrasound observations per animal.

Records of animal body weights and ultrasound measurements in the pre-feed trial period were used to increase the accuracy of the RFI model. In the pretrial period, ADG was determined by a regression of body weight gain on 152 days, equivalent to the number of days of the pretest. Ultrasound observations were computed as the average over the pretrial period, as well as the amount gained over this period. Both were determined using the regression of the six observations.
on the length of the pretrial. Average ultrasound observations were determined from regression of measurements on half the length of the pretrial period. The amount gained of the ultrasound measurement was calculated as the total gain, calculated from the regression on pretrial length, minus the animal’s intercept which is equivalent to the pretrial starting value.

The same approach was used to calculate each of the above components for the trial period when individual feed intakes were measured. Mid-trial body weight (BW) was calculated from the animal intercept of the trial period plus half the trial length, 57 days, multiplied by the ADG. Calculations for the trial period included the 10 weight observations and five ultrasound observations.

Residual feed intake was initially calculated from the model of Koch et al. (1963):

$$\text{ADMI} = \beta_0 + \beta_1 (\text{T}_{\text{ADG}}) + \beta_2 (\text{T}_{\text{ABW}}) + \text{RFI}_{\text{koch}}$$

where ADMI is the average dry matter intake, $\beta_0$ is the regression intercept, and $\beta_1$ and $\beta_2$ are coefficients of the linear regression of ADMI on trial average daily gain ($\text{T}_{\text{ADG}}$), and trial average metabolic body weight ($\text{T}_{\text{ABW}}$). The residual portion of the model is representative of the RFI portion.

Additional RFI models tested included various combinations of the regression of dry matter intake on average daily gain, mid-trial metabolic weight, ultrasound traits measured during the trial period, as well as average daily gain and ultrasound traits measured during the pretrial period. The model chosen to best represent the RFI regression was the one in which the combinations of criterion included in the model resulted in the greatest $R^2$ and lowest Bayesian information criteria (BIC). The most appropriate model for explaining variation in feed intake, similar to that described by Montanholi et al., (2009), had an $R^2$ of 0.34 and the lowest BIC and was the following:
ADMI = \beta_0 + \beta_1 (T_{ADG}) + \beta_2 (T_{ABW}) + \beta_3 (T_{ABFT}) + \beta_4 (T_{AIFT}) + \beta_5 (T_{AREA}) + \beta_6 (T_{ARFT}) + \beta_7 (PT_{ADG}) + \beta_8 (PT_{ABFT_G}) + \beta_9 (PT_{AIFT_G}) + \beta_{10} (PT_{AREA_G}) + \beta_{11} (PT_{ARFT_G}) + RFI_{bestfit}.

where \beta_3, \beta_4, \beta_5, \beta_6, \beta_7, \beta_8, \beta_9, \beta_{10}, \beta_{11} are coefficients of the linear regression of ADMI on trial average back fat, trial average intramuscular fat, trial average rib-eye area, trial average rump fat, pretrial average daily gain, pretrial average back fat gain, pretrial average intramuscular fat, pretrial average rib-eye area gain, and pretrial average rump fat gain, respectively. The residual portion, RFI_{bestfit}, of the model is representative of the RFI portion based on Koch’s original equation plus these added traits from both the trial and pretrial periods.

Statistical Analysis

Data were analyzed using mixed model binary logistic procedures, and regression procedures of SAS (2008; SAS Institute Inc., Cary, NC, USA). Residual feed intake and pubertal status were included as two binary traits representative of positive RFI animals and negative RFI animals and whether pubertal or not. Logistic regression methodology was utilized to model categorical outcomes of RFI group. RFI groups were defined as group 1 having RFI < 0 and group 0 with RFI > 0. The logistic regression model fitted was

\[
\ln \left( \frac{p}{1 - p} \right) = b_0 + \sum_{i=1}^{n} b_i x_i + e
\]

where \( p \) represents the probability of the event 1, \( x_{i,n} \) (n = 9) which included end-of-test BW, age, ultrasound measurements including intramuscular fat, back fat, rib-eye area, rump fat, average plasma progesterone, average fecal progesterone metabolites and age at puberty, and \( e \) is the residual error. A step-wise selection criterion of P < 0.2 was utilized for inclusion of independent variables in the model.

The above model was also fitted for logistic regressions on the sexual maturity event \( x_{i,n} \) (n = 4) which included the BW, age, plasma progesterone, and fecal progesterone metabolites from
the time of sampling. Again a step-wise selection criterion of $P < 0.2$ was utilized for inclusion of independent variables in the model.

In addition, the general linear model of SAS was employed to compare means between high and low RFI groups. The correlation procedure of SAS was also used to verify the association between the different traits studied. Data was considered statistically significant at $P \leq 0.05$ and was considered a trend toward significance at $P$ values $> 0.05$ and $\leq 0.10$.

**RESULTS**

Descriptive statistics of the mean feed intake and efficiency measurements for all animals over the 114-day feeding trial are shown in Table 3.2. The average DMI and ADG for all animals were 10.33 kg/day and 0.79 kg/day, respectively. Residual feed intake ranged from -2.47 kg DM/day in the most efficient animal to 2.41 kg DM/day in the least efficient animal. Mean RFI values for low and high RFI groups were -0.98 and 0.89 kg/day DM, respectively ($P < 0.001$; Table 3.3). The difference of 1.87 kg/day of DM between the average low and high RFI animals is equivalent to 5.79 kg/day on an as fed basis with a 32.28 % DM diet. The average high RFI animal consumed 11.22 kg DM, while the average low RFI animal consumed 9.35 kg DM without differences in ADG, body fat composition measures and rib-eye area, as these factors were adjusted for in the RFI calculation.

Plasma progesterone concentrations were used as criteria for sexual maturity in the current study. Figure 3.1 depicts the percentage of non-pubertal heifers over the period of sampling for the onset of sexual maturity. Six heifers (12%) reached sexual maturity at or before the average of 301 days of age. Three heifers (6%) had not reached puberty by the end of the sampling period and were removed from the analysis. The mean, standard deviation, minimum and maximum values of
age, body weight and body ultrasound measurements of the group of heifers at the onset of sexual maturity can be found in Table 3.2. The mean age at puberty and corresponding weight were 384 days and 387 kg, respectively.

Table 3.4 shows the mean, standard deviation, minimum and maximum values of both plasma progesterone concentrations, and fecal progesterone metabolites. The continuation of elevated mean values of blood progesterone and fecal progesterone metabolite concentrations after sexual maturity has occurred, indicates that the determination of sexual maturity is possible. Fecal progesterone metabolites were assessed for their ability to predict pubertal onset (Figure 3.2). A 95% confidence interval level for the prediction of sexual maturity using fecal progesterone metabolite concentrations resulted from the detection of fecal progesterone concentrations of 250 ng/g or greater.

Statistical models were tested for their ability to predict age at sexual maturity. The variables included in each model and their associated coefficients of determination (R^2) and Bayesian information criterion (BIC) values are shown in Table 3.5. The model that included intramuscular fat score as a predictor of sexual maturity had a R^2 of 0.57. The addition of body weight, age, back fat, rib eye area, and rump fat to intramuscular fat score increased the R^2 to 0.67.

The comparisons between the means for sexual maturity traits, reproductive characteristics, and traits relating to calving by feed efficiency classification of low RFI and high RFI animals can be found in Table 3.3. Low RFI heifers tended to reached puberty at an earlier age compared to high RFI heifers (P = 0.07). No differences were observed in body weight, or any of the ultrasound traits at the onset of sexual maturity between the low RFI and high RFI animals (P > 0.10). There were no differences between the high and low group means for age at first service and number of times serviced (P > 0.10), but there was a tendency for the low RFI group to have an earlier age at conception (P = 0.08). Calf weight was also shown to differ significantly between the two RFI groups (P = 0.006), with low RFI heifers delivering calves of greater body weights.
DISCUSSION

Feed efficiency, as measured by RFI, is a trait which can be used to aid in the selection of more feed efficient cattle, thus lowering feed costs associated with production (Exton et al., 2000). Dry matter intake is one of the measurements used in the calculation of RFI, and a lower RFI value indicates a more efficient animal (Koch et al., 1963). The average DMI of 10.33 kg/day found in this study is comparable to the average DMI in growing beef heifers of 10.81 kg/day reported by Kelly et al. (2010b).

Using these 47 replacement heifers, with the most efficient animal having a RFI of -2.47 kg DM/day and the most inefficient animal with a RFI of 2.41 kg DM/day, the results agreed with past work suggesting a great variation in RFI exists within cattle (Arthur et al., 2004). This is further demonstrated through mean values for the low RFI group of -0.98 kg DM/day and 0.89 kg DM/day of the high RFI group (P < 0.001). Statistical differences between these averages allow for a comparison that shows a difference in RFI of 1.87 kg DM/day between the mean RFI values of the low and high groups. This value was slightly higher than the values obtained by Arthur et al. (2001) of 1.39 kg DM/day with Angus heifers; however, the observed difference between the two studies may be the result of a difference between a pelleted diet and a total mixed ration diet. The values of feed intake, and RFI observed here are therefore in agreement with other studies in the literature.

Physiological maturity should be taken into account when measuring animals for RFI (Loyd et al., 2011). However, feed intake measurement of young cattle for efficiency assessment typically occurs shortly after weaning (Basarab et al., 2011). The current study has an advantage in its feed intake measurements, as the majority of the heifers were sexually mature at the initiation of intake measurements. Two of the five heifers that were not sexually mature by the initiation of the
feed trial reached sexual maturity within the first four days of feed intake measurements. This study is thus able to demonstrate greater distinctions between RFI and age at puberty.

The association of RFI with the onset of sexual maturity was achieved by using plasma progesterone concentrations as the indicator trait of the latter; a standard method used in many studies (Donaldson et al., 1970; Ferrell, 1982; Wehrman et al., 1996; Cooke and Arthington, 2009). Alternative methods for determining sexual maturity exist (Dodson et al., 1988, Anderson et al., 1991). The applicability of fecal progesterone metabolites to measure sexual maturity in beef heifers remained unknown, however, although data have shown that progesterone in systemic circulation is metabolized and excreted primarily through the feces (Williams, 1962; Estergreen et al., 1977). The corresponding levels of fecal progesterone metabolites to those observed in the plasma do appear, but there is a lag time of 12 to 24 hours from blood to the feces in ruminants (Schwarzenberger et al., 1996b). The ability to monitor ovarian function through fecal progesterone metabolites has been shown possible in numerous species including cattle (Desaulniers et al., 1989; Graham et al., 2001). It is, therefore, completely plausible that sexual maturity in beef heifers may also be determined through this measurement.

Fecal progesterone metabolite concentrations observed in this study were similar to values reported in the literature, with values ranging from close to zero upwards to 500 ng/g (Schwarzenberger et al. 1996b; Rabiee et al., 2001). The levels of plasma progesterone and fecal progesterone metabolites did not always coincide, possibly because of the simultaneity of sample harvest and the lag time between the plasma progesterone and fecal progesterone metabolites levels. Fecal progesterone metabolite concentration values at or above 250 ng/g were found to be indicative of sexual maturity with a 95% confidence interval level. This result indicated, therefore, that fecal progesterone metabolites present an alternative method for the determination of the onset of sexual maturity.
Blood sample collection for sexual maturity determination was initiated at an average age of 275 ± 16 days. The specific definition of sexual maturity used in this study as well as others (Wehrman et al., 1996) helps to avoid improper identification of the onset of sexual maturity. Heifers with the onset of luteal function before 300 days of age are considered to have a greater chance of displaying precocious puberty (Wehrman et al., 1996; Gasser et al., 2006). Figure 3.1 shows the cumulative percentage of sexually immature heifers, with the intercept of the graph at 301 days of age being selected to prevent improper positive identification of sexual maturity. Six heifers (12%) were found to have reached sexual maturity at or before the average of 301 days of age. Blood sample collection ceased before the observation of sexual maturity in three of the heifers in the study (6%), with only one of these three animals conceiving successfully before the end of the breeding season.

Age at puberty is an important trait in beef production that influences reproductive efficiency (Brinks, 1994), and is of particular importance when heifers are required to conceive successfully at 15 months of age in order deliver their first calf at 24 months of age (Bellow and Short, 1994). Mean age at sexual maturity of 384 ± 42 days in this study, was greater than that reported by Jones et al. (1991) who reported an average age 321 days in Angus heifers and average age of 361 days in Simmental heifers. The difference may be due to a lack of rigidity in the specifications of the criterion used for indicating pubertal onset in the Jones et al. (1991) study. Puberty was indicated through one sample with concentrations of serum progesterone greater than 1 ng/mL. Stricter requirements for progesterone concentrations defining pubertal onset would result in the increase in the values of age and weight at puberty, however, bringing those results closer to the values determined in this study. The average age at sexual maturity found in the current study falls below that reported by Hall et al. (1995) who indicated an average age of 399 days in British x British, and British X Continental cross-bred heifers. The high age at puberty is likely due to the strict onset criterion used by Hall et al. (1995), reported as the occurrence of
estrus, followed by the formation of a corpus luteum detected by ultrasonography, and serum progesterone levels exceeding one ng/mL. The values found in the current study therefore fall between those reported by Jones et al. (1991) and Hall et al. (1995).

Body weight is another important trait in addition to age that influences when an animal becomes sexually mature. Body weight at sexual maturity in the current study was 387 ± 45 kg. This value is similar to the value reported by Basarab et al. (2011) of 367 ± 45 kg in cross-bred heifers. A correlation of age at sexual maturity to body weight of 0.34 was observed in this study (P = 0.025). This observation was as expected, as a greater age at puberty would allow for an increased number of days of growth, and therefore an increase in body weight at the onset of sexual maturity.

Physiological maturation of the reproductive axis has been associated with the point of inflection on an animal’s individual growth curve (Joandet and Cartwright, 1969), where the rate of growth and protein deposition begins to slow in combination with a transition toward greater fat deposition—referred to as Brody’s Law (Brody 1945; Pittroff et al., 2008). Fat deposition in live cattle can be estimated using ultrasound measurements (Houghton and Turlington, 1992), so that changes in body composition as measured through ultrasound may be detectable around the time of sexual maturity in replacement beef heifers.

At the onset of sexual maturity in this study, the correlations of ultrasound measurements to body weight were 0.28 (P = 0.07) for marbling score, 0.48 (P = 0.001) for back fat thickness, 0.39 (P = 0.008) for rump fat thickness, and 0.65 (P < 0.001) for rib eye area. Ultrasound measurement correlations of back fat to rump fat, back fat to rib eye area and rib eye area to rump fat were all correlated to one another with correlations of 0.79 (P ≤ 0.001), 0.33 (P = 0.02) and 0.27 (P = 0.08), respectively. These measures demonstrate that an animal with a greater body weight will tend to have a body composition consisting of greater quantities of fat reserves.
Intramuscular fat, however, was not correlated to back fat, rump fat, or rib eye area measurements at sexual maturity ($P \geq 0.67$), indicating that changes in marbling can occur without changes being reflected in the other ultrasound measurements. A significant correlation ($P < 0.001$) of 0.76 was found between intramuscular fat score and age at puberty, thus indicating that an animal with an increased age at sexual maturity will also have an increased marbling score. This correlation reinforces the phenomenon that, at the period around sexual maturity, an animal’s lean growth rate will begin to slow and greater fat stores will be deposited. The prediction models for age at puberty, additionally highlights the importance of intramuscular fat on predicting age at sexual maturity with an $R^2$ of 0.57. The additions of bodyweight, age, and the other body compositions into the prediction model only increased the $R^2$ by 0.10, therefore displaying their inferior predictive capabilities of age at sexual maturity compared to intramuscular fat score. This research agrees with the findings of Hall et al. (1995) that sexual maturity of heifers occurs at dissimilar body compositions, while further indicating that as intramuscular fat increases, the likelihood of the animal having reached sexual maturity also increases.

Body composition and its association with RFI has been previously reported in the literature with small positive correlations between RFI and body fatness (Arthur et al, 2001; Richardson et al., 2001; Basarab et al., 2003; Kelly et al., 2010a). Fortunately, ultrasound measurements can be included in the RFI model to account for this factor making RFI more independent from body composition. As shown in this study, when ultrasound data is included in the RFI prediction model, no difference were observed between low and high RFI animals for any of the body composition measurements at sexual maturity ($P \geq 0.36$).

No difference was found in this study between low and high RFI animals for bodyweight at the onset of sexual maturity ($P = 0.64$). The results do, however, indicate a difference in age at sexual maturity between low and high RFI animals, with low RFI animals displaying a lower average age at puberty ($P = 0.08$). This report of the increased probability of being in the high RFI
category as age at puberty increases contradicts other suggestions (Arthur et al., 2005; Basarab et al., 2007; Donoghue et al., 2011) and findings currently in the literature (Basarab et al., 2011; Shaffer et al., 2011). Other results could differ from the current findings due to the effects of intake measurements taken from a mixture of pre- and post-sexually mature animals, a lack of adjustment for ultrasound measurements, as well as selectively breeding for divergent RFI lines.

Despite the result showing that low RFI animals reached puberty at an earlier age in this study, average age at first service and services per heifer did not differ between the low and high RFI animals ($P \geq 0.41$). Pregnancy rate was not related to RFI ($P = 0.47$) and was not affected by BW or any of the ultrasound body measurements ($P \geq 0.12$), which are similar to other findings (McAllister et al., 2011).

Earlier age of sexual maturity in low RFI heifers does, however, seem to correspond to the earlier age at conception shown in these results ($P = 0.08$). This conclusion is further supported through an increased fertility and conception rates in the ovulations following pubertal estrus (Byerley et al., 1987; Kinder et al., 1994). An earlier age at sexual maturity allows a heifer to experience a greater number of estrous cycles prior to breeding time, with each cycle adding to the development of the uterine environment, thus aiding in the pregnancy process (Kinder et al., 1995). Additionally, animals that became pregnant in this study, regardless of RFI group, had a lower average age at sexual maturity (379 days of age) compared to heifers that did not become pregnant (410 days of age; $P = 0.07$) supporting the observation of increased conception rates in heifers with an earlier age at sexual maturity.

Low RFI heifers in the current study delivered calves with higher birth weights ($P = 0.006$). The difference in average calf weight of 3.94 kg between the low and high RFI heifers was found, without any differences in gestation length ($P = 0.88$) or heifer weight at calving ($P = 0.51$). This observation was also independent of calf gender, as the difference in calf weight of 1.7 kg between the average bull and heifer calves was not significant ($P = 0.27$). A larger calf size in the
low RFI heifers increase the fetus to pelvic disproportions and therefore greatly increases the probability of dystocia (Meijering, 1983; Mee, 2008); with the chance of dystocia increasing 13% for every kilogram increase in calf weight (Johanson and Berger, 2003). Greater probability of dystocia increases the postpartum anestrous recovery period, thus leading to delayed pregnancy in the following breeding season (Short et al., 1990). Therefore, calf size could be responsible for the later calving dates of low RFI heifers in subsequent calving seasons reported in other studies (Basarab et al., 2007; Donoghue et al., 2011).

Significant differences in feed intake between low and high RFI heifers were found in this study. Selection for RFI in the cow-calf sector has the ability to reduce feed requirements therefore reducing costs of production and increasing profitability (Exon et al., 2000). Differences in reproductive traits between low and high RFI heifers have been established in this study, as well as others (Basarab et al., 2011; Donoghue et al., 2011; Shaffer et al., 2011). Importance lies in the discovery of traits that differ between low and high RFI animals so that possible undesirable side effects of selection for RFI can be avoided (Rauw et al., 1998) or properly managed to increase the economic efficiency of beef production.

CONCLUSION

Measurements of fecal progesterone metabolites present a promising non-invasive technique for determining sexual maturity in replacement beef heifers. Fecal progesterone metabolite concentration values of 250 ng/g or greater were found be indicative of sexual maturity with a 95 percent confidence interval. Intramuscular fat score was associated with the onset of sexual maturity in these heifers (correlation = 0.76) indicating the significance of body composition to reproductive maturation. Reproductive traits, specifically those of age at sexual
maturity, and age at conception were found to be favourably associated with RFI adjusted for body composition. These findings support the importance of including ultrasound measurements in the determination of RFI. Further emphasis should be placed on the obtainment of feed intake measurements from animals at similar physiological states to allow for better comparisons between animals. The discovery in this study of low RFI heifers delivering heavier calves at birth may lead to increased dystocia in these animals and thus, an increased post-partum anestrus period and a subsequent delayed pregnancy in the second breeding season.

Acknowledgements

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Table 3.1. Diet composition

<table>
<thead>
<tr>
<th>Ingredient</th>
<th>NE (Mcal/kg DM)</th>
<th>% as fed</th>
<th>% of DM</th>
</tr>
</thead>
<tbody>
<tr>
<td>Diet</td>
<td>1.60&lt;sub&gt;m&lt;/sub&gt;; 0.99&lt;sub&gt;g&lt;/sub&gt;</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Corn Silage</td>
<td>49.75</td>
<td>50.29</td>
<td></td>
</tr>
<tr>
<td>Haylage</td>
<td>49.75</td>
<td>48.17</td>
<td></td>
</tr>
<tr>
<td>Premix A&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.50</td>
<td>1.53</td>
<td></td>
</tr>
</tbody>
</table>

DM = dry matter; NE = net energy.

<sup>a</sup> Contains 40% of calcium phosphate, 60% trace mineralized salt (96.5% NaCl, 7500 mg/kg Zn, 5000 mg/kg Mn, 2500 mg/kg Cu, 1600 mg/kg Fe, 70 mg/kg I, 40 mg/kg Co).

<sup>m</sup> Net energy for maintenance calculated according to Weiss et al., (1992) and NRC (1996).

<sup>g</sup> Net energy for growth calculated according to Weiss et al., (1992) and NRC (1996).
Table 3.2. Descriptive statistics of feed efficiency traits and measurements at onset of sexual maturity

<table>
<thead>
<tr>
<th>Traits (abbreviation; unit)</th>
<th>Mean</th>
<th>S.D. (^a)</th>
<th>Minimum</th>
<th>Maximum</th>
</tr>
</thead>
<tbody>
<tr>
<td>Feed efficiency traits(^b)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Feed intake (FI; kg as fed/d)</td>
<td>32.00</td>
<td>4.18</td>
<td>24.13</td>
<td>41.33</td>
</tr>
<tr>
<td>Dry matter intake (DMI; kg/d)</td>
<td>10.33</td>
<td>1.35</td>
<td>7.79</td>
<td>13.34</td>
</tr>
<tr>
<td>Average daily gain (ADG; kg/d)</td>
<td>0.79</td>
<td>0.15</td>
<td>0.40</td>
<td>1.03</td>
</tr>
<tr>
<td>Residual feed intake (RFI; kg DM/d)</td>
<td>0.00</td>
<td>1.16</td>
<td>-2.47</td>
<td>2.41</td>
</tr>
<tr>
<td>Measurements at onset of sexual maturity(^c,d)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Age (d)</td>
<td>384</td>
<td>42</td>
<td>283</td>
<td>455</td>
</tr>
<tr>
<td>Body weight (BW; kg)</td>
<td>387</td>
<td>45</td>
<td>316</td>
<td>482</td>
</tr>
<tr>
<td>Back fat (BFT; mm)</td>
<td>4.05</td>
<td>1.58</td>
<td>2.00</td>
<td>7.90</td>
</tr>
<tr>
<td>Intramuscular fat (IFT; score)</td>
<td>6.72</td>
<td>0.55</td>
<td>4.98</td>
<td>7.53</td>
</tr>
<tr>
<td>Rib eye area (REA; cm(^2))</td>
<td>59.25</td>
<td>7.04</td>
<td>44.32</td>
<td>72.15</td>
</tr>
<tr>
<td>Rump fat (RFT; mm)</td>
<td>4.18</td>
<td>0.15</td>
<td>1.80</td>
<td>8.10</td>
</tr>
</tbody>
</table>

\(^a\) S.D. = Standard deviation
\(^b\) summary for all replacement heifers over the feed trial
\(^c\) Sexual maturity is defined as two consecutive concentrations of progesterone each greater than 1.00 ng/mL, or one concentration greater than 2.00 ng/mL followed by continued cyclic profiles
\(^d\) Three animals were excluded from the analysis as they had not reached sexual maturity by the end of the sampling period
Table 3.3. Residual feed intake group means for feed efficiency, traits at sexual maturity, reproductive traits, and calving traits

<table>
<thead>
<tr>
<th>Traits (abbreviation; unit)</th>
<th>Low RFI</th>
<th>High RFI</th>
<th>P value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Measures over feed trial</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dry matter intake (DMI; kg/d)</td>
<td>9.35</td>
<td>11.22</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Residual feed intake (RFI; kg DM/d)</td>
<td>-0.98</td>
<td>0.89</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>At sexual maturity&lt;sup&gt;a&lt;/sup&gt;&lt;sup,b&lt;/sup&gt;</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Age (d)</td>
<td>373</td>
<td>395</td>
<td>0.082</td>
</tr>
<tr>
<td>Body weight (BW; kg)</td>
<td>389</td>
<td>383</td>
<td>0.643</td>
</tr>
<tr>
<td>Back fat (BFT; mm)</td>
<td>4.16</td>
<td>3.94</td>
<td>0.652</td>
</tr>
<tr>
<td>Intramuscular fat (IFT; score)</td>
<td>6.64</td>
<td>6.80</td>
<td>0.360</td>
</tr>
<tr>
<td>Rib eye area (REA; cm&lt;sup&gt;2&lt;/sup&gt;)</td>
<td>58.38</td>
<td>60.21</td>
<td>0.395</td>
</tr>
<tr>
<td>Rump fat (RFT; mm)</td>
<td>4.28</td>
<td>4.08</td>
<td>0.673</td>
</tr>
<tr>
<td>Reproductive&lt;sup&gt;b&lt;/sup&gt;</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Age at first service (d)</td>
<td>445</td>
<td>448</td>
<td>0.611</td>
</tr>
<tr>
<td>Services per heifer</td>
<td>1.8</td>
<td>2.0</td>
<td>0.412</td>
</tr>
<tr>
<td>Age at conception (d)</td>
<td>454</td>
<td>468</td>
<td>0.079</td>
</tr>
<tr>
<td>Pregnancy Rate</td>
<td>0.85</td>
<td>0.83</td>
<td>0.466</td>
</tr>
<tr>
<td>Gestation length (d)</td>
<td>277</td>
<td>278</td>
<td>0.857</td>
</tr>
<tr>
<td>Calving&lt;sup&gt;b&lt;/sup&gt;</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Heifer weight at first calving (kg)</td>
<td>623</td>
<td>605</td>
<td>0.514</td>
</tr>
<tr>
<td>Calf birth weight (kg)</td>
<td>35.25</td>
<td>31.31</td>
<td>0.006</td>
</tr>
</tbody>
</table>

<sup>a</sup> Sexual maturity is defined as two consecutive concentrations of progesterone each greater than 1.00 ng/mL, or one concentration greater than 2.00 ng/mL followed by continued cyclic profiles

<sup>b</sup> Three animals were excluded from the analysis as they had not reached sexual maturity by the end of the sampling period
Table 3.4. Summary of plasma progesterone and fecal progesterone metabolites before, at, and after sexual maturity in beef replacement heifers

<table>
<thead>
<tr>
<th>Traits (abbreviation; unit)</th>
<th>Mean</th>
<th>S.D. (^a)</th>
<th>Minimum</th>
<th>Maximum</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Measurements before sexual maturity</strong>(^b)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Plasma Progesterone (PP(_4); ng/mL)</td>
<td>0.219</td>
<td>0.216</td>
<td>0.001</td>
<td>1.498</td>
</tr>
<tr>
<td>Fecal Progesterone Metabolites (FP(_4)M; ng/g)</td>
<td>53</td>
<td>25</td>
<td>8</td>
<td>238</td>
</tr>
<tr>
<td><strong>Measurements at sexual maturity</strong>(^b,c)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Plasma Progesterone (PP(_4); ng/mL)</td>
<td>5.237</td>
<td>3.120</td>
<td>1.15</td>
<td>13.456</td>
</tr>
<tr>
<td>Fecal Progesterone Metabolites (FP(_4)M; ng/g)</td>
<td>144</td>
<td>76</td>
<td>38</td>
<td>395</td>
</tr>
<tr>
<td><strong>Measurements after sexual maturity</strong>(^b,c)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Plasma Progesterone (PP(_4); ng/mL)</td>
<td>5.730</td>
<td>3.971</td>
<td>0.043</td>
<td>17.482</td>
</tr>
<tr>
<td>Fecal Progesterone Metabolites (FP(_4)M; ng/g)</td>
<td>136</td>
<td>114</td>
<td>17</td>
<td>1086</td>
</tr>
</tbody>
</table>

\(^a\) S.D. = Standard deviation

\(^b\) Sexual maturity is defined as two consecutive concentrations of progesterone each greater than 1.00 ng/mL, or one concentration greater than 2.00 ng/mL followed by continued cyclic profiles

\(^c\) Three animals were excluded from the analysis as they had not reached sexual maturity by the end of the sampling period
### Table 3.5. Models for age at sexual maturity and associated coefficients of determination values and Bayesian information criterion

<table>
<thead>
<tr>
<th>Variables included in model</th>
<th>Coefficient of determination (R(^2))</th>
<th>Bayesian information criterion (BIC)</th>
</tr>
</thead>
<tbody>
<tr>
<td>In Singular</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Intramuscular fat (IFT; score)</td>
<td>0.57</td>
<td>297</td>
</tr>
<tr>
<td>Body weight (BW; kg)</td>
<td>0.09</td>
<td>327</td>
</tr>
<tr>
<td>Rib eye area (REA; cm(^2))</td>
<td>0.05</td>
<td>329</td>
</tr>
<tr>
<td>Rump fat (RFT; mm)</td>
<td>0.04</td>
<td>329</td>
</tr>
<tr>
<td>Age (d)</td>
<td>0.03</td>
<td>330</td>
</tr>
<tr>
<td>Back fat (BFT; mm)</td>
<td>0.03</td>
<td>330</td>
</tr>
<tr>
<td>In combinations</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Age + IFT</td>
<td>0.59</td>
<td>297</td>
</tr>
<tr>
<td>BW + IFT</td>
<td>0.58</td>
<td>298</td>
</tr>
<tr>
<td>IFT + REA + RFT + BFT</td>
<td>0.66</td>
<td>294</td>
</tr>
<tr>
<td>BW + IFT + REA + RFT + BFT</td>
<td>0.67</td>
<td>296</td>
</tr>
<tr>
<td>Age + IFT + REA + RFT + BFT</td>
<td>0.66</td>
<td>296</td>
</tr>
<tr>
<td>BW + Age + IFT + REA + RFT + BFT</td>
<td>0.67</td>
<td>298</td>
</tr>
</tbody>
</table>
Figure 3.1. Cumulative percentage of sexually immature replacement heifers.
Figure 3.2. Probability of predicting the onset of sexual maturity using fecal progesterone metabolites with a 95 percent confidence interval. The shaded area around the line represents the standard error in the estimate. The probability of 0.00 is indicative of a non-sexually mature status, while the probability of 1.00 indicates that sexual maturity has been obtained.
Chapter 4*

CIRCADIAN PLASMA TRIIODOTHYRONINE (T3) LEVELS OVER THREE STAGES OF REPLACEMENT BEEF HEIFER DEVELOPMENT AND THEIR ASSOCIATION WITH RESIDUAL FEED INTAKE

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Triiodothyronine and feed efficiency in beef heifers
**ABSTRACT.** Low cost alternatives to the individual measurement of feed intake for the prediction of feed efficiency would be beneficial in screening for feed efficient cattle. Therefore, the potential of triiodothyronine (T3) plasma concentrations to predict feed efficiency was evaluated, along with the role of factors such as age, body weight, days in gestation, and body composition on the observed concentrations in circulation. Animal body measurements were collected from 36 crossbred replacement heifers for a period initiated shortly after weaning up until one week before calving. Body measurements consisted of biweekly bodyweights, and ultrasound body composition measurements of back fat (BFT; mm), rib eye area (REA; cm²), intramuscular fat (IFT; score) and rump fat (RFT; mm) collected every 28 days. Individual feed intake measurements were collected for a period of at least 286 days prior to calving and were used in the calculation of residual feed intake (RFI). Triiodothyronine concentrations were determined from hourly blood samples harvested over a 24 h period from each heifer on three separate sampling occasions corresponding approximately to the yearling, early gestation, and late gestation stages of development. Triiodothyronine concentrations were found to exhibit a diurnal pattern and average concentrations had a correlation of -0.59 with age; -0.60 with days in gestation; -0.53 with body weight; -0.62 with BFT; -0.44 with REA; and -0.56 with RFT (P < 0.001). Individual animal T3 concentrations at the yearling stage sampling period had a correlation of 0.30 (P = 0.002) with RFI. The correlation between RFI and T3 concentrations was not significant at the latter two sampling periods. Triiodothyronine concentrations incorporated into a quadratic model to predict RFI were found to have the greatest correlation of 0.58 (P = 0.001) during the first sampling period corresponding to the yearling stage. A positive correlation of 0.33 with this quadratic prediction model of RFI in the third sampling period was also observed (P = 0.05). Comparisons of T3 concentrations between animals should be made with animals similar in development stage and age when possible. Since T3 concentrations at the yearling sampling stage were correlated with RFI,
the period surrounding this or leading up to the yearling stage may provide the greatest opportunity to determine T3 differences associated with low and high RFI heifers.

**Key words**
beef cattle, bio-indicators, biological indicators of efficiency, cow-calf, thyroid hormones

**Implications**
Adoption of feed efficiency measurement in cattle is limited by costs associated with the measurement of individual animal feed intake and the facilities required to do so. Using biological indicators of feed efficiency aids selection for efficient animals without the expenses associated with measuring individual intake for long periods. Efficient animals utilize fewer resources while producing similar outputs and, thus, have reduced environmental demand and impact. Biological indicators of efficiency are required to aid in the selection of feed efficient animals in order to lower input cost of production, as well as to aid in the management for volatile markets, surging land and input costs, and a more sustainable beef production system.

**INTRODUCTION**

Improvements in feed efficiency within the beef industry would lower costs of production, reduce environmental impact, make beef more competitive against other protein sources and would help to ensure the sustainability of production. Animals with improved feed efficiency would consume less feed, and lower the feed costs which comprise the single greatest variable cost in any beef production system (Taylor, 1994; Arthur et al., 2004). It has been suggested that using residual feed intake (RFI) in a selection program would be a reliable way to improve feed
utilization and reduce costs in the beef production system (Carstens and Tedeschi, 2006). The concept of RFI, first introduced by Koch et al. (1963) for beef cattle, is calculated as the difference between observed dry matter intake and the expected dry matter intake for a given level of production (Archer et al, 1999; Arthur and Herd, 2008). Animals with intake less than that expected for the given production level will have a negative RFI, while those with intake greater than expected for the level of production will have a positive RFI. Thus, a negative RFI is indicative of an efficient animal, and a positive RFI indicates an inefficient animal (Okine et al., 2004). The time period required and costs associated with individual animal feed intake measurements for the assessment of feed efficiency are great deterrents to industry-wide adaption (Tatham et al., 2000). Thus, alternative methods that could be implemented for the assessment of feed efficiency are warranted.

Residual feed intake calculated from intake, weight records, and ultrasound measurements such as those used in this study, means a greater benefit over other feed efficiency measures due to its relative independence from production traits (Richardson et al., 2001). This factor enables the RFI to be more reflective of background energy requirements than other methods (Archer et al., 1999), and allows for closer comparison between animals regardless of production level (Carstens and Tedeschi, 2006). The adoption of RFI is particularly beneficial when investigating biological processes and mechanisms that contribute to differences observed in feed intake (Arthur and Herd, 2008). Metabolic differences between efficient and inefficient animals based on RFI have been reported in the literature (Herd et al., 2004; Richardson and Herd, 2004; Kelly et al., 2010). However, there are in reality, few individual traits that can be used effectively to identify efficient animals in any given population.

Investigations into the relation between low and high RFI animals take us much closer to understanding corresponding differences between these groups (Herd et al., 2004). Blood and its constituents provide an opportune means of determining differences between animals, as blood
represents the distribution system of key hormones and metabolites throughout the body (Cunningham, 2002) and is easily accessed. Previous work has examined relationships between RFI and key hormones and metabolites such as leptin (Bottje and Carstens, 2009), fecal cortisol metabolites (Montanholi et al., 2009), non-esterified fatty acids, and beta-hydroxybutyrate (Kelly et al., 2010). These biological indicators, however, have not been able to replace the requirement of feed intake measurement in the assessment of feed efficiency. Thus opportunities exist in the determination of additional hormonal or metabolic measures that may better predict or add to the overall predictive ability of those previously identified. For example, although the thyroid hormones have been shown to have extensive effects on metabolism (Kunde, 1927; de Lange et al., 2001), few studies have determined their association with RFI.

The thyroid hormones are under the control of the hypothalamic–pituitary–thyroid axis (Cunningham, 2002). Triiodothyronine (T3) has greater biological activity compared to tetraiodothyronine (Gross, 1993) and quantities in circulation are dependent upon production and clearance rates. The extent of the effects of T3 is concentration-dependent (Hulbert, 2000) with the main function as an oxidative metabolism stimulant (Scheele et al., 1992; Wang et al., 2000). Cattle with differences in efficiency as measured using RFI have been shown to have different rates of metabolism as measured by serial slaughter (Castro Bulle et al., 2006) and calorimetry (Nkrumah et al., 2006). Given this functionality, T3 levels can be offered as a possible biological indicator of feed efficiency. Results showing significantly differing levels of T3 in pullets divergently selected for RFI at 17 weeks of age (Bordas and Minvielle, 1999; Van Eerden et al., 2006) indicate that T3 has potential as an indicator of feed efficiency. To date, however, relationships between RFI and T3 levels in beef cattle have not been reported in the literature.

This study was initiated to determine the relationship between T3 and RFI, age, body weight, days in gestation, and body composition. The objectives of this study were to examine the
usefulness of T3 as a biological indicator of feed efficiency as measured by RFI and to verify potential relationships between T3 levels and age, body composition, and pregnancy.

**MATERIALS AND METHODS**

**Animals**

Thirty-six cross-bred replacement heifers from the Elora Beef Research Centre, University of Guelph, were used for this study. Average breed composition of the heifers consisted of 63.4% Angus, 24.3% Simmental, 2.9% Gelbvieh, 2.7% Piedmontese, 1.9% Charolais. The remaining breeds, each with a presence between 0.3% and 1.5% in the overall breed composition include: Hereford, Maine-Anjou, Tarentaise, Salers, and South Devon. Heifers were handled and monitored to meet or exceed the recommendations of the Canadian Council of Animal Care guidelines (1993). All procedure protocols were approved by the University of Guelph’s Animal Care Committee.

**Management during feed efficiency assessment**

Animals were housed in pens of six, with each animal having individual feed access through the use of Calan gates ® (American Calan Inc., Northwood, NH, USA). Calan gates, secured to tombstone style head gates, limit access by requiring the detection of a specific electronic key in close proximity to the head gate, for the locking mechanism to be disengaged. Electronic keys attached to a collar around the heifer’s neck are unique to each individual animal and only allow entrance to one feeder within the pen. Each pen had a depth of 10.8 m, and a width of 5.4 m, and a total of 58.3 m². Pens were semi-sheltered, with a sheltered portion of 29.2 m². This
sheltered area contained a bedding pack of the same dimensions. The bedding, consisting of straw, was kept dry through addition of straw at weekly or at a greater frequency if necessary.

A total mixed ration was offered in the morning once daily and feed refusals were removed and measured at least once weekly in order to maintain fresh bunks. Feed refusals were measured two times per week during the warmer months when weather was conducive to that of feed spoilage. Animals were offered feed for *ad libitum* intake at a rate of 105 - 110 percent of actual intake to make certain access to feed was unlimited, with adjustments in offerings calculated from the previous week’s intake levels. Two total mixed ration diets, A and B, were fed over the duration of feed intake measurements (Table 4.1). Diet 1 was fed from weaning at an average age and body weight of 191 ± 17 days and 242 ± 43 kg (mean ± standard deviation), until an average age and body weight of 584 ± 17 days and 575 ± 63 kg, respectively. Diet 2, of lower energy density, was fed from this point through to calving. Individual animal weights were recorded biweekly, with ultrasound body measurements taken every 28 days while animals were properly restrained within a hydraulic squeeze chute (Silencer® Hydraulic Squeeze Chute; Moly Manufacturing Inc., Lorraine, KS, USA). Briefly, the ultrasound measurement were obtained with the use of an Aloka SSD-500 ultrasound unit, 3.5 MHz long probe (Corometrics Medical Systems, Wallingford, CT, USA) and Auskey program (Animal Ultrasound Services, Ithaca, NY, USA) to measure back fat (mm), rib eye area (cm²), intramuscular fat (score) and rump fat (mm).

**Residual feed intake calculation**

The complete trial was initiated at an average days of age of 247 ± 17 and weight of 275 ± 47 kg occurring shortly after weaning, and concluded the week before calving for each animal. Over the duration of this entire period, ultrasound body composition measurements at 28 day intervals and animal body weights at 14 day intervals were collected for data extraction and
inclusion into the RFI model. The ultrasound body measurements obtained by a trained technician were similar to those used in the studies by Bergen et al. (2005) and Montanholi et al. (2009).

The complete trial was further subdivided into pre-feed trial period (PT), and a feed trial period (T). The pretrial period covered the first 178 days of the trial and did not include the measurement of individual animal feed intake. Measurements obtained over the pretrial period were used to determine pretrial average daily gain (PT_ADG), as well as the change (Δ), or slope of the ultrasound measurements over this period. Pre-trial average daily gain was determined from a regression of body weight on the pretrial length. Change in the pretrial ultrasound measurements of back fat (PTΔ_BFT), rib eye area (PTΔ_REA), intramuscular fat (PTΔ_IFT), and rump fat (PTΔ_RFT) were determined from a regression of seven observations over the period of the pretrial length.

The feed trial period consisted of the 286 to 342 days of the study remaining after the pretrial period, and also included the collection of biweekly body weights, and ultrasound measurements collected every 28 days. Dry matter content of the diet, used for calculating dry matter intake, was determined by drying weekly pooled diet samples in a ventilated oven at 65°C for 96 h. Feed intake measurement compromised by malfunctioning gates or lost neck keys accounted for 3.7% of the entire dataset and was excluded from the analysis.

Measurements calculated from the trial period include averages, mid-point values, as well as the change in values over this period. Trial average daily gain (T_ADG) was calculated from the regression of body weight the trial period length. Mid-trial body weight (BW) was calculated from the animal’s intercept for the trial period regression analyses plus half the trial period length multiplied by the trial period ADG, therefore determining trial period average body weight (T_ABW). Trial period mid-point back fat (T_ABFT), rib eye area (T_AREA), intramuscular fat (T_AIFT), and rump fat (T_ARFT) were calculated from the regression of 13 measurements multiplied by half the trial length. The change, or slope, of the trial period ultrasound
measurements were also determined obtained over this period, similar to the calculations for the pre-feed trial period measurements.

Residual feed intake was calculated using the general linear model (GLM) procedure of SAS (Statistical Analysis Software, 2008). Models were tested using the Koch et al. (1963) multiple regression model where dry matter intake is regressed on average daily gain, mid-trial period body weight, and also included average ultrasound body measurements, change in ultrasound body measurements, age and various combinations thereof to determine RFI. The model with the greatest $R^2$ and lowest Bayesian information criterion—BIC (Burnham and Anderson, 2004) was chosen to represent the most accurate predictor of RFI. This regression model had an $R^2$ of 0.51 and was determined as the following:

$$ADMI = \beta_0 + \beta_1 (\text{age}) + \beta_2 (T\_\text{ADG}) + \beta_3 (T\_\text{ABW}) + \beta_4 (T\_\text{ABFT}) + \beta_5 (T\_\text{AIFT}) + \beta_6 (T\_\text{AREA}) + \beta_7 (T\_\text{ARFT}) + \beta_8 (T\Delta BFT) + \beta_9 (T\Delta REA) + \beta_{10} (T\Delta IFT) + \beta_{11} (T\Delta RFT) + \beta_{12} (PT\_\text{ADG}) + \beta_{13} (PT\Delta BFT) + \beta_{14} (PT\Delta REA) + \beta_{15} (PT\Delta IFT) + \beta_{16} (PT\Delta RFT) + RFI_{\text{bestfit}}$$

Where $ADMI$ is the average dry matter intake, $\beta_0$ is the regression intercept, $\beta_1$, $\beta_2$, $\beta_3$, $\beta_4$, $\beta_5$, $\beta_6$, $\beta_7$, $\beta_8$, $\beta_9$, $\beta_{10}$, $\beta_{11}$, $\beta_{12}$, $\beta_{13}$, $\beta_{14}$, $\beta_{15}$, $\beta_{16}$, are the coefficients of the linear regression of $ADMI$ on age, the trial period: average daily gain, average body weight, average back fat, average intramuscular fat, average rib-eye area, average rump fat, change in back fat, change in intramuscular fat, change in rib eye area, change in rump fat, and the pretrial period: average daily gain, change in back fat, change in intramuscular fat, change in rib-eye area, change in rump fat, respectively. The residual portion of the model, $RFI_{\text{bestfit}}$, is representative of the RFI portion from Koch’s original equation with the addition of traits from the pretrial and trial periods.
Animal training and acclimation to sampling procedures

Four stalls, each measuring 2.5 m long by 1.1 m wide and bedded with wood shavings, were used to house the heifers during blood sample collection. Heifers were fitted with halters and tethered to a feed chamber located at the front of each stall to facilitate sample collection. Feed and water were provided for ad libitum intake within the feed chamber throughout the duration of the sampling. The lighting in the room during sampling was controlled in order to mimic the lighting normally experienced by the animal in its regular pen setting. Stalls were kept clean and dry with the addition of shavings as required.

Groups of four heifers were each moved into individual stalls on three different occasions for sample collection. Table 4.2 shows the average age, weight, and days of gestation for each sampling period. Halters were placed and remained on the heifers for a two-week period prior to sampling. Heifers were adapted to the sampling environment, stall, and feed chamber for the two days prior to each day of blood sampling. Over the course of the first day of adaptation, heifers were introduced to the stall and surrounding setting, customized to a loosely tied halter within the feed chamber, and familiarized with the experimental conditions. The second day of adaptation included tying the heifer, with halter closer to the chamber to facilitate the proximity required for harvesting of blood samples. This proximity to the feed chamber provided enough room to allow unrestricted movement to eat, drink, stand, and lie down. Heifers were maintained in this setting, identical to that of the sampling setting, for a minimum of five hours or until they were at ease. Each sampling collection consisted of 24 consecutive hours of blood sampling, with samples harvested on an hourly basis.

Blood collection and triiodothyronine (T3) determination

Total T3 was determined from plasma samples obtained from each of the 24-consecutive-hour blood sample collections. An indwelling jugular catheter (14 GA 2.1 x 133 mm, Angiocath®;
BD Inc., Franklin Lakes, NJ, USA) was used to collect the hourly blood samples over the sampling period. Prior to jugular catheter insertion, heifers were mildly sedated with xylazine (0.02 mg/kg; Rompun®; Bayer Inc., Bergkamen, Germany), and a local ring block with lidocaine 2% (3 mL/block, Lidocaine Hydrochloride Injection USP; Alveda Pharmaceuticals Inc., Toronto, ON, Canada) was performed around the insertion site. Catheters were connected to tubing, which ran up the heifer’s neck to stop at the withers, an arrangement that facilitated blood sampling while enabling the heifer to have freedom of movement within the feed chamber. The catheter, secured in place with two sutures, and the connected tubing were protected by a covering of bandage wrap.

Hourly blood sample collection was initiated at 08:15 on the day of sampling, and was concluded with the last sample drawn at 07:15 the following day. Five mL of a heparinized saline solution (30 USP units/mL, Heparin Sodium Injection, USP; Pharmaceutical Partners of Canada Inc., Richmond Hill, ON, Canada; 0.9% NaCl) was administered into the tubing and catheter after each blood sample harvest to prevent any blood from clotting within. Before drawing blood for the hourly sample, the five mL of the saline solution in the tubing and catheter, in combination with five mL of fresh blood mixture, were removed so that the harvested sample consisted solely of blood constituents. Blood samples of 10 mL were withdrawn from the catheter and tubing with disposable 20 mL syringes (BD Inc., Franklin Lakes, NJ, USA). The blood sample was immediately placed into 10 mL blood collection tube containing sodium heparin (Vacutainer®; BD Inc., Franklin Lakes, NJ, USA) and placed on ice.

Blood samples were allowed to cool on ice until centrifuging for 30 minutes with a 45 degree fixed angle bench-top centrifuge (Fisher Scientific 225 Centrifuge Benchtop Centrifuge, Thermo Fisher Scientific Inc., Waltham, MA, USA). Aliquots of plasma were then placed into 1.5 mL micro-centrifuge tubes (Thermo Fisher Scientific Inc., Waltham, MA, USA) and stored at -20°C for 24 hours, before being moved into a -80°C freezer. Plasma samples were maintained at -80°C until further analysis for T3 was performed.
Total triiodothyronine (T3) plasma concentrations were measured using a commercially available radioimmunoassay kit (Coat-A-Count, Diagnostics Products Co-operations, Los Angeles, CA, USA) that has been previously validated for use with cattle samples (Williams et al., 1987). The same kit lot and batch were used for all determinations. Standards were prepared by using bovine plasma stripped with charcoal and a solution of 500 ng/mL of T3 in methanol to ensure that both the standards and plasma were of similar bovine origin. Two serial dilutions starting from 5 ng/mL and from 4 ng/mL of T3 in stripped bovine plasma were performed to produce various points along the standard curve. These points corresponded to T3 concentrations of 5.0 ng/mL, 4.0 ng/mL, 2.5 ng/mL, 2.0 ng/mL, 1.25 ng/mL, 1.0 ng/mL, 0.625 ng/mL, 0.5 ng/mL, 0.313 ng/mL, and 0.25 ng/mL.

Before T3 analysis, plasma samples were removed from the -80°C freezer and allowed to thaw slowly in a refrigerator for 16 hours. Both the plasma samples and the T3 kit contents were removed from their respective refrigerators and brought to room temperature for two hours prior to sample incubation. Incubation of the samples with radioactive tracer lasted 20 hours at room temperature. The ideal duration for the incubation was determined in preliminary tests. Following the incubation within the labeled tubes, the contents were aspirated. All tubes were then rinsed with 1 mL of a phosphate buffered saline solution containing gelatin, and then aspirated again to remove any residual tracer from the tube. A gamma counter (Wallac 1274 RIA Gamma Counter; Perkin Elmer, Inc., Boston, MA, USA) was used to read the tubes on the day of aspiration and rinse. Inter-assay coefficient of variability was 3.7 %.
STATISTICAL ANALYSIS

Area under the sampling curves for the hourly T3 samples of the three sampling periods was calculated utilizing the trapezoid algorithm expanded procedure of SAS (2008; SAS Institute Inc., Cary, NC, USA). Logistic regression methodology was utilized to model categorical outcomes of RFI group within sampling periods. RFI groups were defined as group 1 having RFI < 0 and group 0 with RFI > 0. For each sampling period the logistic regression model fitted was

\[
\text{Ln}[p/(1-p)] = b_0 + \sum_{i=1}^{n} b_i x_i + e
\]

where \( p \) represents the probability of the event 1, \( x_{i..n} \) (n = 7) which included ultrasound measurements of intramuscular fat, back fat, rib eye area, rump fat, linear, quadratic and cubic area under T3 curve, and \( e \) is the error.

Similar to the logistic model for each sampling period, a linear model was fitted to individual RFI values

\[
RFI_i = b_0 + \sum_{i=1}^{n} b_i x_i + e_i
\]

where \( x_{i..n} \) (n = 7) which included ultrasound measurements for intramuscular fat, back fat, rib eye area, rump fat, linear, quadratic and cubic area under T3 curve, and \( e_i \) is the error for individual \( i \).

The correlation procedure of SAS was used to verify associations between different traits studied. Statistical significance was reported at \( P \leq 0.05 \) and a trend toward significance was considered at \( P \) values \( > 0.05 \) and \( \leq 0.10 \).

RESULTS

Body measurements collected from a period shortly after weaning until calving, feed data collected for a 286- to 342-day period before calving, and three sets of hourly blood sample
analyses were obtained. Mean values with their standard deviation, along with the minimum and maximum values of traits measured over the feeding period are shown in Table 4.2.

The average DMI was 10.91 kg/day, with a nadir of 9.14 kg/day and a zenith of 13.19 kg/day. Residual feed intake had a standard deviation of 0.65 kg DM, with consumption by the most feed efficient heifer 1.31 kg DM/day less than expected, while the most inefficient heifer exceeded her expected intake by 1.74 kg DM/day. The mean of the total T3 concentrations over the three sampling periods was 0.873 ng/mL as shown in Table 4.2. Triiodothyronine values observed in the study ranged from 0.032 ng/mL to 1.796 ng/mL.

Residual feed intake group means are shown in Table 4.3. There was a RFI difference of 0.99 kg DM/day between the average low and average high animal’s intake. Triiodothyronine values differed by 0.05 to 0.08 ng/mL between low and high RFI heifers and did not show a consistent trend through the sampling periods.

Mean T3 concentrations at each sampling period are shown in Table 4.4. Individual animal T3 concentrations during the first sampling period had a correlation of 0.29 with REA (P = 0.09), and 0.30 (P = 0.002) with RFI. Triiodothyronine concentrations were not correlated with IFT (P > 0.10). No correlation between T3 concentrations and RFI was found in either of the two samplings that followed, but a correlation of 0.44 between animal T3 concentrations and age was observed (P < 0.001) in the second sampling period. A correlation of -0.33 between T3 concentration and BFT was observed in the third sampling period (P < 0.001) and was the only one found to have a significant value in this period.

Table 4.4 shows the correlation of T3 concentrations to predictions from models of RFI derived from regression analysis. A quadratic model resulted in the greatest correlations, followed by the linear model; the cubic did not result in any significant correlations. The first sampling period resulted in significant correlations for both the linear and quadratic prediction models, reinforcing the initial association between RFI and T3 concentrations during this period.
The least square means of T3 concentrations of low and high RFI animals over the circadian period in yearling heifers are shown in Figure 4.1. This graphical representation displays the diurnal pattern that exists in T3 circulating concentrations. Observed differences in hourly least square means of T3 plasma concentrations between low and high RFI animals were found from 09:00 to 15:00 h, and from 20:00 to 02:00 h.

DISCUSSION

Profit is the difference between revenue and expenses. Since feed costs are the singular greatest cost in any beef production system (Taylor, 1994), one successful approach to increase profitability would be the reduction of feed costs. Difficulty lies in the identification of feed-efficient animals without the costly requirements of obtaining individual animal feed intakes over a lengthy period (Tatham et al., 2000). Biological indicators of feed efficiency aid in the selection of efficient animals without limitations of feed intake measurements. When the examination of mechanisms and processes responsible for differences in feed efficiency is the focus of a study, RFI has been recommended as the feed efficiency measure (Arthur and Herd, 2008). Thus, RFI was used in this study to investigate the usefulness of T3 as an indicator of feed efficiency in the beef replacement heifer.

Feed intake measurements were obtained from 36 replacement heifers over several months prior to calving. Dry matter intake (DMI) of the heifers ranged from 9.14 kg/day to 13.19 kg/day, and had an average value of 10.91 kg/day. The average DMI reported were observed to be similar to those of Kelly et al. (2010b) for growing heifers and therefore fell within levels consistent with other literature.
Statistical differences were observed between the mean RFI value of the low RFI group at -0.58 kg DM/day and the mean value of the high RFI group at 0.41 kg DM/day. The difference in feed intake of 0.99 kg DM/day is similar to the value of 0.87 kg DM/day found by Durunna et al. (2012) in cross-bred replacement heifers, but is less than the values of 1.44 kg DM/day in young growing cattle reported by Basarab et al. (2003), and 1.39 kg DM/day in Angus heifers reported by Arthur et al. (2001). The higher values of Basarab et al. (2003) are likely due to a larger population and the use of steers instead of heifers, while the values of Arthur et al. (2001) are likely due to selection of high and low RFI groups from divergent selection lines. Nonetheless, the difference in RFI between low and high RFI groups in this and other studies demonstrates the existence of variation in RFI between animals (Arthur et al., 2004) and suggests that a reduction in feed consumption could be achieved by feeding low RFI animals in place of high RFI animals (Arthur et al., 2001).

Triiodothyronine concentrations observed in the study ranged from 0.032 ng/mL to 1.796 ng/mL, had an average of 0.873 ng/ml and a standard deviation of 0.247 ng/mL. The average is comparable to Williams et al. (1987), who observed 1.0 ng/mL in beef steers, and is in proximity to the value of 1.45 ng/mL found by Aldrich et al. (1995) in beef heifers. The average T3 value of 1.85 ng/mL determined by Bitman et al. (1984) in pregnant dairy heifers is greater than ours. Triiodothyronine concentrations exhibit baseline levels from 04:00 to 10:00 h, increase to higher values from 12:00 to 22:00 h, then regress back to the low levels by 04:00 h (Refsal et al., 1980). The discrepancy of the inflated mean triiodothyronine value found by Bitman et al. (1984) could be due to sample collection between 08:00 and 20:00 h where higher circulating concentrations are sustained (Refsal et al., 1980). Nonetheless, triiodothyronine values reported here agree with other biological concentrations reported in other studies in the literature involving cattle (Kahl et al., 1977; Christopherson et al., 1979; Bitman et al., 1994).
No differences were found in any of the ultrasound traits between the RFI groups during the feed trial or at any of the sampling periods. This result was expected, since RFI was adjusted for body composition using ultrasound measurements (Basarab et al., 2003) and demonstrates that this adjustment helps to maintain independence of RFI from body composition. Slightly numerically higher values for the majority of the body fat measurements in the high RFI heifers, however, agrees with others reports of high RFI animals having a greater chemical fat composition (Richardson et al., 2001; Kelly et al., 2010a). Despite differences in efficiency between the low and high groups, no statistical differences were observed in the T3 means between these groups at any of the sampling periods, similar to findings of comparisons between mean T3 values of high and low milk producing groups (Bitman et al., 1984). Thus, the use of raw T3 concentration means over the circadian cycle does not appear to be an effective method for detecting differences between RFI groups.

Raw concentration means are effective in determining correlations of T3 with other measures such as age, DIG, BW and ultrasound measurements. The correlation of -0.59 between average T3 concentration and age, agrees with the findings of reduced deiodination and the subsequent T3 levels observed with ageing (Margarity et al., 1985). The finding of an increased T3 level after weaning in heifer calves by Iveta et al. (2011), also supports the higher T3 values found at the yearling sampling stage in this study. T3 was found to have a correlation of -0.60 with DIG, which supports the findings of declining free T3 levels during pregnancy (Lof et al., 2005). The proximity of the timing of the third sampling to calving could have contributed to lower T3 levels observed at this time point, as decreased thyroid hormone levels in cows have been observed in the the last month of gestation (Iveta et al., 2011). A decrease in T3 levels at this time could be due to greater energy requirements for fetal growth resulting in a negative energy balance (Klimienë et al., 2008). Therefore, the overall trend observed was a decline in T3 levels as age and DIG increase. Difficulty arises, however, in the separation of the effects of these two factors in this
study as T3 levels have been found to be influenced by age (Bordas and Minvielle, 1999; Delange, 2000) and reproductive status (Iveta at al., 2011). Decreasing T3 concentrations were observed at higher body weights as well, as shown by the correlation value of -0.53. On a body mass basis, animals with a smaller mass have greater metabolic rates than those of a larger mass (Kleiber, 1961), while metabolic rate has been associated with increased levels of T3 (Wang et al., 2000). Accordingly, smaller animals are likely to have greater metabolic rates and higher associated T3 levels. Ultrasound measurements values of BFT, RFT, and REA increased with body weight in this study, supporting the results from Lofgreen et al. (1962) of greater carcass weights from animals with increased body weights and a correlation of 0.84 between percent body fat and body weight. Low thyroid hormone production has been associated with obesity (Cunningham, 2002), supported by findings here of T3 correlations of -0.62 with BFT and -0.56 with RFT. The lack of significance in the correlation between T3 and IMF is likely due to the relative consistency of IMF values between the three sampling periods.

Triodothyronine concentrations for individual yearling heifers at the first sampling had a correlation of 0.29 (P = 0.002) with RFI, despite the fact that there was no difference in T3 means between the RFI groups (P > 0.10). Significant correlations of individual animal concentrations were not found for either of the two successive samplings. Therefore, individual animal T3 concentrations and their correlation to RFI differ according to animal physiology. This finding of an optimal sampling time having greater associations between T3 levels and RFI has also been found in pullets (Bordas and Minvielle, 1999; Van Eerden et al., 2006). Significantly higher T3 concentrations in high RFI pullets were found at 16 weeks of age, however, these animals had depressed values compared to the low RFI group at 19 weeks of age (Van Eerden et al., 2006). Thus, the most appropriate time to sample replacement beef heifers to determine differences in RFI from T3 samples occurred at one year of age in this study.
Individual animal T3 concentrations at the yearling sampling indicated a correlation of 0.29 with REA. Growth at the yearling stage of heifers promotes that of frame and muscle (Fox and Black, 1984). Higher T3 levels at this sample time could relate to the stimulative effect they have on the production of myosin heavy chains and sarcoplasmic reticulum pumps (Hulbert, 2000), resulting in a greater REA and associated correlation. The correlation of 0.44 of individual animal T3 levels to age at the second sampling period could indicate that age begins to contribute a larger influence on T3 levels observed at this time. Back fat thickness could have a larger influence on individual animal T3 concentrations during the third sampling period as a correlation of -0.33 was determined in this period. These results indicate that influence of particular physiological factors on T3 levels could vary dependent on the period of sampling.

The usefulness of T3 as an indicator of feed efficiency was tested using correlations of actual T3 values to the RFI prediction models. A linear model revealed a correlation of 0.44 between T3 values and RFI at the first sampling period, with no correlations in either of the successive samplings. A correlation to the model at the first sampling at the yearling stage was as expected, since this period was the only sampling period where individual animal T3 concentrations had a correlation with RFI. The use of a quadratic prediction model increased the correlation between T3 values and predicted RFI from the model to 0.58. However, correlations of T3 concentrations to those predicted from the cubic model of RFI were not significant. Therefore, T3 concentrations from samples taken at the yearling stage in heifers had the greatest correlation to a quadratic prediction model of RFI. Increases in the correlation of the quadratic prediction model of RFI over that of the linear model in the first sampling period is likely a response due to the changes in T3 values over the circadian cycle.

A diurnal pattern exists for the anterior pituitary secretion of thyroid stimulating hormone, which in turn controls thyroid hormone production (Hulbert, 2000). Circadian patterns in T3 plasma concentrations have been observed in other studies (Refsal et al., 1980; Bitman at al.,
with the patterns in this study, shown in Figure 4.1, following a similar trend. Fluctuations in T3 values over the circadian cycle emphasize the influence of timing of sample collection on T3 concentrations. No statistical differences in hourly samples between high and low RFI animals at the first sampling period were identifiable over the circadian cycle using least square means comparisons. Differences, however, can be observed graphically in Figure 4.1. Observed differences in T3 plasma concentrations between low and high RFI animals for hourly least square means can be observed in two periods from 09:00 to 15:00 h, and from 20:00 to 02:00 h. These two periods represent the most appropriate time points for sample collection in yearling heifers to observe differences in T3 concentrations that have the greatest probability of indicating differences in RFI.

Significant differences in RFI were observed among the heifers used in this study, enabling the comparison of biological factors that may correspond or contribute to differences in feed efficiency (Herd et al., 2004). Triiodothyronine concentrations over the circadian cycle did not differ between RFI groups, and was found to vary with age, gestation, and body composition. A correlation between T3 concentrations and RFI at the yearling stage indicates that samples collected around or before this time point may provide the greatest insight into the association between T3 concentrations and RFI. However, sampling in the initial few weeks of life in cattle for T3 concentrations should be avoided as they have been shown to alter significantly in this period (Iveta et al., 2011).

CONCLUSION

Triiodothyronine concentrations were found to be negatively correlated with age, DIG, BW, BFT, REA, and RFT. Difficulty exists in the differentiation of the effects the individual
factors have on circulating T3 concentrations. Residual feed intake exhibited a positive correlation of 0.29 with T3 concentrations at the yearling stage in replacement heifers. This correlation was not maintained at early and late gestation samplings which indicates that associations between RFI and T3 concentrations are more probable around or before the yearling stage in beef replacement heifers. Furthermore, samples aiming to determine differences in feed efficiency should be obtained within the two periods from 09:00 to 15:00 h, and from 20:00 to 22:00 h where differences in T3 concentrations are the greatest between low- and high-RFI heifers. Additional biological indicators of efficiency, or more in combinations, may be more effective as an indirect screening method for feed efficiency in cattle.

Acknowledgements

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Table 4.1. Diet composition

<table>
<thead>
<tr>
<th>Diet</th>
<th>NE (Mcal/kg DM)</th>
<th>% as fed</th>
<th>% of DM</th>
</tr>
</thead>
<tbody>
<tr>
<td>Diet 1</td>
<td>1.60(_m); 0.99(_g)</td>
<td>49.75</td>
<td>50.29</td>
</tr>
<tr>
<td>Corn Silage</td>
<td></td>
<td>17.00</td>
<td>15.60</td>
</tr>
<tr>
<td>Haylage</td>
<td></td>
<td>74.97</td>
<td>65.90</td>
</tr>
<tr>
<td>Premix A(^a)</td>
<td></td>
<td>0.50</td>
<td>1.53</td>
</tr>
<tr>
<td>Diet 2</td>
<td>1.41(_m); 0.82(_g)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Corn Silage</td>
<td></td>
<td>49.75</td>
<td></td>
</tr>
<tr>
<td>Grass Haylage</td>
<td></td>
<td>74.97</td>
<td></td>
</tr>
<tr>
<td>Wheat Straw</td>
<td></td>
<td>7.30</td>
<td></td>
</tr>
<tr>
<td>Premix B(^b)</td>
<td></td>
<td>0.73</td>
<td></td>
</tr>
</tbody>
</table>

DM = dry matter; NE = net energy.

\(^a\) Contains 40% of calcium phosphate, 60% trace mineralized salt (96.5% NaCl, 7500 mg/kg Zn, 5000 mg/kg Mn, 2500 mg/kg Cu, 1600 mg/kg Fe, 70 mg/kg I, 40 mg/kg Co).

\(^b\) Contains 43% of calcium phosphate, 57% trace mineralized salt (96.5% NaCl, 7500 mg/kg Zn, 5000 mg/kg Mn, 2500 mg/kg Cu, 1600 mg/kg Fe, 70 mg/kg I, 40 mg/kg Co).

\(^m\) Net energy for maintenance calculated according to Weiss et al., (1992) and NRC (1996).

\(^g\) Net energy for growth calculated according to Weiss et al., (1992) and NRC (1996).
Table 4.2. Descriptive statistics

<table>
<thead>
<tr>
<th>Traits (abbreviation; unit)</th>
<th>Mean</th>
<th>S.D.</th>
<th>Minimum</th>
<th>Maximum</th>
</tr>
</thead>
<tbody>
<tr>
<td>Performance traits(^a)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dry matter intake (DMI; kg /day)</td>
<td>10.91</td>
<td>0.93</td>
<td>9.14</td>
<td>13.19</td>
</tr>
<tr>
<td>Residual Feed Intake (RFI; kg DM/day)</td>
<td>0.00</td>
<td>0.65</td>
<td>-1.31</td>
<td>1.74</td>
</tr>
<tr>
<td>Average body weight (kg)</td>
<td>553</td>
<td>58</td>
<td>420</td>
<td>667</td>
</tr>
<tr>
<td>Ultrasound measurements(^b)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Back fat (BFT; mm)</td>
<td>7.27</td>
<td>2.11</td>
<td>3.74</td>
<td>12.76</td>
</tr>
<tr>
<td>Rib eye area (REA; cm(^2))</td>
<td>80.89</td>
<td>7.32</td>
<td>65.80</td>
<td>93.76</td>
</tr>
<tr>
<td>Intramuscular fat (IFT; score)(^b)</td>
<td>6.93</td>
<td>0.25</td>
<td>6.14</td>
<td>7.42</td>
</tr>
<tr>
<td>Rump fat (RFT; mm)</td>
<td>8.41</td>
<td>2.51</td>
<td>4.38</td>
<td>14.95</td>
</tr>
<tr>
<td>Thyroid hormone concentrations(^c)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total Triiodothyronine (T3; ng/mL)</td>
<td>0.873</td>
<td>0.247</td>
<td>0.032</td>
<td>1.796</td>
</tr>
</tbody>
</table>

\(^a\) Over the duration of feed intake measurements

\(^b\) Intramuscular fat score is on a scale from 1 (trace marbling) to 10 (abundant)

\(^c\) Mean for all samples
Table 4.3. Residual feed intake group means over feed intake measurements, and traits at each sampling period

<table>
<thead>
<tr>
<th>Traits (abbreviation; unit)</th>
<th>Low RFI</th>
<th>High RFI</th>
<th>P value</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Measures over feed trial</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dry matter intake (DMI; kg/d)</td>
<td>10.27</td>
<td>11.36</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Residual feed intake (RFI; kg DM/d)</td>
<td>-0.58</td>
<td>0.41</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Body weight (BW; d)</td>
<td>548</td>
<td>558</td>
<td>0.569</td>
</tr>
<tr>
<td>Back fat (BFT; mm)</td>
<td>6.99</td>
<td>7.46</td>
<td>0.247</td>
</tr>
<tr>
<td>Intramuscular fat (IFT; score)</td>
<td>6.94</td>
<td>6.92</td>
<td>0.684</td>
</tr>
<tr>
<td>Rib eye area (REA; cm²)</td>
<td>80.56</td>
<td>81.13</td>
<td>0.689</td>
</tr>
<tr>
<td>Rump fat (RFT; mm)</td>
<td>8.28</td>
<td>8.51</td>
<td>0.646</td>
</tr>
<tr>
<td><strong>Measures at first sampling</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Age (d)</td>
<td>366</td>
<td>368</td>
<td>0.736</td>
</tr>
<tr>
<td>Body weight (BW; d)</td>
<td>364</td>
<td>373</td>
<td>0.616</td>
</tr>
<tr>
<td>Back fat (BFT; mm)</td>
<td>0.37</td>
<td>0.43</td>
<td>0.296</td>
</tr>
<tr>
<td>Intramuscular fat (IFT; score)</td>
<td>6.87</td>
<td>6.81</td>
<td>0.633</td>
</tr>
<tr>
<td>Rib eye area (REA; cm²)</td>
<td>59.23</td>
<td>61.05</td>
<td>0.512</td>
</tr>
<tr>
<td>Rump fat (RFT; mm)</td>
<td>0.41</td>
<td>0.46</td>
<td>0.301</td>
</tr>
<tr>
<td>Total Triiodothyronine (T3; ng/mL)</td>
<td>1.00</td>
<td>1.05</td>
<td>0.501</td>
</tr>
<tr>
<td><strong>Measures at second sampling</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Age (d)</td>
<td>546</td>
<td>539</td>
<td>0.407</td>
</tr>
<tr>
<td>Body weight (BW; d)</td>
<td>487</td>
<td>496</td>
<td>0.674</td>
</tr>
<tr>
<td>Days in gestation (DIG; d)</td>
<td>83</td>
<td>81</td>
<td>0.851</td>
</tr>
<tr>
<td>Back fat (BFT; mm)</td>
<td>4.70</td>
<td>5.00</td>
<td>0.587</td>
</tr>
<tr>
<td>Intramuscular fat (IFT; score)</td>
<td>7.04</td>
<td>6.99</td>
<td>0.603</td>
</tr>
<tr>
<td>Rib eye area (REA; cm²)</td>
<td>76.56</td>
<td>76.59</td>
<td>0.992</td>
</tr>
<tr>
<td>Rump fat (RFT; mm)</td>
<td>5.66</td>
<td>5.82</td>
<td>0.828</td>
</tr>
<tr>
<td>Total Triiodothyronine (T3; ng/mL)</td>
<td>0.93</td>
<td>0.85</td>
<td>0.156</td>
</tr>
<tr>
<td><strong>Measures at third sampling</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Age (d)</td>
<td>707</td>
<td>701</td>
<td>0.475</td>
</tr>
<tr>
<td>Body weight (BW; d)</td>
<td>656</td>
<td>671</td>
<td>0.462</td>
</tr>
<tr>
<td>Days in gestation (DIG; d)</td>
<td>244</td>
<td>243</td>
<td>0.567</td>
</tr>
<tr>
<td>Back fat (BFT; mm)</td>
<td>11.29</td>
<td>11.73</td>
<td>0.707</td>
</tr>
<tr>
<td>Intramuscular fat (IFT; score)</td>
<td>6.76</td>
<td>6.77</td>
<td>0.928</td>
</tr>
<tr>
<td>Rib eye area (REA; cm²)</td>
<td>90.84</td>
<td>91.95</td>
<td>0.625</td>
</tr>
<tr>
<td>Rump fat (RFT; mm)</td>
<td>13.39</td>
<td>13.50</td>
<td>0.939</td>
</tr>
<tr>
<td>Total Triiodothyronine (T3; ng/mL)</td>
<td>0.73</td>
<td>0.68</td>
<td>0.175</td>
</tr>
</tbody>
</table>
Table 4.4. Average animal parameters and standard deviation for each sampling period and correlation of prediction models to actual animal triiodothyronine concentrations

<table>
<thead>
<tr>
<th>Traits (abbreviation; unit)</th>
<th>First sampling</th>
<th>Second sampling</th>
<th>Third sampling</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Animal parameters</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Approximate stage</td>
<td>yearling</td>
<td>early gestation</td>
<td>late gestation</td>
</tr>
<tr>
<td>Age (d)</td>
<td>367 ± 15</td>
<td>542 ± 23</td>
<td>704 ± 25</td>
</tr>
<tr>
<td>Body weight (BW; kg)</td>
<td>354 ± 49</td>
<td>501 ± 57</td>
<td>645 ± 62</td>
</tr>
<tr>
<td>Days in gestation (DIG; d)</td>
<td>82 ± 24</td>
<td>244 ± 4</td>
<td></td>
</tr>
<tr>
<td><strong>Ultrasound measurements</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Back fat (BFT; mm)</td>
<td>0.40 ± 0.16</td>
<td>4.88 ± 1.57</td>
<td>11.55 ± 3.35</td>
</tr>
<tr>
<td>Rib eye area (REA; cm²)</td>
<td>60.29 ± 8.09</td>
<td>76.58 ± 8.58</td>
<td>91.49 ± 6.60</td>
</tr>
<tr>
<td>Intramuscular fat (IFT; score)</td>
<td>6.83 ± 0.35</td>
<td>7.01 ± 0.26</td>
<td>6.77 ± 0.35</td>
</tr>
<tr>
<td>Rump fat (RFT; mm)</td>
<td>0.44 ± 0.16</td>
<td>5.75 ± 2.08</td>
<td>13.45 ± 4.09</td>
</tr>
<tr>
<td><strong>Thyroid hormone concentrations</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total Triiodothyronine (T3; ng/mL)</td>
<td>1.03 ± 0.23</td>
<td>0.88 ± 0.16</td>
<td>0.70 ± 0.12</td>
</tr>
<tr>
<td><strong>Model correlations to T3 concentrations</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Linear prediction model</td>
<td>0.44 (P=0.008)</td>
<td>0.25 (P=0.144)</td>
<td>0.23 (P=0.186)</td>
</tr>
<tr>
<td>Quadratic prediction model</td>
<td>0.58 (P=0.001)</td>
<td>0.27 (P=0.114)</td>
<td>0.33 (P=0.048)</td>
</tr>
<tr>
<td>Cubic prediction model</td>
<td>0.24 (P=0.159)</td>
<td>-0.17 (P=0.330)</td>
<td>-0.13 (P=0.438)</td>
</tr>
</tbody>
</table>

a Based on the regression of the measurement over the trial period
b Intramuscular fat score is on a scale from 1 (trace marbling) to 10 (abundant)
Figure 4.1. Least square means of triiodothyronine (T3) concentrations of low and high RFI animals over the circadian period in yearling heifers. Standard error bars were not included in the plot due to their relatively large values. The quadratic prediction model had a correlation of 0.58 (P=0.001) to the T3 concentrations in this sampling period.
Replacement heifer feed efficiency was the backbone of this research, with investigations into possible differences in respect to sexual maturity, reproductive characteristics, and triiodothyronine (T3) concentrations. Replacement beef heifers are desirable subjects for feed efficiency determination, as their advancements would have long lasting effects on the cow-calf sector and would permeate all sectors of the beef industry. The significance of feed efficiency is amplified by greater volatility of markets, rising feed prices, surging land and input costs, and decreasing farm profit margins. As productivity gains are achieved through feed efficiency, less feed and resources are required to sustain similar production volumes resulting in increased profitability and a more competitive industry.

Feed efficiency in cattle is of particular importance due to their long generation interval and the normality of a uniparous birth. As a consequence, high maintenance feed costs are associated with every calf that is weaned. The determination of feed efficiency in the female breeding herd is best performed before a heifer delivers her first calf, as the likelihood of being culled from the herd for poor feed efficiency greatly diminishes afterwards. Earlier detection of feed efficiency also increases dispersal options of less desirable animals. Biological indicators of feed efficiency represent an affordable alternative method of selecting and screening for feed efficiency without the prerequisites of individual animal feed intakes and weights over a lengthy period and the costs associated with obtaining these measures.

In Chapter 3, feed efficiency adjusted for body composition was determined, and the onset of sexual maturity was assessed through plasma progesterone measurements. Fecal progesterone metabolites, tested for their usefulness as an indicator of sexual maturity, were able to indicate
sexual maturity in beef heifers. Concentrations equal to or greater than 250 ng/g were found to be indicative of sexual maturity at a 95% confidence interval. Age at sexual maturity was associated with residual feed intake (RFI) in this study, with efficient heifers displaying an earlier age for both sexual maturity and age at conception. Efficient heifers also delivered calves of significantly heavier birth weights independent to the sex status of the calf. Further research is required to determine the effectiveness of fecal progesterone metabolites at indicating sexual maturity compared to other existing methods. This may also help to greater define the specifications in concentrations corresponding to sexual maturity in heifers. Additional research is also needed to determine if the associations found between feed efficiency and reproductive traits carry on into further reproductive seasons.

In Chapter 4, feed efficiency adjusted for body composition was determined, and each animal had hourly plasma samples collected over the circadian cycle on three separate occasions corresponding approximately to the yearling stage, early gestation, and late gestation. Plasma samples were analyzed for their T3 concentration, with these values assessed for their association with age, gestation, body composition, and whether distinguishable differences in these concentrations exist between low and high RFI animals. Triiodothyronine concentrations had a declining trend that was associated with age, days in gestation, body weight, back fat thickness, rib eye area, rump fat. Thus, as an animal grows larger, gains more body fat, and develops further into gestation, its T3 levels will decrease accordingly over time. Triiodothyronine concentrations were found correlated to RFI, but only at the yearling stage. Thus, the yearling stage or the period prior may present the most beneficial sampling period for determining associations between RFI and T3 concentrations between low and high RFI heifers. The times from 09:00 to 15:00 h, and from 20:00 to 02:00 h had the greatest divergence in T3 concentrations between low and high RFI heifers and present the most appropriate timing for sample collection. Further research is required to segregate the effects of age, gestation, body weight and body composition observed with the
declining T3 concentrations. Studies on RFI and T3 should focus on sample collections between the weaning to shortly after the yearling stage as this may present the timing with the greatest associations between the two. Additional biological indicators of feed efficiency or combinations of two or more may be more effective as an indirect screening method of feed efficiency in cattle. A focus on how T3 correlates to energy demanding process, such as heat production, may provide improved results over the single focus of RFI.

Overall, these results suggest an alternative and promising avenue of using plasma progesterone for determining the onset of sexual maturity, and show distinguishable benefits that can be obtained from the selection for RFI. Heifers selected for RFI should also be selected for greater pelvic areas to combat the heavier calf birth weights seen in low RFI heifers. The use of low RFI bulls that have low birth weight estimated breeding values may also prevent calving problems associated with heavier calves. These findings show the opportunities that can be achieved from the raising of efficient animals, and aids in the ability to manage for differences that are associated with animals that have distinct differences in feed efficiencies. Information gained from this study highlights differences between efficient and inefficient animals, enabling benefits associated with increased feed efficiencies to be captured while ensuring reproductive soundness in the breeding herd. Further research will elucidate the effects T3 has on energy utilizing processes and the additive effects these have on RFI in the replacement beef heifer.
Chapter 6

REFERENCES


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Johnson, D. E., Ferrell, C. L., and Jenkins, T. G. (2003). The history of energetic efficiency research: where have we been and where are we going?. Journal of Animal Science, 81, 27–38.


