MAINTENANCE ENERGY REQUIREMENTS IN MATURE BEEF COWS AND RELATIONSHIPS WITH METABOLIC HORMONES, ADIPOSE GENE EXPRESSION, AND CALF PERFORMANCE

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EXPRESSION, AND CALF PERFORMANCE

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Abstract: Nonlactating, spring-calving Angus cows in mid- to late gestation were used during 3 yr to determine variation in maintenance energy requirements (MR) and evaluate relationships between MR and concentrations of triiodothyronine (T_3), thyroxine (T_4), and IGF-I in plasma, genes associated with lipid homeostasis, and calf performance. Cows were individually fed to meet predicted MR (NE_m; Level 1 Model; NRC, 2000) and feed intake was adjusted every other week until constant BW (regression analyses) was achieved. Cows in each year were classified based on MR as low (LMR; > 0.5 SD less than mean MR), moderate (MMR; ± 0.5 SD of mean MR), or high (HMR; > 0.5 SD greater than mean MR). Blood samples were collected at maintenance in each year and during early lactation in yr 1 and 3. During maintenance, cows (yr 2: n = 14; yr 3: n = 20) were infused with thyrotropin releasing hormone (TRH) and blood samples were collected. Plasma concentrations of T_3, T_4, and IGF-I were quantified by RIA. Relative mRNA abundance of lipogenic and lipolytic genes were evaluated in Longissimus dorsi muscle of LMR and HMR cows (n = 12) in yr 3. Mean MR (Kcal•kg $BW^{0.75}$•d^{-1}) of cows was 81.0 ± 1.8, 83.1 ± 1.6, and 88.1 ± 1.3 in yr 1, 2, and 3, respectively. Body weight, BCS, and daily plasma concentrations of T_3, T_4, and IGF-I in cows were not influenced by MR. After infusion of TRH in yr 2, mean plasma concentrations of T_4 were greater in MMR compared with LMR cows, which were greater than in HMR cows and the T_3:T_4 was greater in HMR cows compared with LMR and MMR cows. In yr 3, LMR cows had greater plasma concentrations of T_3 compared with HMR cows after THR infusion. Low MR cows had greater gene expression of *FASN*, as measured by mRNA abundance, compared with HMR cows. Performance of calves before weaning was not influenced by MR of cows. Thyroid hormones, IGF-I, and lipogenic genes may be a component of potential biomarkers for MR of cows and may allow for selection of cows with reduced MR.

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CHAPTER I

INTRODUCTION

Increased global food demand and rising costs of production have renewed interest in enhancing the efficiency of beef cows. Greater production efficiency of beef cows can increase profitability of the cow calf segment. Cost of feed represents the greatest single expense in cattle production and accounts for 50% of the variation in herd profitability (Miller et al., 2001). Arthur et al. (2001a) indicated profitability of growing animals could be enhanced to a greater extent by increasing feed efficiency rather than increasing outputs. Maintenance energy requirements (MR) account for nearly 70% of the total energy required by a cow and for approximately 50% of the total energy required for beef production from birth to slaughter (Ferrell and Jenkins, 1984b). Variation in MR of beef cattle (DiCostanzo et al., 1990; Johnson et al., 2003a; Cooper-Prado et al., 2014) and moderate heritability of metabolizable energy for maintenance (ME_m; Carstens et al., 1989; Hotovy et al., 1991) indicates that cows may be selected for lesser MR. Energetic efficiency of beef cows, whether determined by MR (Shuey et al., 1993; Boehmer et al., 2014; Cooper-Prado et al., 2014) or residual feed intake (RFI; Arthur et al., 2005; Basarab et al., 2007; Shike et al., 2014), has minimal influence on reproductive performance of cows or performance of calves before weaning.

Determination of MR for individual cows is impractical and does not represent common management practices. As a result, biomarkers for MR could be utilized to identify cows with reduced MR. Metabolic hormones including thyroid hormones (TH) and insulin-like growth factor I (IGF-I) regulate many biological processes. Concentrations of metabolic hormones can be easily determined in cattle and may be a potential component of biomarkers for energetic efficiency. Thyroid hormones are important mediators of metabolism, growth, and thermoregulation in beef cattle. Differences in thyroid hormone concentrations may account for a portion of the variation in maintenance energy requirement. Concentrations of thyroxine (T_4) and IGF-I in plasma are related to nutrient intake in cattle (Richards et al., 1995; Ciccioli et al., 2003; Lents et al., 2005). Thyroid hormones may be potential biomarkers for MR. Thyroxine and MR are related in beef cows (Cooper-Prado et al., 2014). Cows with divergent milk production, which is associated with MR (Ferrell and Jenkins, 1984a) differ in concentrations of T_4 (Bitman et al., 1984). Body temperature is related to MR in mice (Kgwatalala et al., 2004) and cattle (Derno et al., 2005) however, the relationship between MR and ruminal temperature have not been clearly defined (Boehmer et al., 2014; Cooper-Prado et al., 2014). Relationships between animal activity and MR suggest animal behavior may influence MR (NRC, 2000; Brosh et al., 2006). Despite these observations, accurate biomarkers for MR have not been established. Utilizing established scientific tools and new technologies may help to identify components of biomarkers for MR.

Identification of viable biomarkers for MR is essential for selection of cattle with greater energetic efficiency. Identification of cows that require less energy input and maintain performance may enhance the production efficiency of beef cows. Therefore, the objectives of this dissertation were to: 1) estimate and describe the variation in MR of mature, non-lactating beef cows during mid- to late-gestation, 2) evaluate relationships between MR and plasma concentrations of T_3, T_4 and IGF-I and rectal temperature, 3) evaluate relationships between MR of cows and mRNA expression of TH responsive genes associated with lipid homeostasis and cow temperament, and 4) evaluate relationships between MR of cows and performance of calves before weaning.

CHAPTER II

REVIEW OF LITERATURE

INTRODUCTION

The origins of nutritional energetics may be traced to early Greek philosophers. Lavoisier (1743-1794) in “Quantitation of Combustion” established the principals relating combustion to metabolism (Baldwin and Bywater, 1984). Elucidation of the laws of thermodynamics and the law of Hess provided the foundation for nutritional energetics (Ferrell and Oltjen, 2008). As reviewed by Ferrell and Oltjen (2008), the primary objectives of nutritional energetics have evolved to a) evaluation of relationships between gas exchange and heat energy, b) determination of base values for evaluation of foods that could be related to energy expenditures, and c) establishing the causes of energy expenditures. Subsequent advancements in technology progressed the understanding of nutritional energetics to its current state (see review; Johnson et al., 2003b).

The ability to define metabolizable energy resulted from the foundational discoveries in nutritional energetics. Metabolizable energy (ME) is defined as: gross energy (E) minus fecal energy (FE), urinary energy (UE), and gaseous energy (GE). As digestible energy is gross energy minus fecal and urinary energy losses, the derivation of metabolizable energy results in:

$$ME = HE + RE,$$

where RE equals retained energy and HE equals heat energy (NRC, 2000).

Profitability of beef production is influenced by maintenance energy requirement (MR) of cows. Nearly 70% of the total energy required by a cow is utilized for maintenance (Ferrell and Jenkins, 1984a). Moderate heritability of MR indicates that beef cows may be selected for energetic efficiency. Previous studies indicate that cows differing in MR are similar in reproductive performance and growth of calves before weaning. Current methods for evaluating MR are expensive, time and labor intensive, or alter the natural environment of the cow. Identification of biomarkers for MR would enhance the ability to select cows with reduced MR. Metabolic hormones, genes, proteins, or body temperature may be components of potential biomarkers for MR. Traditional scientific techniques and new technologies may help to identify potential biomarkers for MR. This review will examine the evaluation of MR, the factors influencing MR, energetic efficiency in beef cows and the influence of energetic efficiency cow reproduction and calf performance before weaning. Potential biomarkers for energetic efficiency in beef cows will be reviewed with emphasis on thyroid hormones (TH).

MAINTENANCE ENERGY REQUIREMENT OF BEEF COWS

The National Research Council (2000) defines MR as the amount of feed energy intake that will result in no net loss or gain of energy from tissues of the animal. Alternatively, MR is defined as "the fraction of energy that keeps an animal in energy equilibrium" (Ensminger, 1983). Maintenance energy requirement can be estimated by different methods and is influenced by many factors. Reducing the MR per unit of body size is feasible given its genetic variation and moderate heritability (Carstens et al., 1989; DiCostanzo et al., 1990; Hotovy et al., 1991; Johnson et al., 2003b).

Estimation of maintenance energy requirements

Maintenance energy requirement can be estimated by several methods. These methods include feeding trials, calorimetric, and comparative slaughter methods. Recently, the use of heart rate (HR) has been described as an alternate method of determining energy expenditure (Brosh, 2007).

During feeding trials, feeds with specific energy contents are fed to animals at fixed amounts. Feeding the animals over an extended period of time allows the determination of energy requirement for maintenance of body weight. Regression models for energy intake, live weight, and changes in weight and body condition score can be utilized to normalize small gains or losses when determining MR (McDonald et al., 2002). Feeding trials allow animals to be managed under equal or similar conditions to their normal production system and large numbers of cattle can be evaluated.

Calorimetric methods allow estimation of MR directly or indirectly. Direct calorimetry requires confinement of the animals in respiratory chambers and heat production (energy for maintenance) is measured. Indirect calorimetry measures respiratory exchange, oxygen consumption, and carbon dioxide production to determine heat production. Indirect calorimetry relies on the close relationship between respiratory quotient and heat production. Because respiratory chambers/equipment are utilized, calorimetric methods are expensive and complicated (McDonald et al., 2002). Calorimetric methods are limited; the respiratory equipment alters normal animal behavior, or animals are managed in conditions that differ from natural environments or free-ranging conditions (McDonald et al., 2002).

Heart rate has been utilized to determine energy expenditure of free-ranging farm animals. As reviewed by Brosh (2007), the relationship between heat production (HP) and oxygen consumption with HR provides the basis for determination of energy expenditure. Energy expenditure, ME intake, and HR are highly correlated in free-ranging and confined cows (Brosh et al., 2004; 2006; 2010). Use of HR for determination of energy expenditure requires further validation in other species and environments and is currently cost prohibitive for producers (Brosh, 2007).

The comparative slaughter method (Lawes and Gilbert, 1861; Garrett et al., 1959) measures initial and final body composition, energy intake, and retained energy. Maintenance requirements are calculated by differences between inputs and outputs. This method has the advantage of minimally influencing the normal environment or behavior of the animal. The method requires an accurate estimation of body composition at the beginning and at the end of the trial and some animals must be sacrificed (NRC, 2000).

The California Net Energy System for beef cattle (Lofgreen and Garrett, 1968) was adopted by the NRC (NRC, 1984). Based on the comparative slaughter method, measurements of ME intake (MEI) and RE were utilized to determine heat production (HP). Estimates of ME_m were calculated as the MEI when RE is equal to zero (NRC, 2000). Estimates of fasting heat production (FHP), or net energy requirements for maintenance (NE_m), occur as derivations of the intercept of the regression log of HE on MEI (NRC, 2000). The NE_m for growing beef steers and heifers is calculated as:

$$NE_m = 0.077 \text{ Mcal} \cdot EBW^{0.75}$$

were EBW is the average empty body weight in kilograms. Calculated values of NE_m require adjustments for animal type when different than that used to derive the formula (NRC, 2000). Estimation of NE_m for beef cows utilizes adjustments for breed, physiological state, activity, BCS (an indicator of animal insulation and energy stores), and environment (Level 1; NRC, 2000).

Factors affecting maintenance energy requirement

Maintenance energy requirements are influenced by a number of factors related to the animal, its level of production, and environment. These factors have been described by Ferrell and Jenkins (1985a), Crooker et al. (1991), and the National Research Council (NRC, 2000) and include breed, body composition, sex, size, visceral organ mass, physiological status, level of production, health status, activity, and environment. As evaluations of MR are unique to animals and environments in which studies were conducted, comparison of MR must consider differences in these factors.

***Breed*:** Armsby and Fries (1911) were among the first to describe differences in MR between Angus and dairy type "scrub" steers. Subsequent work has established that MR differs for cattle of different breeds. Metabolizable energy required for maintenance of beef cows range from 123 to 169 $Kcal \cdot BW^{0.75} \cdot d^{-1}$ and breed differences were associated with different potential for milk production (Thompson et al., 1983; Ferrell and Jenkins, 1984a; Solis et al., 1988; Montaño-Bermudez et al., 1990; Laurenz et al., 1991; Reid et al., 1991). Metabolizable energy for maintenance of Angus x Hereford, Charolais x Angus or Hereford, Jersey x Angus or Hereford, and Simmental x Angus or Hereford cows were 130, 129, 145, and 160 $Kcal \cdot BW^{0.75} \cdot d^{-1}$, respectively (Ferrell and Jenkins, 1984a). Fasting heat production in Hereford bull calves was 14% less than Simmental bull calves (Ferrell and Jenkins, 1985b). Fasting heat production was 20% greater in Ayrshire steers compared with Angus steers (Blaxter and Wainman, 1966) and MR was 12% greater in Holstein steers compared with Hereford steers (Garrett, 1971). Maintenance energy requirement of Angus x Hereford cows tended to be greater than in Angus x Holstein cows and averaged 127.6 and 140.3 $Kcal \cdot BW^{0.75} \cdot d^{-1}$, respectively (Thompson et al., 1983). Nellore x *Bos taurus* had greater ME_m compared with purebred Nellore cows (Calegare et al., 2007). Growing dairy or dual purpose cattle have 20% greater MR compared with beef cattle (NRC, 2000). The NRC (2000) indicates that growing *Bos indicus* cattle require 10% less energy for maintenance compared with *Bos taurus* cattle and crosses are intermediate. In contrast, Ferrell and Jenkins (1998) observed ME_m of *Bos taurus* and *Bos indicus* sired steers were similar.

Body composition: Maintenance energy requirements are influenced by body composition. Although visceral organ mass has the greatest effect on HP, lean mass has a greater influence on HP than fat (Thompson et al., 1983; Tess et al., 1984). Lobley et al. (1980) estimated the energetic requirement for protein synthesis accounted for 30% of HP. The requirement for protein and fat synthesis in sheep was 8.14 and 1.10 Kcal ME/Kcal, respectively (Rattray et al., 1974b). Fasting heat production in swine was influenced by mass of body protein, whereas body fat had minimal to no relationship with FHP (Tess et al., 1984; Noblet et al., 1999). Similar relationships between body protein, body fat, and FHP occur in cattle (Webster, 1977; Baker et al., 1991), and other species (Webster, 1977). Estimated requirement for maintenance of protein tissue was greater than fat tissue in Angus x Hereford cows (Thompson et al., 1983). Fat Angus x Hereford cows had decreased MR compared with thin Angus x Hereford cows (Thompson et al., 1983). Fat and moderately conditioned Charolais x Angus cows required 22 and 18% more energy, respectively, for maintenance of body weight compared with cows in lesser body condition (Houghton et al., 1990a). Metabolizable energy for maintenance was greater in moderately conditioned (BCS 5), mature, non-lactating, non-pregnant Hereford cows compared with cows in fat (BCS 7) or thin (BCS 3) body condition (Wagner et al., 1988). In experiments with mature, non-pregnant, non-lactating Angus cows, DiCostanzo et al. (1990) estimated the ME required to deposit 1 Kcal protein (5.56 Kcal) was greater than 1 Kcal of fat (1.26 Kcal). Additionally, when cows had similar fat masses, cows with greater lean masses had increased ME requirements for maintenance compared with cows with lesser lean (DiCostanzo et al., 1990). Fat deposition provides insulation during exposure to cold environments. During the winter, greater amounts of fat tissue reduce energy requirements in pigs (Tess et al., 1984) and cattle (Thompson et al., 1983; Wagner et al., 1988). Internal fat deposition is increased and external fat deposition is decreased in dairy cows compared with beef cows. As a result, dairy cattle have reduced insulation during exposure to cold environments. Reductions in MR, due to insulative properties of fat, were observed by (Thompson et al., 1983) where fat Angus x Hereford cows had a 6.1% decrease in MR (ME_m) compared with thin cows. Decreased MR, as a result of fat insulation, was not observed in Angus x Holstein cows and was attributed to differences in fat distribution between dairy and beef type breeds (Cundiff, 1970). Fasting heat production (MJ·kg $BW^{0.75}$) was greater in thin (≤ 2.9 mm, 0.463) than moderately conditioned Holstein cows (≥ 4.5 mm; 0.359; Birnie et al., 2000)

Visceral organ mass: Energy intake influences mass and metabolic activity of visceral organs (Ferrell and Jenkins, 1988). The visceral organs, while only accounting for 5 to 7% of total body protein mass in steers, account for 32 to 45% of protein synthesis in the body and 23% of total energy expenditure (Lobley, 2002). In contrast, skeletal muscle consumes 25 to 30% of total energy expenditure and accounts for 15 to 20% of the protein synthesis, yet comprises 50% of the total body protein (Lobley, 2002). Increased rates of fractional protein synthesis occur in liver and GI tract tissues and account for the increased energy expenditure of these organs (Lobley et al., 1980; Crooker et al., 1991; Lobley, 2002). Visceral organ mass was correlated with FHP or oxygen consumption of sheep (Ferrell et al., 1986; Burrin et al., 1990; Wester et al., 1995). Changes in feed intake can influence the mass of visceral organs and oxygen consumption increased with increased organ mass in sheep (Burrin et al., 1990; Wester et al., 1995; Caton et al., 2009) and cattle (Ferrell et al., 1976; Reynolds et al., 1991; Hersom et al., 2004a). The energy expenditure of visceral tissues in cattle accounted for 40% of energy utilized for maintenance but only 6% of empty body weight (Ferrell, 1988). In a study evaluating non-pregnant, non-lactating Angus cows, DiCostanzo et al. (1990) observed that liver and heart weights were positively correlated with ME_m in beef cows, indicating metabolically active organs contribute to variation in energy expenditures. In mature, non-lactating, non-pregnant Hereford x Angus x Red Poll x Pinzgauer cows, changes in GI tissue and liver metabolism may account for differences in HP during nutrient restriction and realimentation (Freetly et al., 2006). The energetic requirement of visceral organs was greater than of lean mass in pigs (Milgen et al., 1998) and accounted for three times greater ME_m (Noblet et al., 1999). Increased potential for milk production was related to increased visceral organ mass in beef cows (Ferrell and Jenkins, 1984a).

Environment: Ambient temperature, wind, precipitation, and radiation are environmental factors that influence MR. Cows maintain temperature homeostasis, producing more heat when ambient temperatures are below or dissipating heat when ambient temperatures are above thermoneutral zones. Increased surface area of cows increases potential for evaporative heat loss. Evaporative heat loss of cows is minimal when cows are at or below their thermoneutral zone and increases in warm ambient temperatures (Ehrlemark and Sällvik, 1996). Hair and wool coats of cattle and sheep, respectively, decreased heat loss during increasing wind speeds and decreasing temperatures (Ames and Insley, 1975). Precipitation decreases the insulative property of hair coat in winter and increases evaporative cooling in the summer. Thermal load associated with greater afternoon temperatures was decreased when beef steers were exposed to sprinklers (Mader et al., 2007). Airflow greatly influenced heat exchange between cows and the environment (Gebremedhin and Wu, 2003). Access to shade, thereby decreasing solar radiation, increased gain and feed efficiency of beef steers when exposed to a warm environment compared with when steers had no access to shade (Mader et al., 1999). In cold (-10°C) environments, energy requirements increased 7 Mcal/d and were further increased by wind (Berman, 2004). Maintenance energy requirements increase as animals utilize energy to regulate body temperature (NRC, 2000). The energy required to maintain body weight of Angus and Simmental cows was less (122.6 and 91.4 kg ME·kg $BW^{-.75}$, respectively) in summer than winter (145.9 and 109.3 kg ME·kg $BW^{-.75}$, respectively; Laurenz et al., 1991). Well conditioned, Angus x Hereford cows required 6.1 to 8.9% less energy than thin cows during the winter (Thompson et al., 1983; Wagner et al., 1988). Thompson et al. (1983) suggested the reduced MR of fat Angus x Hereford cows in winter compared with thin cows, at similar lean body mass, may have resulted from the greater insulative property of fat or the reduced requirement for maintenance of fat tissue. In contrast, season did not influence thermoneutral FHP of Hereford steers in Colorado (Birkelo et al., 1991). Behavioral and physiological adaptations to environmental changes can vary greatly among breeds and genotypes (NRC, 2000).

Health: Maintenance energy requirements are increased in cattle with compromised health. Synthesis of acute phase proteins in response to an immune challenge may alter amino acid requirements and MR (Krehbiel et al., 2012). Infection with nematodes can increase maintenance energy expenditure (Van Houtert and Sykes, 1996). While the effect of illness on MR has not been established, the immune response requires energy and may increase MR (NRC, 2000).

Physiological state: Maintenance energy requirement of beef cows is influenced by gestation and lactation. Maintenance energy requirements of non-pregnant heifers were similar to heifers in mid to late gestation (Ferrell et al., 1976). Similar observations have occurred in ewes, where MR did not differ between non-pregnant ewes and those in mid to late gestation (Rattray et al., 1974a). Koong et al. (1982) observed ME_m did not differ between heifers and cows during late gestation. Maintenance energy requirement tended to be greater in Hereford heifers and cows gestating twins compared with single calves (Koong et al., 1982). During two consecutive lactations, Montaño-Bermudez et al. (1990) determined that lactating Hereford x Angus, Red Poll x Angus, and Milking Shorthorn x Angus cows required 18% greater ME_m than during gestation. Hereford cows in peak lactation required 31 and 41% more energy for maintenance compared with non-lactating cows (Neville and McCullough, 1969; Neville, 1974; respectively). Fasting heat production was 9% greater in dairy cows during late lactation than after lactation had ceased (Holter, 1976). Early weaning of calves decreased MR of postpartum beef cows compared with cows with suckling calves (Houghton et al., 1990a).

Feed allowance: Plasticity in MR is observed when animals are adapted to different amounts of feed. Maintenance energy requirement is influenced by previous plane of nutrition or compensatory gain (NRC, 2000). Fasting heat production was altered when sheep were adapted to different planes of nutrition (Marston, 1948; Ferrell et al., 1986). Heat production was decreased during feed restriction of beef steers (Birkelo et al., 1991; Murphy and Loerch, 1994), beef heifers (Yambayamba et al., 1996; Freetly et al., 2003), non-pregnant, non-lactating beef cows (Freetly et al., 2006), and pregnant cows (Freetly et al., 2008). Severity and duration of feed restriction, type of restricted nutrient(s), animal genotype, and other factors influence an animal's response to nutrient restriction (NRC, 2000). Metabolic rates of cattle fluctuate as a consequence of changes in nutrient availability. Fasting heat production increased 7% in steers maintained on greater amounts of nutrition compared with steers on a lesser plane of nutrition (Birkelo et al., 1991). At 1.9% DMI/BW, FHP was similar in Hereford and Simmental cows, however FHP of Simmental cows was greater than for Hereford cows when feed was reduced and lesser when feed was increased (Jenkins et al., 1991b). Hereford steers on a greater plane of nutrition (251.1 Kcal ME·kg $BW^{0.75}$·d^{-1}) had 7 and 14% greater FHP and ME_m, respectively, compared with steers on a lesser plane of nutrition (133.5 kcal ME·kg $BW^{0.75}$·d^{-1}; Birkelo et al., 1991). Feed intake influences HP in non-lactating, non-pregnant (Freetly and Nienaber, 1998; Freetly et al., 2006) and pregnant (Freetly et al., 2008) beef cows where increased HP occurred during nutrient restriction and returned to pre-restriction levels during realimentation. Feed restriction induces a decrease in basal metabolism caused by decreased volume and metabolic activity of the viscera and alterations in growth hormone, insulin-like growth factor I (IGF-I), insulin, and TH (Hornick et al., 2000). Concentrations of T_3 and T_4 were decreased throughout periods of feed restriction and returned to basal concentrations 31 d after realimentation in beef heifers (Yambayamba et al., 1996). During nutrient restriction, a reduction in concentrations of T_3 and T_4 may decrease basal metabolism and decrease energy expenditure (Hornick et al., 2000).

Efficiency of energy utilization can be reduced in high performing cows when environments limit nutrient quality or availability (Ferrell and Jenkins, 1985a; Jenkins and Ferrell, 1994, 2007). Feed intake influences HP in beef cows. Shifts in metabolism of beef cows occur during periods of reduced energy intake (Freetly and Nienaber, 1998; Freetly et al., 2006, 2008). Breeds with greater genetic potential for growth or milk production (Charolais, Braunvieh, Simmental, Pinzgauer and Limousin) were more efficient (g calf weaned $\cdot$kg $DMI^{-1}\cdot d^{-1}$) when fed 6,000 kg DM/yr and efficiency of energy utilization decreased with reduced DMI (Jenkins and Ferrell, 1994). In contrast, Red Poll cows had greater feed conversion when fed less than 4,000 kg DM/yr, but efficiency declined when DMI increased (Jenkins and Ferrell, 1994). Calegare et al. (2007) indicated that lactating Angus x Nellore cows with adequate nutrition had greater efficiency (g BW gain of calf•Mcal of ME $intake^{-1}$) compared with purebred Nellore cows. Ultimately, it is essential to match the performance potential of beef cows to an environment with adequate nutrition to maximize productivity (Jenkins and Ferrell, 1994; Calegare et al., 2007).

Sex: The influence of sex and castration on body composition and MR is well established (NRC, 2000). Bulls have 15% greater MR compared with heifers and steers (NRC, 2000). Metabolizable energy for maintenance (Kcal•kg $BW^{0.75}$•d^{-1}) of beef steers was greater compared with that of beef heifers (Hotovy et al., 1991; NRC, 2000). Metabolizable energy requirement for maintenance (kJ•kg $BW^{0.75}$•d^{-1}) was 11% greater in Hereford and Simmental bulls compared with heifers (Ferrell and Jenkins, 1985b). Feed conversion and HP in Hereford x Friesian bulls was increased by 9 and 7%, respectively compared with steers when fed the same ME (Webster, 1977). In purebred and crossbred Nellore heifers, steers, and bulls, neither sex nor castrate status influenced NE_m (Kcal•kg $BW^{0.75}$•d^{-1}; Chizzotti et al., 2008). Similarly, NE_m (Kcal•kg $BW^{0.75}$•d^{-1}) did not differ between Nellore bulls and steers (Tedeschi et al., 2002).

Other factors: Animal behavior may influence MR. Energetic cost of horizontal movement was 2 J•kg^{-1}·min^{-1}and vertical movement was 26.2 J•kg^{-1}•vertical m^{-1} in Hereford x British Friesian steers (Ribeiro et al., 1977). Brosh et al. (2006) estimated the total energy expenditure of grazing activity was 12.92 J•kg BW$^{0.75}$•m^{-1}. Heat production in beef cattle is increased by physical activity (NRC, 2000). In contrast, chute scores, chute exit velocity, and pen score were not influenced by residual feed intake (RFI) in heifers and when evaluated as cows (Black et al., 2013b). Similarly, Nkrumah et al. (2007) observed that flight speed was not related to RFI. Aggressive temperament of cows may influence MR as energy expenditure may be elevated when cows are nervous (Crooker et al., 1991).

EFFICIENCY OF BEEF COWS

Energetic efficiency of cattle is generally represented in terms of outputs relative to inputs. Johnson et al. (2003b) indicated three primary components of efficiency ratios; diet energy cost of maintaining the animal per unit time, diet energy cost per unit of product, and efficiency ratio (fixed maintenance cost). Berry and Crowley (2013) classified feed efficiency calculations as ratios of traits or residual and regression traits. Calculation of energetic efficiencies can be complicated by adaptation to feeding levels, changes in digestibility of diets, fermentation, microbial growth, protein supply, nutrient flux metabolism, hormonal regulation, and product composition (Johnson et al., 2003b).

Efficiency in maintenance requirement

Energy requirement variation of cows within a herd indicates that different energetic efficiencies can occur (DiCostanzo et al., 1990). Variation in MR within different breeds and herds ranges from 5 to 33% (Taylor et al., 1986; DiCostanzo et al., 1990; Shuey et al., 1993; Johnson et al., 2003b; Derno et al., 2005; Cooper-Prado et al., 2014). The greatest difference in ME_m within a herd was 26.6% for non-pregnant, non-lactating Angus cows (DiCostanzo et al., 1990), 32.3 and 47.2% in peripartum Hereford x Angus cows (Shuey et al., 1993), and 22.8% for Hereford steers (Derno et al., 2005). Similarly, Cooper-Prado et al. (2014) observed the greatest within herd difference in NE_m averaged 26% in two experiments with Angus cows.

Efficiency of ME_m utilization can be influenced by type of animal or breed. Efficiency of ME_m utilization (FHP/ME_m) in beef steers ranged from 0.62 and 0.83 (Birkelo et al., 1991) and 0.64 to 0.84 in peripartum Hereford x Angus cows (Shuey et al., 1993). Efficiency in maintenance energy utilization (kg $BW^{0.75}$•d^{-1}•ME_m^{-1}) was greater in Hereford and Angus cows (0.15 and 0.14, respectively) compared with Friesian and Jersey cows (-0.18 and -0.15, respectively; Taylor et al., 1986). Mature, non-lactating, non-pregnant beef cows were 23% more efficient at body weight equilibrium than dairy cows (Taylor et al., 1986). Efficiency of ME use for maintenance was not influenced by sex in Angus x Hereford and Barzona x Hereford monozygotic twin calves (Hotovy et al., 1991). Efficiency of energy utilization for maintenance (FHP/ ME_m) was greater in Hereford cattle compared with Simmental cattle, and heifers tended to be more efficient than bull calves (Ferrell and Jenkins, 1985b).

Energetic efficiency of cows may be quantified relative to calf production, the primary product of the cow/calf industry. Relating production to energy utilization, Ferrell and Jenkins (1984a) indicated potential for differences in cow production per annual MR (calf WW•exposed cow^{-1}•annual MR^{-1}). Energetic efficiency of cow/calf pairs (Kcal calf retained energy/Mcal MEI of cow/calf pair) was greater in Angus than in Simmental cow/calf pairs (Calegare et al., 2007). In contrast, production efficiency (calf WW/ MEI of cows and calves) of Hereford x Angus cows was not influenced by either ME_m or FHP (Shuey et al., 1993). Heritability of ME_m in monozygous twin beef cattle was 0.71 at 9 mo of age and 0.49 at 20 mo of age (Carstens et al., 1989). Similarly, Hotovy et al. (1991) indicated a moderate heritability (0.52) for ME_m and suggested a genetic component for MR; as variation in MR between pairs of monozygotic twin beef calves was greater than MR variation within pairs. Reproductive performance of cows and performance of calves before weaning was not influenced by MR of dams (Boehmer et al., 2014; Cooper-Prado et al., 2014). Given the moderate heritability of MR of cows and the similar performance of calves from cows differing in MR, selection of cows for reduced MR may be feasible.

Residual feed intake

Residual feed intake (RFI), initially described by Koch et al. (1963) as a measure of feed efficiency related to DMI, is not influenced by growth or mature body size (Herd and Arthur, 2009). Primary factors influencing RFI include intake and digestion of feed, metabolism, activity, and thermoregulation (Herd and Arthur, 2009). The comparison of expected and actual feed intakes results in residual values for feed intake. Deviations from expected feed intake, termed residuals, are then used to classify animals as having greater or lesser efficiency (negative RFI and positive RFI, respectively). Studies evaluating growing cattle have established relationships between RFI, available ME, HP, and visceral organ mass (Basarb et al., 2003; Nkrumah et al., 2006). Increased visceral organ mass occurs in less efficient pigs (Tess et al., 1984; Noblet et al., 1999), sheep (Burrin et al., 1990), and cattle (Ferrell and Jenkins, 1984a; Wagner et al., 1988; Reynolds et al., 1991). Muscle from more efficient pigs had reduced 20S proteasome activity and troponin-T degradation product compared with less efficient pigs and indicated reduced protein degradation enhances efficiency (Cruzen et al., 2013). The greater efficiencies of animals identified by RFI may be a result of decreased methane production, metabolic efficiency, increased digestibility, or altered mitochondrial function (Nkrumah et al., 2006; Hegarty et al., 2007; Bottje and Carstens, 2012).

Although estimation of RFI is typically used in growing animals, recent efforts have focused on enhancing cow efficiency. When classified by RFI as heifers, RFI and RFI ranking were not correlated with RFI or RFI rank as cows (Black et al., 2013b). Residual feed intake of heifers was negatively correlated with RFI as mature cows (Bradbury et al., 2011). In contrast, RFI of heifers was moderately correlated with subsequent RFI as mature cows (Archer et al., 2002; Morgan et al., 2010) (Morgan et al 2010, Archer et al 2002). Heifers classified as high and moderate RFI were less efficient as cows at 2 yr of age and had greater RFI and DMI during lactation and subsequent gestation (Shike et al., 2014). Cows that were the most efficient as heifers, as classified by RFI, had decreased DMI compared with less efficient cows (Black et al., 2013b). Reproductive performance of cows and preweaning calf performance did not differ among cows classified by RFI (Arthur et al., 2005; Basarab et al., 2007; Shike et al., 2014). Feeding behavior in offspring, muscle fiber abundance and proportion, and carcass characteristics may be influenced by divergent selection for RFI (Welch et al., 2012; Welch et al., 2013; McGee et al., 2014). Using RFI as a tool for selection of growing animals with increased energetic efficiency may reduce maintenance cost by 9 to10% and feed intake by 10 to 12% (Nkrumah et al., 2006; Hegarty et al., 2007). Together, information from animal physiological and molecular genetic evaluations of efficiency will lead to the ultimate goal of developing an accurate, cost effective commercial test for selection of efficient animals (Herd and Arthur, 2009).

Feed conversion

Feed conversion efficiency differs among breeds of cattle and crosses of breeds. Cows produced by breeding Angus, Hereford, Chianina, Gelbvieh, Maine Anjou, and Red Poll bulls to Angus and Hereford cows differed in efficiency (g gain of calf•adj Mcal•d^{-1}) and was greater in cows sired by Angus or Hereford (35.8), Red Poll (35.7), or Maine Anjou sires (35.6) than in cows sired by Chianina (33.1) or Gelbvieh (33.7) bulls (Jenkins et al., 1991a). Feed conversion to kg of weaned calves was greater in cows with a greater potential for growth or milk production compared with cows that have reduced potential for milk production (Jenkins and Ferrell, 1994). The mechanisms regulating efficiency of feed conversion have not been defined. Hong et al. (2015) suggested selection for oxygen consumption in mice induced changes in basal metabolism; state 2 mitochondrial respiratory activity, and therefore, mitochondrial activity was greater in mice with increased oxygen consumption compared with mice having lesser oxygen consumption rates (Hong et al., 2015). Mitochondrial respiratory chain complex activity was not different between sheep with a high or low feed conversion ratio (FCR; Sharifabadi et al., 2012). Selection of Angus cows for feed conversion did not alter FCR in offspring, but increased gain and subcutaneous fat occurred when offspring had increased FCR (Bishop et al., 1991). Feed conversion ratio of beef cattle was negatively correlated with maternal WW (Crowley et al., 2011) and weight of calves at 200 and 400 d of age (Arthur et al., 2001b).

BIOLOGICAL MARKERS FOR MAINTENANCE ENERGY REQUIREMENT

Increased interest in enhancing the profitability of beef production has stimulated research to determine biomarkers for animal efficiency. Development of practical methods for determination of MR in beef cattle is necessary because determination of MR in individual animals is difficult, cost prohibitive, or time and labor intensive. Several hormones, proteins, and genomic messages have been evaluated as biomarkers for MR without success. Concentrations of IGF-I, insulin, and TH (T_3, triiodothyronine; T_4, thyroxine) have been evaluated relative to feed efficiency or energy balance in cattle.

IGF-I and insulin

Insulin-like growth factors and insulin regulate growth and metabolism. Serum concentrations of IGF-I are correlated with post weaning BW and gain in growing Angus cattle divergently selected for greater or lesser IGF-I (Davis and Simmen, 2006; Huang et al., 2011). The relationship between IGF-I and feed efficiency in growing animals has not been firmly established. Feed efficiency and IGF-I in growing beef cattle have been reported to be positively related (Johnston et al., 2002; Moore et al., 2005), or minimally to unrelated (Lancaster et al., 2008; Kelly et al., 2010a). Concentrations of IGF-I in plasma did not differ in beef cows with different MR fed to maintain body weight (Cooper-Prado et al., 2014), however IGF-I was negatively correlated with MR during ad libitum grazing. Decreased concentrations of IGF-I occur when cattle are in a negative energy balance (Reynolds et al., 1991; Keisler and Lucy, 1996; Bossis et al., 1999) and concentrations of IGF-I increased when cattle consumed greater amounts of energy (Bossis et al., 2000). Angus cows fed to lose 1% of BW per wk had lesser concentrations of insulin in plasma compared with cows fed to maintain BW (Richards et al., 1989; Bossis et al., 1999). Concentrations of insulin were increased in less efficient Brangus steers compared with more efficient Angus steers (Beaver et al., 1989) and were greater in Angus heifers with a negative (more efficient) RFI classification than heifers with a positive (less efficient) RFI classification (Walker et al., 2015). Although concentrations of insulin and IGF-I in plasma were not influenced by MR of Angus cows during maintenance of body weight, concentrations of IGF-I were positively related to MR during early lactation (Bailey, 2009; Pye, 2011; Cooper-Prado et al., 2014). Thus, plasma concentrations of IGF-I, not insulin, may be a potential biomarker for MR of grazing beef cows.

Thyroid hormones

Thyroid hormones are dynamic homeostatic regulators that maintain the balance between energy turnover and metabolism (Hulbert and Else, 2004). Triiodothyronine, the more biologically active thyroid hormone, is produced from deiodination of T_4. Triiodothyronine and T_4 are transported by binding proteins to cellular targets where they elicit homeostatic effects (see reviews; Bartalena, 1990; Lazar, 1993). The remainder of this section of the review focuses on the synthesis and effects of TH.

Synthesis and regulation: The importance of the thyroid gland in regulation of metabolism was first demonstrated by Magnus-Levy (1895). Thyroxine was first isolated in 1914 by Kendall (1964, 1983) and T_3 was later identified concurrently by (Gross and Pitt-Rivers, 1952) and Roche et al. (1952a, b). Synthesis of TH is controlled by the hypothalamus, where sensory neurons stimulate production of the tripeptide, thyrotropin-releasing hormone (TRH; Guillemin, 1964; Schally et al., 1966b; Schally et al., 1966a). Thyrotropin releasing hormone is transported to the anterior pituitary to stimulate secretion of thyroid stimulating hormone (TSH, Uhlenhuth, 1927) in thyrotrophic cells. Thyroid stimulating hormone stimulates production of thyroglobulin by thyroid follicular cells (see reviews; Magner, 1990; Szkudlinski et al., 2002). In concert, sodium iodide symporters in thyroid follicular cells concentrate inorganic iodine from extracellular fluid. Both thyroglobulin and iodine are transported to the follicular lumen where iodination of tyrosine residues occur within the thyroglobulin matrix. The primary TH, T_4 (3,5,3',5'-tetraiodo-L-thyronine) and, the more biologically active, T_3 (3,5,3'-triiodo-L-thyronine) are formed within the thyroglobulin matrix though the self-coupling of diiodotyrosyl (DIT) residues or coupling of a DIT residue with a monoiodotyrosyl (MIT) residue, respectively. Returning to the follicular cell, MIT, DIT, T_3, and T_4, result from proteolytic cleavage of thyroglobulin by 5'-deiodinase. Only 3 to 4 molecules of T_4 are produced within a single thyroglobulin molecule and the ratio of T_4 to T_3 synthesis in human thyroglobulin is approximately 15:1 (Lingvay and Holt, 2012). In circulation, T_3 and T_4 are bound to serum proteins (thyroid hormone-binding protein, transthyretin, and albumin) which influence bioavailability and metabolism of TH (Schussler, 1990). The ratio of free to bound TH is species dependent but generally is less than 0.3% for T_3 and 0.03% for T_4. In the thyroid and other tissues, T_4 is converted to T_3 by 5'-deiodinase (Moreno et al., 2008). As reviewed by Hennemann et al. (2001), passage of TH through the plasma membrane occurs by passive diffusion and by energy dependent transporters. Effects of TH occur via binding with nuclear TH receptors (THR); THR have a 10-15 fold greater affinity for T_3 compared with T_4 (Sinha and Yen, 2000; Visser, 2000). Secretion of T_3 and T_4 is controlled by negative feedback mechanisms and influences gene expression in most tissues of the body. Ablation of the paraventricular nucleus reduced TRH and TSH secretion in rats while stimulation of the PVN increases secretion of both (Degreef et al., 1992). Relative to euthyroid controls, hypothyroid Brahman cows had increased and hyperthyroid cows had decreased serum concentrations of TSH (De Moraes et al., 1998).

Similarly, hyperthyroid steers have decreased secretion of TSH compared with euthyroid controls (Kahl et al., 1992). The molar ratio of T_4 to T_3 in Shorthorn and Africander x Shorthorn cattle was rapidly reduced in response to TRH (Slebodzinski and Wallace, 1977).

Factors influencing thyroid hormones: Thyroid hormones are necessary for development of bovine embryos (Ashkar et al., 2010). Concentrations of T_4 and thyroid binding globulin increase during fetal development until birth and rapidly decline to adult concentrations within a week of birth (Hernandez et al., 1972). Basal metabolic rate of calves was less than 40 $cal \cdot kg\ BW^{-1} \cdot d^{-1}$ at birth, increased to 49 $cal \cdot kg\ BW^{-1} \cdot d^{-1}$ within 3 d after birth, and decreased to 41 $cal \cdot kg\ BW^{-1} \cdot d^{-1}$ within 1 wk (Hernandez et al., 1972).

Concentrations of T_4 in beef cattle are approximately 40 fold greater than concentrations of T_3 (Kahl et al., 1978; Ellenberger et al., 1989; Kahl et al., 1992; Hersom et al., 2004b; Flores et al., 2008). Because of the relationships between metabolism and milk production, TH have been evaluated to a greater extent in dairy cattle than in beef cattle. Decreased 5'deiodinase activity occurs in plasma of dairy cows during early lactation and indicates a tissue specific regulation of metabolism (Pezzi et al., 2003). Concentrations of TH in milk available to calves contributed minimally to the TH requirements for metabolic functions of calves (Akasha and Anderson, 1984).

Diurnal variation occurs in concentrations of T_3 and T_4. Maximum concentrations of T_3 and T_4 in serum and milk of lactating dairy cows occurred in the afternoon and the nadir occurred in the morning (Bitman et al., 1984). Similarly, diurnal patterns occurred for plasma concentrations of T_3 and T_4 in lactating dairy cows with maximum concentrations of T_4 occurring 2 h after maximum concentrations of T_3 (Bitman et al., 1994). Concentrations of free and bound T_3 and T_4 change throughout the year and increases in TH are associated with reduced ambient temperature (Nixon et al., 1988). Exposure to elevated ambient temperature and relative humidity decreases concentrations of T_3 and T_4 in beef (Pratt and Wettemann, 1986; Biggers et al., 1987; Richards et al., 1995) and dairy cattle (Johnson et al., 1991). In non-pregnant, yearling, Angus heifers, serum concentrations of T_4 increased 21% in the winter compared with summer (ambient temperatures ranged from -9.6 to 5.2°C and 19.9 to 34.2°C, respectively) but concentrations of T_3 were not influenced by season (Mader and Kreikemeier, 2006).

Effects of thyroid hormones: Thyroid hormones are essential for development, growth, and maintenance of body weight and condition. Thyroxine and T_3 are primary regulators of basal metabolic rate in cattle (Yousef and Johnson, 1966; Yambayamba et al., 1996), sheep (Hornick et al., 2000), and rats (Moreno et al., 2002; Klieverik et al., 2009). Excess T_4 increased total and resting energy expenditure in rats, whereas hypothyroid rats had decreased total and resting energy expenditure (Klieverik et al., 2009). Body weight, height, growth, reproduction, and metabolism were decreased in thyroidectomized, Jersey heifers (Brody and Frankenbach, 1942). Thyroid hormones are permissive to the biological activity of growth hormone (GH; Hornick et al., 2000). Thyroid status did not influence serum concentrations of insulin or GH in Brahman cows (De Moraes et al., 1998). Thyroid status of Brahman cows influenced BW and BCS; hypothyroid cows gained and hyperthyroid cows lost BW and BCS relative to euthyroid controls (De Moraes et al., 1998). Serum concentrations of T_3 and T_4 were greater in moderate body condition cows compared with low body condition cows (Flores et al., 2008). Hyperthyroid rats had greater feed intake (18%) compared with euthyroid controls, but feed intake did not differ between hypo-and euthyroid rats (Klieverik et al., 2009). Plasma concentrations of T_3 and T_4 were decreased in Chianina steers (Hayden et al., 1993) and fed lesser amounts of energy compared with controls and increase after realimentation.

Thyroid hormones are primary regulators of metabolism in cattle. Thyroxine increased metabolic rate in lactating dairy cows as determined by oxygen consumption (Yousef and Johnson, 1966). The magnitude of milk production in dairy cows treated with T_4 was greater in thermoneutral environments compared with when cows were exposed to elevated ambient temperatures (Shibata et al., 1983). Resting metabolism was decreased 40% in thyroidectomized dairy calves (Brody and Frankenbach, 1942). In beef cows, concentrations of T_4 in plasma are influenced by feed intake (Ciccioli et al., 2003; Lents et al., 2005) and concentrations of T_4 decrease with feed restriction (Richards et al., 1995). Concentrations of T_4 and T_3 were reduced in nutrient restricted beef steers (Ellenberger et al., 1989; Hayden et al., 1993; Murphy and Loerch, 1994), beef steers grazing low quality forage (Hersom et al., 2004b), and Holstein-Friesian bulls (Keogh et al., 2015). Thyroxine and T_3 in serum were positively associated with energy balance in dairy cows during the first 10 wk of lactation and estimation of energy balance was enhanced in models including T_4 (Reist et al., 2002; Pezzi et al., 2003). Concentrations of T_4 were reduced in primiparous beef cows divergently selected for reduced milk production (Bitman et al., 1984). As variation in MR is associated with potential for milk production (Ferrell and Jenkins, 1984a), TH may be a potential biomarker for MR. In support of this concept, there was a tendency for concentrations of T_4 in plasma to differ in Angus cows classified as high, moderate, or low MR (Cooper-Prado et al., 2014). Plasma concentrations of T_3 and T_4 were positively correlated with RFI classification in Angus heifers (Walker et al., 2015). However, concentrations of T_4 were not influenced by MR in ad libitium fed mice (Kgwatalala and Nielsen, 2004). Body temperature is influenced by thyroid status of cattle. Rectal temperatures were increased in T_3 induced hyperthyroid Brahman cows compared with hypo- or euthyroid controls (De Moraes et al., 1998). Similarly, TRH increased core body temperature in hamsters (Schuhler et al., 2007). Thus, changes in body temperature may impact the relationship between TH and MR.

Thyroid hormones influence reproduction in cattle. Hyperthyroid, Brahman cows had an increased incidence of anestrous compared with hypo- and euthyroid cows (De Moraes et al., 1998). In contrast, cyclic cows had greater serum concentrations of T_4 compared with anestrous cows (Flores et al., 2008). Follicular dynamics and serum concentrations of progesterone were not affected by thyroid status of Brahman cows (De Moraes et al., 1998). Serum concentrations of T_3, but not T_4, were positively correlated with largest follicle diameter (Flores et al., 2008). Feed intake influences secretion of thyroid hormones and ovarian activity (Ciccioli et al., 2003). Thyroid hormones directly influence ovarian activity and likely serve in a multihormonal complex that regulates follicular steroidogenesis in cattle (Spicer et al., 2001). Thyroid hormones also influence secretion of luteinizing hormone and follicle stimulating hormones in beef cows (Stewart et al., 1994b), but do not influence estrous behavior or length of estrous cycle in beef heifers (Stewart et al., 1994a). Increased concentrations of T_4, dominant follicle size, and decreased postpartum interval occurred in well conditioned, Angus cows on a high plane of nutrition compared with thinner cows or cows receiving lesser amounts of nutrition prior to the first postpartum estrus (Ciccioli et al., 2003). Although total serum concentrations of T_4 were greater in dairy cows with a prolonged luteal phase compared with cows exhibiting normal luteal function, dairy cows with normal luteal activity had increased serum concentrations of free T_4 compared with cows that had delayed luteal activity (Kafi et al., 2012). This indicates that concentrations of free and total T_3 and T_4 need to be evaluated to better understand TH physiology.

Thyroid hormones are critical for milk secretion in lactating cattle. Thyroxine increased milk production in dairy cows in thermoneutral and elevated ambient temperatures (Yousef and Johnson, 1966). During lactation, mammary glands of dairy cows maintain a euthyroid state due to increased 5'-deiodination of T_4, while the remainder of the body is hypothyroid as T_4 conversion to T_3 is reduced (Tucker, 2000). Concentrations of T_3 and T_4 are greater in heifers with increased potential for milk production (Bitman et al., 1984) and milk yield was increased by 10 to 40% after treatment with thyroxine (Meites, 1961; Bauman and McCutcheon, 1984).

Thyroxine increased lactose and fat yield in milk and plasma glucose in Jersey cows (Davis et al., 1988).

Genes regulating lipid homeostasis

Although lean mass, not adipose, is a primary determinant for MR of cattle (Thompson et al., 1983) and rats (Pullar and Webster, 1977), evaluation of adipose stores is important as the kinetics of energy utilization are influenced by tissue mobilization (Berry and Crowley, 2013). Adipose tissue has the lowest priority for nutrients and indicates a greater potential for adipose tissue mobilization when nutrients are limited (Hammond, 1952). Transcription of *PPARG* is essential for adipocyte differentiation (Rosen and Spiegelman, 2006) and *PPARG* binds PPAR response elements to stimulate expression of adipogenic genes (Colin et al., 1995; Lemberger et al., 1996; Hausman et al., 2009). In cattle, sterol regulatory element binding factor 1 (*SREBF1*) is a well established target of *PPARG* (Hausman et al., 2009; Kadegowda et al., 2009; Graugnard et al., 2010). The SREB transcription factors are global regulators of lipid homeostasis by controlling expression of enzymes responsible for cholesterol, fatty acid, triacylglycerol, and phospholipid synthesis (Eberlé et al., 2004). Transcriptional activity of *SREBF1* is regulated by the interaction of THR with *SREBF1* (Yin et al., 2002). The gene products of fatty acid synthase (*Fasn*) and diacylglycerol acyltransferase 2 (*Dgat2*) function in lipogenesis and are transcriptionally regulated by the *Sreb* family in mice (Liang et al., 2002; Horton et al., 2003; Griffin et al., 2007). Decreased lipogenesis and increased lipolysis was associated with increased expression of *SREBF1* and *FASN* during early lactation in dairy cows with increased milk yield compared with cows with reduced milk yield (Khan et al., 2013). Muscle energy homeostasis is regulated by carnitine palmitoyltransferase 1B (*CPT1B*), a lipolytic gene product that is essential in catabolism of fatty acids (Eaton et al., 2001). Translocation of fatty acids to the mitochondria for β-oxidation is facilitated by *CPT1* (McGarry and Brown, 1997). Malonyl CoA is a potent inhibitor of *CPT1* and its degradation to acetyl CoA is stimulated by acetyl CoA carbocylase-1

(Huang and Freake, 1998; Clarke, 2000). Expression of FASN and DGAT2, but not CPT1B, was positively correlated with intramuscular adipose tissue deposition in Korean steers (Jeong et al., 2012).

***TH and lipid homeostasis*:** Lipid homeostasis is regulated by TH. Zhu and Cheng (2010) reviewed the influence of thyroid hormone receptors (THR) on lipid homeostasis and indicated the necessary role of TH in adipogenesis and lipid metabolism. Transcription of acetyl CoA carboxylase-1 is stimulated by T_3 (Huang and Freake, 1998). Plasma concentrations of T_3 and T_4 were correlated with mRNA expression of *CPT1A* and *CPT2* 10 wk before calving and at 4 wk postpartum (van Dorland et al., 2009). A net loss of body fat occurs in rats when increased concentrations of TH stimulate lipogenesis and lipolysis (Oppenheimer et al., 1991).

MAINTENANCE AND PERFORMANCE OF BEEF CALVES

Primary factors influencing the maintenance and performance of calves before weaning are sex of the calf, nutrition, and genetics. The effect of sex on calf growth is well established. Growth rate of bull calves is greater than steers (Marlowe and Gaines, 1958; Bailey et al., 1966; Cundiff et al., 1966). Steer calves have greater ADG compared with heifers (Marlowe and Gaines, 1958; Neville, 1962; Cundiff et al., 1966). Growth of calves was influenced by breed of cows (Reynolds et al., 1978; Freetly and Cundiff, 1998; Brown and Brown, 2002) and crossbreeding (Cundiff, 1970; Koger et al., 1975; Reynolds et al., 1978; Brown and Brown, 2002), however these are generally associated with milk production potential of cows. Breed of calf influences growth prior to weaning (Turner and McDonald, 1969; Reynolds et al., 1978; Prichard et al., 1989).

Milk yield of cows influences weaning weights of calves. Cows with increased milk yield have heavier calves at weaning. Correlations between milk yield of cows and ADG of calves range from 0.51 to 0.88 (Neville et al., 1962; Furr and Nelson, 1964; Reynolds et al., 1978;

Clutter and Nielsen, 1987; Marston et al., 1992). Milk yield of cows accounted for 60 to 66% of the variation in WW of calves (Rutledge et al., 1971; Reynolds et al., 1978; Clutter and Nielsen, 1987). Greater milk quality enhanced growth of calves prior to weaning (Brown and Brown, 2002). Supplementing creep feed increases the WW and ADG of calves at weaning (Furr and Nelson, 1964; Tarr et al., 1994) and may decrease the influence of cow milk production on WW of calves (Lusby et al., 1976; Marshall et al., 1976).

Pre-weaning growth enhances post-weaning growth of calves. Increased WW occurred in calves from beef cows with increased milk yield compared with low yielding cows (Clutter and Nielsen, 1987). Dairy calves consuming greater amounts of milk had increased BW at harvest and required fewer days on feed to achieve a targeted 12th rib fat thickness compared with calves consuming less milk prior to weaning (Abdelsamei et al., 2005). After weaning, calves from beef cows with increased milk yield maintained a 65% advantage in growth rate compared with calves from cows with lesser milk production (Clutter and Nielsen, 1987).

SUMMARY

Enhancing the production efficiency of beef cows can increase the profitability of the cow calf segment. Maintenance energy requirements account for 70% of the total energy requirement of beef cows and approximately 50% of the variation in herd profitability. Selection of cows with reduced maintenance energy requirement is feasible considering the variation and moderate heritability. Current methods for determining MR in individual cows are expensive and require substantial time and labor inputs. Identification of biomarkers for maintenance energy requirements could be utilized to identify cows with reduced MR. Potential biomarkers for maintenance energy requirement include metabolic hormones and genes that regulate adipose tissue homeostasis. Metabolic hormones including T_3, T_4, and IGF-I regulate metabolism, growth, and thermogenesis and are influenced by feed intake. The transcription factor *SREBF1* regulates expression of *FASN* and *DGAT2*, which are critical in lipogenesis, and *CPTIB*, which serves in the catabolism of lipids. Maintenance energy requirement may be influenced by activity or temperament of cows. Determining the influence of MR on calf performance is necessary, as selection for reduced MR should not result in decreased calf performance. Selection of cows with reduced MR while maintaining calf performance may enhance production efficiency in the cow calf segment. Therefore, the objectives of these experiments were to 1) estimate and describe the variation in MR of mature beef cows during mid- to late gestation, 2) determine relationships between MR of cows and concentrations of T_3, T_4, and IGF-I in plasma, 3) evaluate relationships between MR of cows and mRNA expression of TH responsive genes associated with lipid homeostasis, and 4) evaluate the influence of MR on calf performance before weaning.

CHAPTER III

MAINTENANCE ENERGY REQUIREMENTS IN MATURE BEEF COWS AND RELATIONSHIPS WITH METABOLIC HORMONES, ADIPOSE GENE EXPRESSION, AND CALF PERFORMANCE

ABSTRACT**:** Nonlactating, spring-calving Angus cows in mid to late gestation were used to determine variation in maintenance energy requirements (MR) and evaluate relationships between MR and concentrations of triiodothyronine (T_3), thyroxine (T_4), and IGF-I in plasma, genes associated with lipid homeostasis, and calf performance. Cows (4 to 7 yr of age) were evaluated in 3 yr (yr 1: n = 31; yr 2: n = 30; yr 3: n = 34) during mid to late gestation. Cows were individually fed a complete diet to meet predicted MR (NE_m; Level 1 Model; NRC, 2000). Body weight of cows was recorded twice weekly and feed intake was adjusted every 14 d until constant BW (regression analyses) was achieved for at least 28 d (maintenance). Cows in each year were classified based on MR as low (LMR; > 0.5 SD less than mean MR), moderate (MMR; ± 0.5 SD of mean MR), or high (HMR; > 0.5 SD greater than mean MR). Blood samples were collected at maintenance in each year and during early lactation in yr 1 and yr 3. During maintenance, cows (yr 2: n = 14; yr 3: n = 20) were infused with thyrotropin releasing hormone (TRH) and blood samples were collected frequently from 60 min before to 360 min after TRH infusion. Plasma concentrations of T_3, T_4, and IGF-I were quantified by RIA. Longissimus dorsi muscle (LM) of LMR and HMR cows (n = 11) was biopsied at maintenance in yr 3. Relative mRNA abundance for sterol regulatory element binding factor 1 (*SREBF1*), fatty acid synthase (*FASN*), diacylglycerol acyltransferase 2 (*DGAT2*), and carnitine palmitoyltransferase 1B (*CPT1B*) was evaluated. Maintenance energy requirement (Kcal•kg $BW^{0.75}$•d^{-1}) of cows was 81.0 ± 1.8, 83.1 ± 1.6, and 88.1 ± 1.3 in yr 1, 2, and 3, respectively. Body weight, BCS, and daily plasma concentrations of T_3, T_4, and IGF-I in cows were not influenced by MR. After infusion of TRH in yr 2, mean plasma concentrations of T_4 were greater ($P < 0.001$) in MMR compared with LMR cows, which were greater than in HMR cows and T_3:T_4 was greater ($P = 0.004$) in HMR cows compared with LMR and MMR cows. In yr 3, LMR cows had greater ($P = 0.001$) plasma concentrations of T_3 compared with HMR cows after TRH infusion. Low MR cows had greater ($P = 0.04$) expression of *FASN* mRNA compared with HMR cows. Performance of calves before weaning was not influenced ($P \geq 0.37$) by MR of cows. Thyroid hormones, IGF-I, and lipogenic genes may be components of potential biomarkers for MR of cows. Identification of biomarkers for MR may allow for selection of cows with reduced MR.

Key words: beef cattle, maintenance energy requirements, thyroid hormones

INTRODUCTION

The increased cost of beef production has renewed interest in enhancing efficiency in the cow-calf segment of the industry. Maintenance energy requirements (MR) account for approximately 70% of the total energy required by cows (Ferrell and Jenkins, 1984b). Maintenance energy requirement (NE_m) varies in beef cattle (DiCostanzo et al., 1990; Johnson et al., 2003a; Cooper-Prado et al., 2014). Metabolizable energy for maintenance is moderately heritable (ME_m; Carstens et al., 1989; Hotovy et al., 1991). Despite the potential for enhanced efficiency when cows are selected for reduced MR, biomarkers for MR have not been identified.

Metabolic hormones including triiodothyronine (T_3), thyroxine (T_4), and IGF-I regulate many biological process and may contribute to variation in MR. Plasma concentrations of T_4 and

IGF-I are influenced by nutrient intake in cattle (Richards et al., 1995; Ciccioli et al., 2003; Lents et al., 2005). Plasma concentrations of T_4 in beef cows were correlated with MR (Cooper-Prado et al., 2014). Insight to the mechanisms regulating energy utilization may occur by evaluating the expression of genes associated with lipid homeostasis. Lipid homeostasis is regulated by *SREBF* transcription factors (Eberlé et al., 2004), lipogenic enzymes including FASN and DGAT2 (Liang et al., 2002; Horton et al., 2003; Griffin et al., 2007), and lipolytic enzymes including CPT1B (Eaton et al., 2001), however relationships with energetic efficiency remain unclear. Therefore, the objectives of these experiments were to 1) estimate and describe the variation in MR of mature beef cows during mid- to late gestation, 2) determine relationships between MR of cows and concentrations of T_3, T_4, and IGF-I in plasma, 3) evaluate relationships between MR of cows and expression of genes associated with lipid homeostasis and cow temperament, and 4) evaluate the influence of MR on calf performance before weaning.

MATERIALS AND METHODS

Animal management

All experimental procedures used in this study were approved by the Oklahoma State University Animal Care and Use Committee (AG091). Non-lactating, spring calving, Angus cows were assigned to the experiments during 3 yr to determine the influence of MR on cow physiology and calf performance prior to weaning. Cows were AI to a single sire during 3 wk each year and exposed to bulls 15 d after AI. Pregnancy was determined by fetal heartbeat at 31 ± 2 d after AI using ultrasonography (Aloka 500-V with a 7.5-MHz probe; Corometrics Medical Systems; Wallingford, CT). At the initiation of MR determination, nonlactating cows weighed 568.3 ± 8.4 kg (BCS: 4.7 ± 0.1; n = 31), 555.0 ± 8.4 kg (BCS: 4.4 ± 0.1; n = 30), and 571.9 ± 9.6 kg (BCS: 4.8 ± 0.1; n = 34) during yr 1, 2, and 3, respectively. Cows were 160 ± 3, 143 ± 2, and 173 ± 1 d of gestation at the initiation of the MR determination (November to December). Plasma hormones and calf performance were evaluated each year. After cows were challenged with TRH, thyroid hormones were evaluated in yr 2 and 3, and ruminal temperature of cows was evaluated in yr 2. In yr 3, gene expression was evaluated in longissimus dorsi (LM) and cow temperament was characterized.

Estimation of maintenance energy requirements

Cows were maintained in a 0.25 ha dry lot and individually fed a complete diet once daily at 0730 h and ad libitum water. The diet (as fed) consisted of rolled corn (38%), alfalfa pellets (35%), cottonseed hulls (12%), soybean meal (4%), cane molasses (3%), salt (0.2%), and vitamin A-30 (0.01%). Diets were calculated to provide 11.2% crude protein and 1.44 Mcal/kg NE_m. Feed samples were collected weekly, stored at -20°C, and composited at the end of study each year. Composited feed samples were ground in a Wiley Mill through a 2 mm screen prior to analyses (near infrared reflectance spectroscopy; Dairy One, Inc.; Ithaca, NY). Rations were analyzed for NE_m and CP content (as fed) and were 1.67 Mcal/kg and 12.5% in yr 1, 1.64 Mcal/kg and 12.9% in yr 2, and 1.66 Mcal/kg and 12.8% in yr 3. Cows had water ad libitum and mineral supplement (46.1% NaCl, 50.0% dicalcium phosphate, 0.4% copper sulfate, 0.5% zinc oxide, and 3.0% mineral oil) was offered at a target consumption of 113 $g \cdot cow^{-1} \cdot d^{-1}$.

Cows were adapted to the ration for at least 8 d prior to feeding predicted MR (NRC, 2000). Body weight and BCS (1 = emaciate and 9 = obese; Wagner et al., 1988) of cows was determined after adaptation to the diet. After adaptation, individual diets were adjusted to meet Level 1; NRC (2000) estimated maintenance requirements. Maintenance requirements were evaluated for 88 d, 101 d, and 91 d in yr 1 yr 2, and yr 3, respectively. To determine energy requirements for body weight stasis, body weight of cows was determined twice weekly following deprivation of feed (23 h) and water (7 h). Day relative to NRC predicted MR feeding, day of gestation, and daily mean ambient temperature during the 3 d prior to BW determination were regressed on body weight of individual cows to determine changes in cow BW. Only cows with constant BW, defined as having non-significant ($P > 0.10$) linear regression of BW during

28 or more days, were used in analyses. As described by Jenkins and Ferrell (2007), differences in MR can be determined when cows achieve BW equilibrium at constant amounts feed intake. Environmental data was recorded daily (www.mesonet.org) from a weather station 8 km from the experimental site. In yr 1, constant body weight was achieved in 15 cows by 60 d on feed, 20 cows by 70 d on feed in yr 2, and 26 cows by 59 d on feed in yr 3. Cows with a linear regression ($P < 0.10$) of BW on the covariates during the last 28 d of evaluation of MR were excluded from subsequent analyses. This resulted in the exclusion of 16, 10, and 8 cows in yr 1, 2, and 3, respectively. Maintenance energy requirement is defined as the amount of dietary energy intake resulting in no net gain or loss of energy from body tissues (NRC, 2000). Cows were classified by MR as low (LMR, > 0.5 SD less than the yearly mean MR), moderate (MMR; ± 0.5 SD of the yearly mean MR), and high (HMR; > 0.5 SD greater than the yearly mean MR).

After determination of MR, cows were maintained as a group on native range pasture (*Andropogon scoparius*, *Andropogon gerardii*) and received supplemental protein and hay as needed according to their physiological status and pasture availability. Cows received approximately 1.4 kg/d of a 38% CP supplement after determination of MR until parturition. After calving, cows grazed native range pasture and protein supplementation (38 % CP) was increased to 1.8 kg/d. Calves had continuous access to cows except when separated for 7 h for determination of shrunk BW. Body weights at birth and weaning were recorded for calves each year. Calves were weaned at 182 ± 4 d of age in yr 1, 209 ± 3 d of age in yr 2, and 210 ± 1 d of age in yr 3.

Blood samples and hormone assays

Blood samples were collected by caudal venipuncture at maintenance in all years and during early lactation in yr 1 and 3. Cows were sampled 7 d after maintenance was established at 0700 h [after feed (23 h) and water (7 h) deprivation], and at 1400 h [6 h after consumption of feed and ad libitum water] in yr 1. Cows were sampled twice daily at 37 d postpartum on two consecutive days (early lactation) in yr 1. Cows were sampled at 0800 h, immediately after removal from native range pasture and water access, and maintained in a dry lot and deprived of feed and water (7 h) prior to sampling at 1500 h. Cows were returned to native range pasture overnight and sampling procedures were repeated on the second day. In yr 2, blood samples were obtained from cows at maintenance for 30 d, and before parturition at 7 and 22 d after realimentation to pasture at times of day described for yr 1. In yr 3, blood samples were collected after cows were at MR for 20 d and at 28 ± 1 d post partum (early lactation) at times of day described for yr 1. Additional blood samples were collected, prior to tissue biopsy, from LMR and HMR cows when cows were at maintenance for 30 d.

Samples were collected in Monoject blood collection tubes containing EDTA (Tyco Healthcare Group, LP; Mansfield, MA) and stored on ice. Plasma was aspirated from blood samples within 3 h of sampling after centrifugation for 20 min at 2,500 g and 4 °C. Plasma was stored at -20 °C until analyzed. Plasma concentrations of IGF-I in plasma were determined following acid ethanol extraction (16 h at 4°C) by RIA (Echternkamp et al., 1990). Samples for each year were analyzed in an assay. Intraassay coefficients of variation were 10%. Analysis of variance with sample and assay was used to determine coefficient of variation as calculated from estimated mean squares. To determine plasma concentrations of T_3 and T_4, samples for each year were blocked by MR classification and cow, and each assay contained a similar number of cows for each MR (LMR, MMR, and HMR. Three assays were conducted for yr 1, 4 assays for yr 2, and 5 assays for yr 3, for both T_3 and T_4. Total concentrations of T_4 in plasma were determined by solid phase RIA for humans (Coat-A-Count Total T_4 kit, Diagnostic Products Corp., Los Angeles, CA; Ciccioli et al., 2003). Intra- and interassay coefficients of variation (n = 12 assays) were 8 and 16%, respectively. Total plasma concentrations of T_3 in plasma were determined by solid phase RIA for humans (Coat-A-Count Total T_3 kit, Diagnostic Products Corp., Los Angeles, CA). The addition of 0.2, 0.5, 1.0, and 2.0 ng/mL of triiodothyronine (n = 3) to plasma resulted in the recovery of 95, 106, 105, and 99 %, respectively. When 37.5, 50, and 75 μL of bovine plasma were assayed, the concentrations of triiodothyronine (T_3) were parallel to the standard curve. Intra- and interassay coefficients of variation (n = 12 assays) were 6 and 18%, respectively.

TRH challenge

Cows were administered thyrotropin releasing hormone (TRH; Sigma Aldrich Chemical Company; St. Louis, MO) to maximize differences in T_3 and T_4. In yr 2, 14 cows (LMR: n = 5; MMR: n = 5; HMR: n = 4) that had maintained BW for an average of 16 d were stratified by MR and randomly assigned to one of two treatment days occurring 1 d apart. Cows were sampled in two groups to minimize variation in sample collection time. Cows were administered 0.33 μg TRH/ kg BW into the jugular vein within 30 min after daily feeding. Blood samples were collected by caudal venipuncture at 0, 30, 60, 90, 120, 150, 180, and 210 min after TRH challenge in yr 2 and 0, 30, 60, 90, 120, 150, 180, 240, 300, and 360 min after TRH treatment in yr 3. Rectal temperature (RT) was recorded at 0, 30, 60, 90, 120, 150, 180, 210, 240, 300, and 360 min after TRH treatment. Rectal temperatures were recorded at a depth of 12 cm using a digital thermometer (Model M216; G.L.A. Agricultural Electronics; Montclair, CA). In yr 3, cows (LMR: n = 9; MMR: n = 5; HMR: n = 6) that had maintained constant BW for an average of 20 d were stratified by MR, randomly assigned to one of two sequential treatment days, and sampled as described as described for yr 2.

Tissue biopsy

Muscle samples were obtained from the Longissimus dorsi of six LMR and six HMR cows in yr 3. Biopsies were performed after cows consumed actual MR and maintained constant BW for 31 d. Biopsies were performed as described by Winterholler et al. (2008). Longissimus muscle was selected due to the differing metabolism and reduced sensitivity of intramuscular adipose tissue to dietary manipulations compared with subcutaneous adipose tissue (Smith and

Crouse, 1984). Approximately 1 g of tissue was collected from each cow using a sterile biopsy needle. Biopsies were taken approximately 8 cm lateral to the vertebrae and 10 cm caudal to the last rib. Tissues were harvested from each cow and immediately frozen in liquid nitrogen. Biopsies were performed within 3.5 h and tissues were stored at -80°C until analyzed.

Gene expression analyses

Total RNA was isolated from muscle tissues using TRI-reagent (Sigma Aldrich Chemical Company; St. Louis, MO) following the manufacturer's protocol. Quantitation of total RNA was determined in 1.0 μL aliquots using a NanoDrop® ND-1000 spectrophotometer (260 nm; NanoDrop Technologies, Wilmington, DE) and purity was determined as the ratio of 260/280 nm and acceptable values occurred between 1.8 and 2.2. RNA quality was determined by gel electrophoresis.

Quantitative real-time PCR (qRT-PCR) was used to determine mRNA expression of sterol regulatory element binding factor 1 (*SREBF1*), fatty acid synthase (*FASN*), diacylglycerol acyltransferase 2 (*DGAT2*), and carnitine palmitoyltransferase 1B (*CPT1B*) relative to glyceraldehyde-3-phosphate dehydrogenase (*GAPDH*). Primers for target genes and endogenous controls are presented in Table 1. Selected primers were previously validated (Lancaster et al., 2014) and each primer pair was evaluated for complementarity of forward and reverse primer sequences using OligoAnalyzer 3.1 (Integrated DNA Technologies, Coralville, IA).

Amplification of cDNA via qRT-PCR was conducted using an iTaq Universal SYBR Green One-Step kit (Bio-Rad Laboratories; Hercules, CA). Optimized qRT-PCR reactions for *FASN*, and *DGAT2* contained 10 μL of iTaq Universal SYBR Green Reaction Mix (2x; Bio-Rad Laboratories), 0.25 μL iScript reverse transcriptase, 1.6 μL of 25 μM forward primer (400 nM), 1.6 μL of 25 μM reverse primer (400 nM), and 5.0 uL of RNA (200 ng). Optimized qRT-PCR reactions for *SREBF1*, *CPT1B*, and *GAPDH* contained 10 μL of iTaq Universal SYBR Green

Reaction Mix (2x), 0.25 μL iScript reverse transcriptase, 1.6 μL of 25 μM forward primer (200 nM), 1.6 μL of 25 μM reverse primer (200 nM), and 5.0 uL of RNA (100 ng). Reaction mixes were brought up to 20 μL total volume with RNase free water. Reactions were conducted using a CFX96 Real Time PCR detection system (Bio-Rad Laboratories). Thermal cycling parameters were 50°C for 10 min during reverse transcription, 95°C for 1 min for polymerase activation and DNA denaturation, followed by 45 cycles of 95°C for 10 sec for denaturation, and optimum annealing temperature for 30 sec. Following amplification, a melt curve analysis was performed to verify the specificity of the reaction. For each gene, melting peaks were evaluated for a single (± 0.5°C) melt peak to ensure amplification of a unique product. Amplifications resulting in more than one melt peak were omitted. Because the total number of samples was greater than the 96-well plate capacity, samples for each gene were amplified on a single plate and individual samples were run in duplicate.

Gene expression was evaluated by setting an arbitrary threshold (Ct) on log transformed SYBR curves in the geometric portion of the qRT-PCR amplification plot. Comparative threshold cycle methods were used for relative quantification of target gene mRNA (Voge et al., 2004a; Voge et al., 2004b; Spicer and Aad, 2007). Briefly, threshold cycle (Ct) values of each target gene were subtracted from Ct of endogenous control genes (ΔCt). The ΔΔCt was determined as the greatest ΔCt (least expressed unknown) minus individual ΔCt values. Relative abundance in mRNA expression was determined as $2^{-\Delta\Delta Ct}$ (Voge et al., 2004a; Voge et al., 2004b).

Cow temperament

Cow temperament was evaluated in yr 3 after cows were acclimated to the handling process by movement through the chute for 13 wk during biweekly BW measurements that commenced at the initiation of the trial. Cows were at MR for 29 d prior to evaluation of temperament. Cows were randomly allotted to one of six pens (32 m^2) with an average of 5 cows per pen. Temperament of cows was assessed by pen score, chute score, and exit velocity. Pen score was based on a 5 point scale where 1= calm, no movement; 2 = restless, slight shifting; 3 = nervous, frequent movement; 4 = flighty, agitated; 5 = aggressive. Cows were observed in pens from a distance of 5 m for 10 min then approached by a handler. After cows were observed in the pen, cows were obliged to move through an alley into a chute and restrained in a headgate. Chute score was assessed on a 5-point scale where 1 = calm, no resistance; 2 = restless, occasional shifting; 3 = nervous, frequent movement; 4 = flighty, constant movement; 5 = aggressive, struggling movement. Pen and chute scores were similar to those described by Voisinet et al. (1997). Exit scores were assigned upon release from the chute as 1 = walk; 2 = trot; 3 = run. Evaluations of temperament were independently observed by two trained observers and averaged prior to analyses. Because all cows observed during the experiment were well adapted to the handling procedures and aggression was not observed during the experiments, pen scores of 4 and 5, and chute scores of 5 were not assigned to any cow.

Calf performance

Calving occurred 35 ± 4 d (range: 7 to 70 d), 35 ± 3 d (range: 11 to 58 d) and 14 ± 1 d (range: 5 to 31 d) after cows were at maintenance in yr 1, 2 and 3, respectively. Body weight of calves was recorded within 24 h of birth. Calves remained with cows until weaning at 182 ± 4 d of age in yr 1, 209 ± 3 d of age in yr 2, 210 ± 1 d of age in yr 3. Weaning weights (WW) were adjusted to 205 d of age and 205 d WW was used for determination of ADG of calves. One calf died at birth in yr 1 and was omitted from calf performance. One calf in yr 1, 2 calves in yr 2, and 1 calf in yr 3 died prior to weaning and were omitted from analyses of WW and ADG.

Statistical analyses

Data were analyzed by year using a completely randomized design. Initial BW, BCS, and age of cows were analyzed using a mixed models method (PROC MIXED) with MR as a fixed effect. A mixed models method was used to evaluate the effects of MR and physiological status (maintenance, early lactation, and weaning) on body weight and BCS of cows with cow within treatment as a repeated measure.

A mixed models method was used to evaluate the relationships between MR, fed status, and physiological status on plasma concentrations of T_3, T_4, T_3:T_4, and IGF-I plasma with assay and experimental day (where appropriate) as random effects. Plasma concentrations of T_3, T_4, T_3:T_4, and ruminal temperature after TRH challenge were analyzed with 10 unequally spaced repeated measures of time using mixed models methods. Polynomial response curves of appropriate order were fitted and evaluated for heterogeneity of regression when MR x time interaction was significant (Snedecor and Cochran, 1968) to evaluate MR effects.

Relative fold change of mRNA abundance was analyzed using a general linear models method (PROC GLM; SAS) with MR as a fixed effect. Calf performance data analyzed using a mixed models method with sex of calves as a covariate and year as a random effect. Fishers LSD was used to make preplanned comparisons between means when significant ($P = 0.05$) F-test occurred. Linear relationships among response variables were determined using PROC CORR and PROC REG (SAS). Correlations between MR, plasma hormones, BW, BCS, and temperament of cows were evaluated using PROC CORR (SAS). Data were analyzed using the SAS software (version 9.2). Copyright, SAS Institute Inc. SAS and all other SAS Institute Inc. product or service names are registered trademarks or trademarks of SAS Institute Inc., Cary, NC, USA. Nominal significance level was established at $P = 0.05$.

RESULTS

Trial duration and environmental conditions

Cows were fed a complete diet for 88 d in yr 1, 101 d in yr 2, and 91 d in yr 3 to determine MR (Figure 1). Constant BW was achieved for at least 28 d in yr 1 (n = 15), 31 d in yr 2 (n = 20), and 32 d in yr 3 (n = 26). Maintenance of BW occurred at 218 ± 4, 213 ± 2, and 232 ±

1 d of gestation in yr 1, 2, and 3, respectively. Daily minimum (Tmin), mean (Tamb), and maximum (Tmax) ambient temperature and relative humidity are in Table 2. In yr 1, daily Tamb averaged 5.3 ± 0.7 and 4.8 ± 0.9°C during the NRC adjustment period and at maintenance, respectively. Daily ambient temperatures ranged from -3.0 ± 1.0 to 13.2 ± 0.9°C when cows were at maintenance in yr 1. One d during the NRC adjustment period had a Tmax of 0°C or less. In yr 2, mean daily Tamb during NRC adjustment was 10.1 ± 0.8°C and was 1.2 ± 0.9°C during maintenance. Daily ambient temperatures ranged from -6.2 ± 1.0 to 9.1 ± 1.1°C at maintenance in yr 2. There were 3 d during yr 2 when Tmax was 0°C or less during maintenance. During the NRC adjustment period, mean daily Tamb was 1.7 ± 0.9°C and was 0.3 ± 1.1°C when cows were at maintenance in yr 3. Daily ambient temperature ranged from -6.6 ± 1.0 to 7.1 ± 1.5°C during maintenance in yr 3. Daily Tmax was 0°C or less on 8 d at maintenance in yr 3.

Energy requirements at maintenance

Daily MR of cows maintaining constant BW was 81.0 ± 1.8 Kcal•kg $BW^{0.75}$•d^{-1} in yr 1 (Figure 2). The percent difference between the cow with the greatest and least MR was 31% and the CV for MR was 8.5%. In yr 2, the mean daily MR during the maintenance period was 83.1 ± 1.6 Kcal•kg $BW^{0.75}$•d^{-1} (Figure 3). Cows with the greatest and least MR differed by 41% and the CV for MR was 8.5%. Cows maintaining BW in yr 3 had a MR of 88.1 ± 1.3 Kcal•kg $BW^{0.75}$•d^{-1} (Figure 4). A 32% difference occurred between cows with the greatest and least MR and the CV for MR was 6.4%.

Actual energy requirements for maintenance of BW differed (Table 3) for LMR, MMR, and HMR cows each year. Maintenance energy requirements were greater in HMR cows (P < 0.001; 90.9 ± 1.4 Kcal•kg $BW^{0.75}$•d^{-1}) than in MMR cows (79.2 ± 1.1 Kcal•kg $BW^{0.75}$•d^{-1}) which were greater (P = 0.04) than LMR cows (75.3 ± 1.2 Kcal•kg $BW^{0.75}$•d^{-1}) in yr 1. In yr 2, HMR cows had greater (P < 0.001; 91.1 ± 1.3 Kcal•kg $BW^{0.75}$•d^{-1}) MR compared with MMR cows (84.0 ± 0.9 Kcal•kg $BW^{0.75}$•d^{-1}) and MMR cows had greater (P < 0.001) MR than LMR cows and

LMR cows (73.3 ± 1.3 Kcal•kg $BW^{0.75}$•d^{-1}). Maintenance energy requirements in yr 3 were greater in HMR cows (P < 0.001; 94.3 ± 1.1 Kcal•kg $BW^{0.75}$•d^{-1}) compared with MMR cows (87.1 ± 1.3 Kcal•kg $BW^{0.75}$•d^{-1}) and MR were greater (P < 0.001) MMR than in LMR cows (83.6 ± 1.0 Kcal•kg $BW^{0.75}$•d^{-1}). Metabolic body weight ($BW^{0.75}$) of LMR, MMR, and HMR cows at maintenance did not differ (Table 3; $P \geq 0.28$) in any year. Cows with HMR tended (P = 0.09) to be older (9.5 ± 0.6 yr of age) compared with LMR (7.8 ± 0.5 yr of age) and MMR cows (7.8 ± 0.5 yr of age) in yr 1. Age of cows did not differ ($P \geq 0.79$) between LMR, MMR, and HMR cows in yr 2 and 3.

Maintenance classification of cows influenced the deviation in MR from NRC requirements. In yr 1, HMR cows required 12.9 ± 1.6 Kcal•kg $BW^{0.75}$•d^{-1} more energy at maintenance (Figure 5; P < 0.001) compared with NRC estimates of NE_m, whereas NRC estimates of NE_m and actual requirements for LMR and MMR cows did not differ ($P \geq 0.11$; 0.3 ± 1.3 and 2.3 ± 1.5 Kcal•kg $BW^{0.75}$•d^{-1}, respectively). In yr 2, energy requirements for MMR and HMR cows were greater (P < 0.001; 7.8 ± 1.1 and 12.8 ± 1.6 Kcal•kg $BW^{0.75}$•d^{-1}, respectively) compared with NRC estimated requirements. Requirements of LMR cows in yr 2 were less (P = 0.03; -3.9 ± 1.6 Kcal•kg $BW^{0.75}$•d^{-1}) than NRC requirements. In yr 3, HMR cows had greater energy requirements (P < 0.001; 9.6 ± 1.2 Kcal•kg $BW^{0.75}$•d^{-1}) compared with NRC estimates of NE_m, however, maintenance requirements for LMR (-0.31 ± 1.2 Kcal•kg $BW^{0.75}$•d^{-1}) and MMR cows (2.1 ± 1.3 Kcal•kg $BW^{0.75}$•d^{-1}) did not differ from NRC estimates.

Body weight and BCS

Body weight and BCS were not influenced ($P \geq 0.20$) by MR at the commencement of feeding, during maintenance of BW, early lactation, or weaning in yr 1 (Table 4). At the initiation of the trial, during maintenance of BW, early lactation and weaning in yr 2, BW did not differ ($P \geq 0.28$) among MR (Table 5). During maintenance of BW in yr 2, there was a tendency (P = 0.09) for greater BCS in LMR (4.4 ± 0.2) and HMR (4.4 ± 0.2) cows compared with MMR cows (3.9 ± 0.1). Body condition score was not influenced (*P* ≥ 0.41) by MR at trial commencement, early lactation, and weaning in yr 2. In yr 3, BW and BCS were not affected (*P* ≥ 0.13) by MR of cows (Table 6). Each year cows gained BW from the final day of maintenance of BW until weaning. Change in BW differed (*P* = 0.004; Table 4) among MR from the initiation of the trial to maintenance of BW in yr 1; BW increased in LMR cows (7.2 ± 6.1 kg), and decreased in MMR (-12.3 ± 5.6 kg) and HMR cows (-32.5 ± 6.8 kg). Cows classified as LMR had the greatest change in BW (*P* = 0.004; -43.5 ± 8.2 kg) compared with MMR (-6.4 ± 7.5 kg) and HMR cows (5.0 ± 9.2 kg) between maintenance of body weight and early lactation in yr 1. Change in BW from the initiation of the trial to maintenance of body weight in yr 2 differed (*P* = 0.05; Table 5) between LMR (7.2 ± 5.6 kg) and HMR cows (-13.9 ± 5.6 kg), however BW change in MMR cows (-5.7 ± 4.0 kg) did not differ from LMR or HMR cows. From maintenance of body weight to early lactation, MMR cows gained BW (*P* = 0.05; 16.9 ± 6.7 kg) compared with LMR (-9.5 ± 9.4 kg) and HMR cows (-8.8 ± 10.5 kg) in yr 2. Body weight increased from the initiation of the trial to maintenance of BW in LMR (*P* = 0.05; 8.5± 4.2 kg) compared with HMR cows (-8.2 ± 4.9 kg), and BW change in MMR cows did not differ (*P* ≥ 0.10; 2.8 ± 5.2 kg) from LMR and HMR cows (Table 6). Changes in BCS were not influenced (*P* ≥ 0.12) by MR of cows in any year.

Thyroid hormones

Concentrations of T_3 and T_4 in plasma were not influenced by the MR x fed status interaction (Figure 6; *P* = 0.98, 0.93), MR (*P* = 0.34, 0.24, respectively), or fed status (*P* = 0.79, 0.45, respectively) when cows maintained BW in yr 1. When cows maintained BW, T_3:T_4 was not affected by MR (Figure 7; *P* = 0.52) or fed status (*P* = 0.57) in yr 1. Maintenance energy requirements did not influence (Figure 8; *P* = 0.72, 0.20) plasma concentrations of T_3 and T_4 during maintenance in yr 2. There was a tendency (Figure 9; *P* = 0.06) for greater T_3:T_4 in HMR cows (0.018 ± 0.002) compared with LMR (0.014 ± 0.002) and MMR (0.014 ± 0.002) cows during maintenance of constant BW in yr 2. Plasma concentrations of T_3 and T_4 were not influenced ($P = 0.65$, 0.70, respectively) by MR while cows maintained constant BW in yr 3 (Figure 10). The T_3:T_4 did not differ ($P = 0.85$) due to MR of cows and averaged 0.010 ± 0.001 in yr 3 (Figure 11). Plasma concentrations of T_3 and T_4 and the T_3:T_4 were not influenced (Table 7; $P \leq 0.15$) by MR of cows when muscle tissues were biopsied in yr 3.

Maintenance energy requirement x fed status did not influence ($P \geq 0.33$) concentrations of T_3 and T_4, in plasma or T_3:T_4 during early lactation in yr 1. During early lactation, concentrations of T_3 and T_4 in plasma were not affected (Figure 12; $P \geq 0.24$) by MR or fed status of cows in yr 1. Fed status and MR did not influence (Figure 13; $P \geq 0.12$) the T_3: T_4 in cows during early lactation of yr 1. Concentrations of T_3 and T_4 in plasma were not affected (Figure 14; $P = 0.38$, 0.87, respectively) by MR of cows during early lactation in yr 3. The T_3: T_4 did not differ ($P = 0.93$) due to MR of cows during early lactation in yr 3 (Figure 15). Body weight and BCS of cows at maintenance, early lactation, and weaning, and MR of cow at maintenance, adjusted for year, were not correlated (Table 8; $P \geq 0.15$) with concentrations of T_3, T_4, and T_3:T_4 in plasma during maintenance. Plasma concentrations of T_3, adjusted for year, were correlated ($P < 0.001$) with plasma concentrations of T_4 during maintenance (r = 0.72) and at early lactation ($P = 0.99$).

IGF-I

Plasma concentrations of IGF-I were not influenced by the interactions between MR, fed status, and physiological state (Figure 16; $P \geq 0.11$) or by MR and fed status of cows ($P \geq 0.18$) during maintenance of yr 1. Concentrations of IGF-I in plasma were greater ($P < 0.001$; 22.6 ± 1.3 ng/mL) in cows during maintenance than during early lactation (6.7 ± 1.0 ng/mL). The MR x physiological state interaction did not influence ($P = 0.16$) concentrations of IGF-I in plasma of cows in yr 2. There was a tendency for greater plasma concentrations of IGF-I (Figure 17; $P = 0.07$) in MMR cows (22.1 ± 2.2 ng/mL) compared with LMR (15.5 ± 3.1 ng/mL) and HMR cows

(13.6 ± 3.1 ng/mL) in yr 2. Plasma concentrations of IGF-I were greater ($P < 0.001$; 21.3 ± 1.8 ng/mL) when cows consumed maintenance diets compared with when cows were realimented to ad libitum pasture (7 d: 15.8 ± 1.7 ng/mL; 22 d: 14.2 ± 1.7 ng/mL). In yr 3, plasma concentrations of IGF-I were not influenced ($P \geq 0.17$) by the MR x physiological status and MR of cows (Figure 18). Plasma concentrations of IGF-I were greater when cows consumed maintenance diets ($P = 0.002$; 16.1 ± 2.7 ng/mL) compared with when cows were realimented to pasture during early lactation (6.6 ± 1.9 ng/mL) in yr 3. Concentrations of IGF-I in plasma were not correlated (Table 8; $P \geq 0.16$) with BW, BCS, metabolic BW, NRC estimated MR, and actual MR of cows at maintenance and BW at early lactation and weaning. There was a tendency for plasma concentrations of IGF-I to be correlated with BCS of cows at early lactation (r = 0.29; $P = 0.06$) and at weaning (r = 0.29; $P = 0.06$). During maintenance, plasma concentrations of IGF-I were correlated ($P = 0.05$) with T_3, but not ($P \geq 0.27$) with plasma concentrations of T_4 or T_3:T_4. Plasma concentrations of IGF-I, adjusted for year, were correlated (P < 0.001) with plasma concentrations of T_3, T_4, and T_3:T_4 during early lactation.

TRH challenge

Concentrations of T_3 and T_4 in plasma, T_3: T_4, and RT were not affected ($P \geq 0.65$) by the MR x time interaction after the TRH challenge in yr 2. Mean concentrations of T_3 in plasma tended to be greater (Figure 19; $P = 0.08$) in MMR (0.66 ± 0.03 ng/mL) cows compared with LMR (0.62 ± 0.03 ng/mL) cows; HMR cows (0.63 ± 0.03 ng/mL) had similar ($P \geq 0.25$) concentrations of T_3 in plasma compared with LMR or MMR cows. After administration of TRH, concentrations of T_3 in plasma increased linearly ($P < 0.001$). A cubic response curve was the best fit for concentrations of T_4 in plasma after TRH (Figure 20). After TRH, plasma concentrations of T_4 were greater in MMR ($P < 0.001$; 44.2 ± 2.8 ng/mL) compared with LMR cows (39.8 ± 2.8 ng/mL), and LMR cows had greater concentrations ($P < 0.001$) than in HMR cows (36.7 ± 2.8 ng/mL). The T_3: T_4 was best fit by a linear regression equation and was not affected (Figure 21; $P = 0.65$) by time relative to TRH administration. The T_3: T_4 after TRH was greater in HMR cows ($P \leq 0.002$; 0.017 ± 0.001) compared with LMR (0.015 ± 0.001) and MMR cows (0.015 ± 0.001). Rectal temperature increased ($P < 0.001$) after administration of TRH and was best fit by a cubic regression equation. Mean RT from 0 to 360 min after TRH administration was greater in LMR cows (Figure 22; $P < 0.001$; 38.85 ± 0.10°C) compared with HMR (38.69 ± 0.11°C) and MMR cows (38.65 ± 0.10°C).

In yr 3, concentrations of T_3 and T_4 in plasma and T_3: T_4 were not influenced ($P \geq 0.76$) by the MR x time interaction. There was a quadratic response ($P < 0.001$) for concentrations of T_3 in plasma after TRH administration. Maintenance requirement of cows influenced (Figure 23; $P = 0.001$) plasma T_3 in yr 3 and concentrations after TRH were greater in LMR cows (0.64 ± 0.03 ng/mL) than in HMR (0.58 ± 0.03 ng/mL) and MMR cows (0.60 ± 0.03 ng/mL). Plasma concentrations of T_4 increased ($P < 0.001$) after TRH and were best fit by a linear regression equation. There was a tendency ($P = 0.06$) for plasma concentrations of T_4 to be greater in LMR cows (49.29 ± 2.34 ng/mL) than HMR cows (46.03 ± 2.45 ng/mL) but did not differ between MMR (47.71 ± 2.45 ng/mL) and LMR or HMR cows (Figure 24). In yr 3, T_3: T_4 was influenced ($P = 0.003$) by time relative to TRH administration and was best fit by a quadratic regression equation ($P = 0.01$); MR did not affect (Figure 25; $P = 0.65$) the T_3: T_4 in cows. .

Cow temperament

Pen scores were greater in LMR cows ($P = 0.05$; 2.1 ± 0.2) compared with MMR cows (1.5 ± 0.2) and HMR cows (1.8 ± 0.2) did not differ compared with LMR and MMR cows. Chute and exit scores were not influenced ($P \geq 0.42$) by MR of cows. Maintenance energy requirement was not correlated ($P \geq 0.36$) with pen, chute, or exit score of cows.

Gene analyses

Messenger RNA abundance in longissimus muscle of LMR and HMR cows during maintenance of body weight is summarized in Figure 26. Expression of *SREBF1* mRNA did not differ (P = 0.24) between LMR (22.53 ± 10.03) and HMR cows (5.93 ± 7.77). Cows classified as LMR had greater (P = 0.04; 10.00 ± 2.10) mRNA expression of *FASN* compared with HMR cows (2.28 ± 2.10). There was a tendency for greater (P = 0.07) mRNA expression of *DGAT2* in LMR cows (1489.47 ± 408.75) compared with HMR cows (255.97 ± 408.75). Expression of *CPT1B* mRNA did not differ (P = 0.59) between LMR (11.96 ± 10.83) and HMR cows (20.13 ± 9.38).

Calf performance

Calf performance is summarized in Table 9. Birth weights, WW, and ADG of calves were not influenced ($P \geq 0.35$) by MR of cows when data from each year was combined and adjusted for year. Sex of calves tended ($P \leq 0.10$) to influence birth weight and ADG of calves, but not WW of calves when data was combined and adjusted for year.

Correlations between birth weight, WW, and ADG of calves and concentrations of T_3, T_4, IGF-I in plasma and T_3: T_4 of cows at maintenance and early lactation, corrected for year and sex of calves, is summarized in Table 10. Birth weight of calves was correlated (r = -0.31; P = 0.05) with plasma concentrations of IGF-I in cows at maintenance but not ($P \geq 0.25$) concentrations of T_3 and T_4 in plasma or T_3: T_4. Weaning weight of calves was negatively correlated (r = -0.35; P = 0.03) with plasma concentrations of T_4 in cows at maintenance. There was a tendency for WW of calves to be positively correlated with T_3: T_4 (r = 0.26; P = 0.10) in cows at maintenance, however concentrations of T_3 were not correlated (P = 0.15) WW of calves. Average daily gain of calves tended to be positively correlated with T_3: T_4 (r = 0.29; P = 0.07) in cows at maintenance. Plasma concentrations of IGF-I in cows at maintenance were not correlated ($P \geq$ 0.40) with WW and ADG of calves. Birth weight of calves tended to be negatively correlated ($P \leq 0.07$) with concentrations of T_3 (r = -0.30), T_4 (r = -0.31), T_3:T_4 (r = -0.30), and IGF-I in plasma (r = -0.31) of cows during early lactation. Plasma concentrations of T_3 and T_4 in cows during early lactation were positively correlated with WW (r = 0.56, *P* < 0.001; r = 0.53, *P* < 0.001, respectively) and ADG of calves (r = 0.37, *P* = 0.02; r = 0.33, *P* = 0.04, respectively). During early lactation, T_3: T_4 in cows was positively correlated with WW and ADG of calves (r = 0.56, *P* < 0.001; r = 0.37, *P* = 0.02, respectively). Plasma concentrations of IGF-I in cows at early lactation was positively correlated with WW (r = 0.55; *P* < 0.001) and ADG of calves (r = 0.36; *P* = 0.03).

DISCUSSION

Maintenance requirements were 81.0 ± 1.8, 83.1 ± 1.6, and 88.6 ± 1.3 $Kcal \cdot BW^{0.75} \cdot d^{-1}$ in yr 1, 2, and 3, respectively. These MR were determined based on NE_m and are similar to previous estimates of MR using a similar experimental approach. Net energy required for maintenance ranged from 80.7 to 95.5 $Kcal \cdot BW^{0.75} \cdot d^{-1}$ when cows were fed to maintain constant BW (Bailey, 2009; Pye, 2011; Cooper-Prado et al., 2014). Metabolizable energy required for maintenance of beef cattle ranges from 123 to 169 $Kcal \cdot BW^{0.75} \cdot d^{-1}$ (Solis et al., 1988; Laurenz et al., 1991; Reid et al., 1991). Estimates of ME_m are greater than NE_m as heat increment of feed is included in estimates of ME_m but not NE_m (NRC, 2000).

Cows differed in MR while maintaining BW during mid- to late gestation. The greatest differences between the most and least efficient cows were 31, 41, and 32% in yr 1, 2, and 3, respectively. The differences in efficiency of cows observed in these experiments are similar to those of Cooper-Prado et al. (2014). Variation in efficiency of ME_m utilization has been observed in beef steers (Birkelo et al., 1991) and cows (Nielsen et al., 1997a). Mice divergently selected for heat loss and thereby maintenance energy requirement had increased variation in heat loss compared with controls after 15 generations (Nielsen et al., 1997a). A 27% variation in ME_m has been observed in Angus cows (DiCostanzo et al., 1990). In the current experiments, the CV for

MR was 8.5, 8.5, and 7.5% in yr 1, 2, and 3, respectively. The CV for MR in Angus cows ranged from 5 to 7% when MR was determined on a NE_m basis (Bailey, 2009; Pye, 2011; Cooper-Prado et al., 2014) and 11% when MR was determined by ME_m (DiCostanzo et al., 1990). In mice divergently selected for heat production, the heritability for heat loss was 0.28 (Nielsen et al., 1997a). Hotovy et al. (1991) estimated the heritability of ME_m was 0.52 in growing beef cattle. Residual feed intake, a measure of feed efficiency, has been observed to be moderately heritable (0.26 to 0.43) in growing beef cattle (Koch et al., 1963; Arthur et al., 2001a; Crews et al., 2003). Heat production, as estimated by oxygen consumption, was correlated with RFI in beef steers (Nkrumah et al., 2004). Current and previous results support that variation in MR occurs between cows and differences in cow efficiency can be determined. Thus, selection of cows with reduced MR should increase cow efficiency.

Variation in estimates of MR may result from differences in physiological status (Ferrell and Jenkins, 1985a; Montaño-Bermudez et al., 1990), environmental conditions (Laurenz et al., 1991), estimation methodology, and other factors. Cows with greater potential for milk production had greater MR compared with cows with lesser potential for milk production (Ferrell and Jenkins, 1984a). Lactation increased MR 31 and 41% in Hereford cows compared with non-lactating cows (Neville and McCullough, 1969; Neville et al., 1974, respectively). Indirect evidence indicates an increased MR during pregnancy in beef cows (NRC, 2000). Although fetal, placental, and uterine weights increase throughout gestation (Prior and Laster, 1979), less than 1% of the BW of gestating cows was attributed to fetal and maternal tissue growth in the current study. Maintenance energy requirements did not differ between pregnant and non-pregnant Hereford heifers during mid to late-gestation (Ferrell et al., 1976). Similarly, MR for gestating and non-pregnant Targhee ewes in mid to late-gestation did not differ (Rattray et al., 1974a). Maintenance energy requirements increase as animals utilize energy to regulate body temperature (NRC, 2000). In the summer, MR of Simmental and Angus cows was greater than in the winter and was attributed to protein and fat accretion during the summer (Wagner et al., 1988; Laurenz et al., 1991). Increased fat accretion occurring during the winter may reduce MR of cows as a result of increased insulation (Thompson et al., 1983). Mean ambient temperature during maintenance of BW was 4.8°C in yr 1, 1.2°C in yr 2, and 0.3°C in yr 3. Mean ambient temperature from the 3 d preceding each BW measurement was a significate covariate for BW during maintenance, however models including ambient temperature did little to decrease variation in BW during maintenance.

The NRC (2000) estimate for MR of mature cows of average BW (567 kg) is 77 Kcal•kg $BW^{0.75}$•d^{-1}. Energy requirements for LMR and MMR cows differed slightly from NRC estimates, however requirements for maintenance of body weight in HMR cows averaged 15% greater than NRC estimates. Previous studies using similar techniques indicated MR of Angus cows were greater than NRC estimates (Bailey, 2009; Pye, 2011; Cooper-Prado et al., 2014). Adjustments for feed, environment, breed, physiological state, activity, and relative heat production are included in calculations of MR in the Level 1 model (NRC, 2000). Application of these adjustment factors are limited to the conditions in which they were developed (Ferrell and Oltjen, 2008). As a result, further work is needed to increase the accuracy of prediction equations for energy requirements of beef cows.

Feed intake increased with increasing heat loss when mice were divergently selected for heat production and received ad libitum feed; the difference between the greatest and least FI was 15 to 25% (Nielsen et al., 1997b). Feed intake differed by 13% between mice selected for greater and lesser heat loss (Kgwatalala and Nielsen, 2004). Greater MR of cows in yr 3 may have resulted from increased exposure to cold ambient temperatures during the feeding periods. Feed efficiency was increased in nutrient restricted-realimented beef cows compared with cows fed at constant level (Freetly and Nienaber, 1998; Freetly et al., 2008). Freetly et al. (2008) suggested that cows can adapt energy metabolism during periods of moderate feed restriction and are more efficient during realimentation. Similarly, ME_m was increased 14.5% in beef steers on a high plane of nutrition (Birkelo et al., 1991). Cows with reduced MR should have decreased ad libitum FI and selection of cows with reduced MR may increase profitability of the cow-calf industry.

Maintenance energy requirement were not related to BW or metabolic BW ($BW^{0.75}$) of cows during maintenance. Body condition score was not related to MR of cows except for a tendency for increased BCS in MMR cows during maintenance of BW in yr 2. These observations agree with previous results where MR of cows did not influence BW and BCS (Bailey, 2009; Cooper-Prado et al., 2014). Cows were of similar BCS during each experimental period and BCS ranged from 3.9 to 5.6. Change in BCS was not influenced by MR of cows in these experiments and were less than 0.5 between subsequent physiological states. Estimates of fetal and maternal reproductive tissue growth during maintenance (Prior and Laster, 1979) accounted for less than 1% of maternal BW in the current experiments. Similar BW and BCS of cows during early lactation and weaning indicates that MR of cows has little influence on body fat stores when cows have ad libitum energy.

Body weight and BCS of cows during maintenance, early lactation, and at weaning were not correlated with plasma concentrations of T_3, T_4, and T_3: T_4 during maintenance. In contrast, plasma concentrations of T_4 were correlated with BCS of cows in early lactation (Cooper-Prado et al., 2014). Concentrations of T_3 and T_4 in serum were greater in cows with moderate BCS compared with low BCS cows (Flores et al., 2008). Body condition score accounted for 7% of the variation in plasma concentrations of T_4 in gestating beef cows (Lents et al., 2005). Cows fed to maintain greater BCS had increased concentrations of T_4 and IGF-I in plasma compared with low BCS cows (Ciccioli et al., 2003). Body condition score during early lactation and at weaning, but not maintenance, were correlated with plasma concentrations of IGF-I. In the current experiments, cows were fed to maintain constant BW, which may have contributed to the lack of correlation with TH.

Maintenance energy requirements did not influence concentrations of T_3 and T_4 in plasma at maintenance. Similarly, concentrations of T_3 and T_4 in plasma were not affected by the MR of Angus cows during maintenance of BW or during early lactation using similar techniques (Bailey, 2009; Pye, 2011). Plasma concentrations of T_4 were greater in Angus cows with high MR compared with low and moderate MR cows (Cooper-Prado et al., 2014). The effects of TH on metabolism are well established (Brody and Frankenbach, 1942; Yousef and Johnson, 1966; Klieverik et al., 2009). Plasma concentrations of T_4 were positively associated with nutrient intake when cows were fed different amounts of energy (Richards et al., 1995; Ciccioli et al., 2003). In the current study, cows were fed to maintain BW and differences in TH would reflect differences in metabolism of cows at maintenance. Concentrations of T_3 and T_4 are associated with energy balance in lactating dairy cows (Reist et al., 2002; Pezzi et al., 2003) and concentrations of T_4 are influenced by changes in energy balance during the transition from gestation to early lactation in ad libitum fed dairy cows (Kunz et al., 1985; Pethes et al., 1985). Concentrations of T_4 were not influenced by MR in mice with ad libitum feed (Kgwatalala and Nielsen, 2004). These observations indicate T_4 may be a potential biomarker for changes in energy balance associated with differences in energy intake or physiological transitions.

The positive relationship between concentrations of T_3 and T_4 in plasma of cattle has been established (Bitman et al., 1984; Pethes et al., 1985; Tiirats, 1997) and was observed in the current experiments. The T_3: T_4 was not affected by MR of cows in yr 1 and 3 but tended to be greater in less efficient cows (HMR) in yr 2. Plasma concentrations of T_3 decreased ($P < 0.001$) from maintenance to early lactation in yr 1 and increased ($P < 0.001$) in yr 3, whereas, concentrations of T_4 in plasma decreased ($P < 0.001$) from maintenance to early lactation in yr 1 and 3. Concentrations of T_4 were greater before calving in ad libitum fed dairy cows compared with cows fed to MR (Kunz et al., 1985). The increase in T_3:T_4 from maintenance to early lactation in yrs 1 and 3 is likely driven by the decrease in T_4; concentrations of T_3 were variable as cows were realimented to ad libitum pasture. Fed status did not influence concentrations of T_3 and T_4 in plasma or T_3: T_4 in the current experiments. Similarly, plasma concentrations of T_4 in beef cows were not influenced by access to feed during late gestation (Lents et al., 2005). However, when beef cows were fed to lose 1 % of BW per wk, plasma concentrations of T_4 decreased (Richards et al., 1995). It is likely that short term fasting in these experiments was not sufficient to alter the metabolism of cows.

To further evaluate relationships between MR of cows and thyroid hormone status, cows were administered TRH to maximize secretion of TH. The stimulatory effect of TRH on concentration of T_3 and T_4 in plasma is well documented in cattle (Kesner et al., 1977; Perera et al., 1985; Pratt and Wettemann, 1986). In yr 2, increased T_3: T_4 in HMR cows occurred after TRH, compared with LMR cows, as a result of decreased concentrations of T_4 and unaltered concentrations of T_3. Greater concentrations of T_3 and T_4 occurred in LMR cows than HMR cows, but the increase in magnitude of T_3 and T_4 was uniform and the T_3: T_4 was not influenced by MR in yr 3. Time relative to administration of TRH did not affect T_3: T_4 in the current experiments. Increased concentrations of T_3 or a greater proportion of T_3 relative to T_4, indicating a greater bioavailability of T_3, may enhance metabolism in more efficient cows. Serum concentrations of T_3 were not altered by administration of TRH to Friesian x Herford heifers, however, concentrations of T_4 were increased and feed conversion efficiency was improved (Enright et al., 1993). Plasma concentrations of T_3 and T_4 were positively correlated with RFI classification in Angus heifers (Walker et al., 2015). In contrast, RFI was not related to plasma concentrations of T_3 or T_4 in beef steers (Brown et al., 2004) or heifers (Kelly et al., 2010b).

Thyroid hormones are critical regulators of energy homeostasis and body temperature. The effects of ambient temperature on concentrations of thyroid hormones in cattle have been established (Pratt and Wettemann, 1986; Biggers et al., 1987; Richards et al., 1995). Triiodothyronine and T_4 regulate basal metabolic rate in cattle and sheep (Hornick et al., 2000) and T_4 increased metabolic rate in lactating dairy cows (Yousef and Johnson, 1966). Thyroidectomized dairy calves have decreased resting metabolism (Brody and Frankenbach, 1942). Thyroxine and T_3 in serum were positively related to energy balance in dairy cows during early lactation (Reist et al., 2002), and concentrations of T_4 and T_3 in plasma are influenced by feed intake in beef cattle (Hayden et al., 1993; Ciccioli et al., 2003; Lents et al., 2005). Decreased concentrations of T_4 occur during feed restriction in beef (Rasby et al., 1991; Richards et al., 1995) and dairy cows (Kunz et al., 1985; Pethes et al., 1985), and beef steers (Ellenberger et al., 1989) and beef steers grazing low quality forage (Hersom et al., 2004b). Concentrations of T_4 were reduced in primiparous beef cows divergently selected for reduced milk production (Bitman et al., 1984). These observations suggest plasma concentrations of T_3 and T_4 may be a component of potential biomarkers for MR in beef cows.

Rectal temperatures of LMR cows were greater than MMR and HMR cows after TRH administration in yr 2, but differences in RT were less than 0.2°C. Similarly, diurnal ruminal temperatures were greater in Angus cows with low MR compared with moderate and high MR cows (Bailey, 2009). In contrast, ruminal temperatures were not influenced by MR in beef cows in other experiments (Pye, 2011; Cooper-Prado et al., 2014). Rectal temperature was positively correlated with MR in beef steers (Derno et al., 2005). Variation in heat loss has a greater influence on body temperature of cattle than heat production (Refinetti and Menaker, 1992). Heat production and loss was positively associated with MR in rats (Nielsen et al., 1997b) and feed efficiency in beef cattle during growth (Basarb et al., 2003). The current experiments were conducted during the winter, which could greatly influence the rate of heat loss and RT.

Plasma concentrations of IGF-I did not differ between HMR and LMR cows during maintenance of BW or during early lactation. The results of these experiments agree with Pye

(2011) where plasma concentrations of IGF-I in Angus cows at maintenance were similar among cows with differing MR. The greater concentrations of IGF-I in MMR cows compared with LMR and HMR cows in yr 2 and during early lactation of yr 1 are similar to those reported by Bailey (2009) and are likely due to BW gain the MMR cows experienced compared with BW loss in both LMR and HMR cows. Cooper-Prado et al. (2014) determined that concentrations of IGF-I in plasma did not differ in beef cows fed to maintain body weight, but MR of cows was negatively correlated with concentrations of IGF-I in plasma during ad libitum grazing in early lactation. Concentrations of IGF-I were positively correlated with BCS when cows grazed ad libitum during early lactation in the current experiments and is consistent with studies showing nutrient intake is positively related with plasma concentrations of IGF-I in beef cows (Richards et al., 1995; Lents et al., 2005).

Cows produce IGF-I in response to growth hormone (Jones and Clemmons, 1995; Keisler and Lucy, 1996). However, the stimulatory action of GH on IGF-I synthesis is uncoupled during negative energy balance as hepatic GH receptors are downregulated (Thissen et al., 1994). Thus, decreased concentrations of IGF-I and increased plasma concentrations of GH occur when cattle are in a negative energy balance (Reynolds et al., 1991; Keisler and Lucy, 1996; Bossis et al., 1999). After realimentation, concentrations of IGF-I gradually return to pre-restriction levels (Bossis et al., 2000) as the uncoupling of the GH – IGF-I axis is reversed (Thissen et al., 1994). Feed efficiency in growing beef cattle and IGF-I have been reported to be positively related (Johnston et al., 2002; Moore et al., 2005), or minimally to unrelated (Lancaster et al., 2008; Kelly et al., 2010a). Serum concentrations of IGF-I are correlated with post weaning BW and gain in growing Angus cattle divergently selected for greater or lesser IGF-I (Davis and Simmen, 2006; Huang et al., 2011). In the current experiments, plasma concentrations of IGF-I were related to MR of cows during early lactation, but not at maintenance. Together these observations indicate concentrations of IGF-I may be more beneficial for describing energetic efficiency of cows during grazing.

Temperament of cows was not influenced by classification of MR in this experiment. A greater proportion of LMR and MMR cows had exit scores of 1, but the pen and chute scores were similar among LMR, MMR, and HMR cows. Pye (2011), using a similar technique to measure MR, observed no difference in walking activity of cows maintaining BW. Brosh et al. (2006) estimated grazing, standing, and traveling activities increased total energy expenditure of grazing beef cows by 11% relative to resting energy expenditure. Similarly, 11.5% of the variation in heat production of mice, divergently selected for heat loss, was attributed to locomotor activity (Mousel et al., 2001). Average daily gains were greater in beef heifers and steers with calm temperaments (Voisinet et al., 1997; Fell et al., 1999). Differences in activity accounted for 36% of the variation in FI of mice selected for high or low heat production (Mousel et al., 2001). In agreement with the current observations, feed efficiency of lactating beef cows was not related to temperament when efficiency was classified by RFI when they were heifers (Black et al., 2013b). It is possible that the reduced number of observations, and adaptation of cows to the handling procedures, contributed to similarity in temperament of cows with different MR in the current experiment.

Expression of *FASN* in LM was 4.4 fold greater in LMR than in HMR cows and expression of *DGAT2* tended to be greater in cows with lesser MR in this experiment. Expression of *SREBF1* and *CPT1B* in LM were not influenced by MR of cows. Despite the established relationships between body composition and lipogenic and lipolytic gene activity, the relationships between adipose gene expression and MR of cattle are unclear. Expression of *FASN* and *SREBF1* were increased and *CPT1* expression was decreased in subcutaneous adipose tissue of Chinese Yellow x Simmental cattle fed diets with greater energy (Zhang et al., 2015). Greater expression of hepatic *Srebp1*, *Fasn*, and *Dgat2* occurred in mice fed high fat diets compared with control fed mice, and mice fed high fat diets had increased feed efficiency and greater white adipose tissue mass compared with control fed mice (Chan et al., 2008). These observations agree with the current experiment where cows with lesser MR, and required less feed to maintain BW, had increased expression of *FASN* and *DGAT2*. The increased lipogenic and similar lipolytic gene expression suggests cows with reduced MR may utilize energy more efficiently, allowing for increased fatty acid synthesis or decreased adipose turnover. Expression of *SREBF1*, *FASN*, and *DGAT2* mRNA were greater in dairy cows with lesser genetic potential for milk production compared than cows with greater genetic potential for milk production during early lactation (Khan et al., 2013) and agrees with the current experiment. As milk production potential is associated with MR in cattle (Ferrell and Jenkins, 1984a) and lipogenic gene expression differs during early lactation (Khan et al., 2013), expression of lipogenic genes may be useful in identifying cows with reduced MR. Further work is needed to determine if greater enzyme abundance occurs as a result of the increased lipogenic gene expression observed in this experiment.

Thyroid hormones and insulin signaling pathways regulate lipid homeostasis. Increased concentrations of TH in rats stimulates lipogenesis and lipolysis resulting in net loss of body fat (Oppenheimer et al., 1991). Zhu and Cheng (2010) reviewed the influence of TH receptors on lipid homeostasis and indicated the necessary role of THR in adipogenesis and lipid metabolism. As reviewed by Eberlé et al. (2004), the *SREBP* transcription factors are global regulators of lipid homeostasis by controlling expression of enzymes that regulate cholesterol, fatty acid, triacylglycerol, and phospholipid synthesis. Thyroid hormone receptors stabilize *SREBF1* at its binding site, thereby regulating the transcriptional activity of *SREBF1* (Yin et al., 2002). Insulin and T_3 bind T_3 response element in the promoter region of FASN, thereby regulating FASN transcription (Radenne et al., 2008). The insulin signaling pathway may also interact with SREB transcription factors through liver X receptor and peroxisome proliferator-activated receptor -γ regulated co-activator-1β (see review; Raghow et al., 2008). Insulin signaling is positively related to SREB gene expression in rats (Shimomura et al., 1999; Deng et al., 2002; Deng et al., 2007). Enzymes that are products of *Fasn* and *Dgat2*, lipogenic genes, are transcriptionally regulated by the SREB family in mice (Liang et al., 2002; Horton et al., 2003; Griffin et al., 2007). The lipolytic gene *CPT1B* is a critical element in muscle energy homeostasis as it functions in the catabolism of fatty acids (Eaton et al., 2001). Carnitine palmitoyltransferase 1B is indirectly regulated by *SREBF1*; decreased *SREBF1* is associated with decreased malonyl-CoA, a primary inhibitor of *CPT1B* (Clarke, 2000). Triiodothyronine stimulates transcription of acetyl CoA carboxylase-1 (Huang and Freake, 1998) which converts malonyl CoA to acetyl CoA. Malonyl CoA inhibits the action of CPTI thereby decreasing the translocation of fatty acids to the mitochondria for β-oxidation (McGarry and Brown, 1997). In the current experiment, cows with increased expression of *FASN* and *DGAT2* in LM had similar concentrations of T_3 and T_4. Similarly, plasma concentrations of T_3 and T_4 were not correlated with *SREBF1* in subcutaneous adipose tissue of dairy cows, however *CPT1A* and *CPT2* were correlated at 10 wk before calving and at 4 wk postpartum (van Dorland et al., 2009). Increased serum concentrations of insulin and subcutaneous adipose tissue expression of *FASN* and *DGAT2* occurred in gestating dairy cows fed greater amounts of energy compared with control fed cows (Ji et al., 2102). Male sheep, prenatally programed for obesity, had decreased plasma concentrations of insulin, and increased abundance of FASN mRNA and adipose tissue mass compared with controls (Long et al., 2015). The minimal sample size may have resulted in insufficient power to determine if expression of *SREBF-1* and *CPT1B* are influenced by MR of beef cows. Further work is needed to elucidate the mechanisms by which TH influence transcription and translation of genes responsible for increased energetic efficiency.

There was not an adequate number of cows to determine the effect of MR on reproduction in the current experiments. Negative relationships between age at puberty and RFI in beef heifers have been described (Basarab et al., 2011; Donoghue et al., 2011), however 94 and 83% of heifers had reached puberty by 14 mo., respectively. Conception rate to first AI and overall pregnancy rate did not differ in Angus cows classified as heifers by RFI (Shike et al., 2014). Pregnancy rate was not altered in beef cows divergently selected for RFI (Arthur et al., 2005) or by RFI status of beef heifers (Donoghue et al., 2011). Birth weight of calves and weight of calves born per female exposed was not influenced by divergent selection for RFI in Angus cows (Arthur et al., 2005; Donoghue et al., 2011). Angus cows divergently selected for RFI did not differ in weight of calf weaned per cow exposed (Arthur et al., 2005). Reproductive performance of beef cows is influenced by nutrition and BCS of cows at parturition (Randel, 1990; Wettemann et al., 2003). Postpartum anestrus was decreased (Richards et al., 1986) and fertility and pregnancy rates were increased (Selk et al., 1988; Ciccioli et al., 2003; Lents et al., 2008) in cows with moderate BCS compared with cows with low BCS. In the current experiments, BCS of cows was similar during the periparturient period and greater than the ≤ threshold necessary for adequate reproduction (BCS ≤ 4; Selk et al., 1988; Looper et al., 2003; Lents et al., 2008). These observations indicate cows may be selected for reduced MR without negatively influencing reproductive performance.

Birth weights, WW, and ADG of calves were not influenced by MR of the dam when calf performance data were adjusted for year. Overall ADG averaged 1.07 ± 0.03, 1.13 ± 0.03, and 1.08± 0.03 kg/d in calves from LMR, MMR, and HMR cows, respectively. Similarly, dam MR did not influence birth weight or WW of calves (Cooper-Prado et al., 2014). Prior and Laster (1979) observed that maternal dietary energy did not influence fetal weights and composition from 85 to 277 d of gestation. Maternal nutrition influenced birth weight of calves and reduced prenatal nutrition decreased (Wiltbank et al., 1962; Houghton et al., 1990b; Spitzer et al., 1995) or had no effect on birth weight of calves (Hough et al., 1990; Wiley et al., 1991; Martin et al., 2007); amount of restriction was probably responsible for the effect on birth weight. Preweaning performance of calves can be influence by inadequate prenatal nutrient intake (Houghton et al., 1990b; Freetly et al., 2000).

Milk production is positively correlated with WW and ADG of calves (Neville, 1962; Rutledge et al., 1971; Marston et al., 1992). Approximately 60% of the variation in WW of calves was attributed to differences in milk yield from dams (Rutledge et al., 1971; Reynolds et al., 1978; Clutter and Nielsen, 1987). Pre-weaning performance of calves nursing cows with different MR were similar in the current study and indicate differences in MR did not influence milk production of cows. Although milk production accounted for 23% of the variation in MR during lactation, differences in milk production alone were not sufficient to determine differences in MR per metabolic body weight (Montaño-Bermudez et al., 1990). Freking and Marshall (1992) observed that energy intakes of non-lactating cows were not correlated with potential for milk production. Milk yield was not influenced by efficiency of cows when classified by RFI as heifers or cows (Black et al., 2013a). Neither milk yield, nor calf performance was influenced by divergent selection of dams for greater or lesser efficiency (RFI; Arthur et al., 2005). These observations suggest that cows may be selected for greater efficiency without negatively influencing pre-weaning performance of calves.

IMPLICATIONS

The difference in maintenance energy requirement between the greatest and least efficient cows ranged from 31 to 41% in nonlactating, pregnant Angus cows. Therefore, selection of cows for greater energetic efficiency may be feasible. Body weight and BCS were not influenced by MR of cows. Daily concentrations of T_3, T_4, and T_3:T_4 in plasma were not affected by MR of cows. After infusion of TRH in yr 2, plasma concentrations of T_3 and T_4 were greater in MMR cows compared with LMR and HMR cows, and T_3:T_4 was greater in HMR cows than in LMR or MMR cows after infusion of TRH. In yr 3, plasma concentrations of T_3, after

TRH administration, were greater in LMR cows compared with MMR and HMR cows, and concentrations of T_4 tended to be greater in LMR cows than in MMR and HMR cows. Maintenance energy requirement of cows did not influence the T_3:T_4 after the TRH challenge. Although the TH response was variable after TRH administration, differences among MR indicate TH may be of potential biomarkers for MR. Plasma concentrations of IGF-I were not influenced by MR of cows and were greater when cows consumed maintenance diets compared with ad libitum pasture during early lactation. Body condition score of cows during early lactation and at weaning was correlated with concentrations of IGF-I in plasma and may be beneficial in describing MR of cows during grazing. Cows with low MR had greater expression of *FASN* and tended to have greater *DAGT2* mRNA abundance in LM compared with HMR cows. Increased mRNA expression of lipogenic genes may be related to decreased MR in beef cows and may serve as a useful tool in identifying MR of cows. Temperament was not related to MR of cows. Birth weights, WW, and ADG of calves were not influenced by MR of cows. These results indicate that cows may be selected for reduced MR without negatively affecting cow-calf production. Identification of cows with reduced MR may enhance production efficiency of beef cows.

CHAPTER IV

SUMMARY AND CONCLUSIONS

Non-lactating, spring-calving Angus cows were used to determine variation in maintenance energy requirements (MR) and to evaluate relationships between MR and concentrations of triiodothyronine (T_3), thyroxine (T_4), and IGF-I in plasma, expression of genes associated with lipid homeostasis, and calf performance. Maintenance energy requirement of cows were evaluated in 3 yr during mid to late-gestation. Cows were individually fed to meet predicted MR (NRC, 2000) and diets were adjusted until constant BW was achieved. Each year, cows were classified based on MR as low (LMR; > 0.5 SD less than mean MR), moderate (MMR; ± 0.5 SD of mean MR), or high (MMR; > 0.5 SD greater than mean MR). Metabolic hormones and expression of genes associated with lipid homeostasis may be a component of potential biomarkers for MR in beef cows. In yr 2 and 3, cows were infused with TRH to maximize the responsiveness of the pituitary-thyroid axis. Muscle biopsies were performed on LMR and HMR cows during yr 3 and relative mRNA abundance of sterol regulatory element binding factor 1 (*SREBF1*), fatty acid synthase (*FASN*), diacylglycerol acyltransferase 2 (*DGAT2*), and carnitine palmitoyltransferase 1B (*CPT1B*) was quantified. Mean MR (Kcal•kg $BW^{0.75}$•d^{-1}) of cows was 81.0 ± 1.8, 83.1 ± 1.6, and 88.1 ± 1.3 in yr 1, 2, and 3, respectively. The difference between cows with the greatest and least MR was 31, 41, and 32% in yr 1, 2, and 3, respectively. Actual requirements for maintenance were 17, 16, and 14% greater in HMR cows compared with NRC estimates for MR in yr 1, 2, and 3, respectively. Daily plasma concentrations of T_3, T_4, T_3:T_4, and IGF-I were not influenced by MR of cows at maintenance or early lactation, however concentrations of IGF-I decreased after realimentation to ad libitum pasture. Plasma concentrations of T_3 and T_4 were greater in MMR than in LMR and HMR cows in yr 2 and T_3:T_4 was greater in HMR than in LMR or MMR cows after TRH administration. In yr 3, concentrations of T_3 and T_4 were greater in LMR than in MMR and HMR cows after TRH inoculation. Abundance of *FASN* mRNA was greater in LMR cows compared with HMR cows and may have application as a component of potential biomarkers for MR. Maintenance energy requirements did not influence birth weights, WW, or ADG of calves.

In conclusion, MR of beef cows and potential biomarkers for reduced MR were evaluated. These experiments confirm that there is variation in MR of beef cows within a herd. Maintenance energy requirement of beef cows did not influence daily concentrations of T_3, T_4, T_3:T_4, and IGF-I at maintenance or during early lactation. After administration of TRH, the response of cows in T_3 and T_4 was variable; concentrations of T_3 and T_4 were greatest in MMR cows in yr 2 and greatest in LMR cows in year yr 3. Plasma concentrations of IGF-I were correlated with BCS of cows during early lactation and at weaning and may be useful for describing MR of cows during grazing. Abundance of *FASN* and *DGAT2* mRNA were greater in more efficient cows than in less efficient cows. Genes regulating adipose tissue homeostasis may be potential biomarkers for reduced MR in beef cows. Performance of calves before weaning was not influenced by MR of cows. Further research is necessary to determine the effect of MR on TH and expression of genes regulating adipose tissue homeostasis. Identification of biomarkers for maintenance energy requirement will allow for the selection of more efficient cows. Production efficiency of beef cows may be improved by identifying cows that require less energy input and maintain performance.

TABLES

Table 1. Primers used to quantify mRNA abundance (quantitative reverse transcription-PCR) of genes in LM of beef cows with low (LMR) and high (HMR) maintenance energy requirement in yr 3

Gene name[1]	Accession	Forward (5'-3')	Reverse (5'-3')	Product, bp
LM				
SREBF1	NM_001113302	ACACCACCAGCATCAACC	CCATTCATCAGCCAGACC	112
FASN	NM_001012669	AAGCAGGCACACAATATGGAC	TGAAGTCAAAGAAGAAGGAGAGG	244
DGAT2	NM_205793	TCATGGGTGTCTGTGGGTTA	GGAGGAGAGAAGAGGGGTTG	185
CPT1B	NM_001034349	CCATCTTCTTCCACGTCTCC	CCATCTTCTTCCACGTCTCC	139
Reference				
GAPDH	NM_00103404	AGCGACACTCACTCTTCTACCTTC	ACTCTTCCTCTCGTGCTCCTG	191

[1] *SREBF1* = sterol regulatory element binding factor *1*; *FASN* = fatty acid synthase; *DGAT2* = diacylglycerol acyltransferase 2; *CPT1B* = carnitine palmitoyltransferase 1B; *GAPDH* = glyceraldehyde-3- phosphate dehydrogenase

Table 2. Daily environmental conditions during adjustment of NRC diets and when body weight was maintained in yr 1, 2, and 3, respectively

		Daily environmental conditions			
Period	**Days**	**Minimum ambient temperature, °C**	**Mean ambient temperature, °C**	**Maximum ambient temperature, °C**	**Relative humidity, %**
Yr 1					
NRC adjustment	60	-1.5 ± 0.7	5.3 ± 0.7	12.3 ± 0.8	68.5 ± 1.9
BW maintenance	28	-3.0 ± 1.0	4.8 ± 0.9	13.2 ± 0.9	65.4 ± 2.1
Yr 2					
NRC adjustment	70	1.1 ± 0.9	10.1 ± 0.8	19.2 ± 0.8	58.4 ± 1.5
BW maintenance	31	-6.2 ± 1.0	1.2 ± 0.9	9.1 ± 1.1	68.5 ± 1.9
Yr 3					
NRC adjustment	59	-5.4 ± 0.9	1.7 ± 0.9	8.8 ± 1.1	70.2 ± 1.7
BW maintenance	32	-6.6 ± 1.0	0.3 ± 1.1	7.1 ± 1.5	57.6 ± 3.1

Table 3. Maintenance energy requirements (MR) and metabolic body weight (MBW) of beef cows fed to maintain body weight[1] in yr 1, 2, and 3

	Maintenance energy requirement[2]			
Item	**LMR**	**MMR**	**HMR**	***P*-value**
Yr 1				
Cows, no.	5	6	4	
MR, Kcal•kg $BW^{0.75}$•d^{-1}	75.3 ± 1.2[a]	79.2 ± 1.1[b]	90.9 ± 1.4[c]	<.0001
MBW, kg $BW^{0.75}$	119.0 ± 3.3	116.8 ± 3.0	115.0 ± 3.7	0.73
Yr 2				
Cows, no.	5	10	5	
MR, Kcal•kg $BW^{0.75}$•d^{-1}	73.3± 1.3[a]	84.0± 0.9[b]	91.1± 1.3[c]	<.0001
MBW, kg $BW^{0.75}$	117.6± 2.9	113.3± 2.1	110.9± 2.9	0.28
Yr 3				
Cows, no.	11	7	8	
MR, Kcal•kg $BW^{0.75}$•d^{-1}	83.6 ± 1.0[a]	87.1 ± 1.3[b]	94.3 ± 1.1[c]	<.0001
MBW, kg $BW^{0.75}$	119.0 ± 2.5	115.5 ± 3.4	113.8 ± 2.8	0.38

[1] Cows maintained constant BW for 28, 31, and 32 d in yr 1, 2, and 3, respectively.
[2] Maintenance energy requirement was classified as low (LMR; > 0.5 SD less than yearly mean MR), moderate (MMR; ± 0.5 SD of yearly mean MR), or high (HMR; > 0.5 SD greater than yearly mean MR).
[a, b, c] Means for each year within a row with different superscripts differ ($P < 0.05$).

Table 4. Body weight and body condition score of beef cows (n = 15) with low (LMR), moderate (MMR), and high (HMR) maintenance energy requirement in yr 1

	Maintenance energy requirement[1]			
Item	LMR	MMR	HMR	*P*-value
Cows, no.	5	6	4	
BW, kg				
Initial[2]	578.9 ± 21.8	583.2 ± 19.9	592.4 ± 24.3	0.92
Maintenance[3]	586.0 ± 21.8	570.9 ± 19.9	559.9 ± 24.3	0.73
Early lactation[4]	542.6 ± 20.9	564.5 ± 19.1	565.0 ± 23.4	0.70
Weaning[5]	548.3 ± 17.1	581.4 ± 15.6	580.6 ± 19.1	0.33
BW change, kg				
Initial to maintenance	7.2 ± 6.1[a]	-12.3 ± 5.6[b]	-32.5 ± 6.8[c]	0.004
Maintenance to early lactation	-43.5 ± 8.2[a]	-6.4 ± 7.5[b]	5.0 ± 9.2[b]	0.004
Early lactation to weaning	5.7 ± 9.3	16.9 ± 8.5	15.6 ± 10.4	0.65
BCS				
Initial[2]	4.9 ± 0.2	4.6 ± 0.2	4.4 ± 0.2	0.20
Maintenance[3]	4.7 ± 0.2	4.7 ± 0.2	4.4 ± 0.2	0.51
Early lactation[4]	4.2 ± 0.2	4.3 ± 0.2	4.4 ± 0.2	0.82
Weaning[5]	4.1 ± 0.2	3.9 ± 0.2	4.0 ± 0.2	0.80
BCS change				
Initial to maintenance	-0.2 ± 0.1	0.1 ± 0.1	0.0 ± 0.1	0.30
Maintenance to early lactation	-0.5 ± 0.1	-0.3 ± 0.1	0.0 ± 0.2	0.12
Early lactation to weaning	-0.1 ± 0.2	-0.4 ± 0.2	-0.4 ± 0.2	0.44

[1] Maintenance energy requirement was classified as low (LMR; > 0.5 SD less than yearly mean MR), moderate (MMR; ± 0.5 SD of yearly mean MR), or high (HMR; > 0.5 SD greater than yearly mean MR).
[2] Initial feeding occurred at 158 ± 4 d of gestation.
[3] Cows maintained consistent BW for 28 d starting at 218 ± 4 d of gestation.
[4] Cows were 58 ± 3 d postpartum.
[5] Weaning occurred at 182 ± 4 d after calving.
[a, b, c] Means within row differ (*P* = 0.004)

Table 5. Body weight and body condition score of beef cows (n = 20) with low (LMR), moderate (MMR), and high (HMR) maintenance energy requirement in yr 2

	Maintenance energy requirement[1]			
Item	LMR	MMR	HMR	P-value
Cows, no.	5	10	5	
BW, kg				
Initial[2]	569.2 ± 16.8	554.2 ± 11.9	546.8 ± 16.8	0.63
Maintenance[3]	576.3 ± 18.8	548.6 ± 13.3	532.8 ± 18.8	0.28
Early lactation[4]	566.8 ± 23.9	565.5 ± 16.9	526.3 ± 26.7	0.44
Weaning[5]	620.6 ± 27.4	614.4 ± 19.3	608.7 ± 35.3	0.96
BW change, kg				
Initial to maintenance	7.2 ± 5.6[a]	-5.7 ± 4.0[ab]	-13.9 ± 5.6[b]	0.05
Maintenance to early lactation	-9.5 ± 9.4[a]	16.9 ± 6.7[b]	-8.8 ± 10.5[a]	0.05
Early lactation to weaning	53.8 ± 14.3	48.9 ± 10.1	90.6 ± 18.5	0.17
BCS				
Initial[2]	4.5 ± 0.1	4.4 ± 0.1	4.5 ± 0.1	0.63
Maintenance[3]	4.4 ± 0.2[x]	3.9 ± 0.1[y]	4.4 ± 0.2[x]	0.09
Early lactation[4]	4.4 ± 0.2	4.4 ± 0.2	4.3 ± 0.2	0.90
Weaning[5]	4.9 ± 0.2	4.7 ± 0.1	4.5 ± 0.2	0.41
BCS change				
Initial to maintenance	-0.1 ± 0.2	-0.5 ± 0.1	-0.1 ± 0.2	0.17
Maintenance to early lactation	-0.0 ± 0.3	0.5 ± 0.2	-0.1 ± 0.3	0.22
Early lactation to weaning	0.5 ± 0.2	0.3 ± 0.1	0.3 ± 0.2	0.57

[1] Maintenance energy requirement was classified as low (LMR; > 0.5 SD less than yearly mean MR), moderate (MMR; ± 0.5 SD of yearly mean MR), or high (HMR; > 0.5 SD greater than yearly mean MR).
[2] Initial feeding occurred at 143 ± 2 d of gestation.
[3] Cows maintained consistent BW for 31 d starting at 213 ± 2 d of gestation.
[4] Cows were 96.8 ± 3 d postpartum.
[5] Weaning occurred at 209 ± 3 d after calving.
[a, b] Means within row differed ($P \leq 0.05$)
[x, y] Means within row differed ($P \leq 0.09$)

Table 6. Body weight and body condition score of beef cows (n = 26) with low (LMR), moderate (MMR), and high (HMR) maintenance energy requirement in yr 3

	Maintenance energy requirement[1]			
Item	LMR	MMR	HMR	*P*-value
Cows, no.	11	7	8	
BW, kg				
Initial[2]	578.0 ± 16.7	559.5 ± 22.7	559.0 ± 18.5	0.70
Maintenance[3]	586.6 ± 16.6	562.8 ± 22.5	551.7 ± 18.4	0.37
Early lactation[4]	576.7 ± 18.5	569.9 ± 23.9	551.7 ± 19.5	0.64
Weaning[5]	617.2 ± 15.0	614.1 ± 19.4	598.8 ± 15.9	0.68
BW change, kg				
Initial to maintenance	8.5 ± 4.2[a]	2.8 ± 5.2[ab]	-8.2 ± 4.9[b]	0.05
Maintenance to early lactation	2.2 ± 8.1	7.4 ± 9.7	-1.2 ± 9.1	0.81
Early lactation to weaning	40.5 ± 7.4	44.6 ± 8.9	47.2 ± 8.3	0.83
BCS				
Initial[2]	5.0 ± 0.1	4.7 ± 0.2	4.6 ± 0.1	0.13
Maintenance[3]	4.8 ± 0.1	4.5 ± 0.1	4.7 ± 0.1	0.31
Early lactation[4]	4.3 ± 0.1	4.3 ± 0.1	3.9 ± 0.1	0.19
Weaning[5]	5.6 ± 0.2	5.6 ± 0.3	5.1 ± 0.3	0.39
BW change, kg				
Initial to maintenance	-0.2 ± 0.1	-0.1 ± 0.1	0.1 ± 0.1	0.23
Maintenance to early lactation	-0.5 ± 0.1	-0.4 ± 0.2	-0.7 ± 0.2	0.37
Early lactation to weaning	1.4 ± 0.2	1.4 ± 0.3	1.1 ± 0.3	0.76

[1] Maintenance energy requirement was classified as low (LMR; > 0.5 SD less than yearly mean MR), moderate (MMR; ± 0.5 SD of yearly mean MR), or high (HMR; > 0.5 SD greater than yearly mean MR).
[2] Initial feeding occurred at 173 ± 1 d of gestation.
[3] Cows maintained consistent BW for 32 d starting at 232 ± 1 d of gestation.
[4] Cows were 84 ± 1 d postpartum.
[5] Weaning occurred at 210 ± 1 d after calving.
[x, y] Means within row differed ($P \leq 0.06$)

Table 7. The effects of low (LMR) and high (HMR) maintenance energy requirement on concentrations of triiodothyronine (T_3) and thyroxine (T_4) in plasma and the ratio of triiodothyronine to thyroxine (T_3:T_4) in beef cows prior to tissue biopsy[1] in yr 3

	Maintenance energy requirement[2]		
Item	**LMR**	**HMR**	***P*-value**
Cows, no.	6	5	
T_3, ng/mL	0.55 ± 0.03	0.55 ± 0.03	0.98
T_4, ng/mL	49.8 ± 3.9	41.9 ± 3.6	0.17
T_3:T_4	0.011 ± 0.001	0.013 ± 0.001	0.15

[1] Cows maintained constant BW for 32 d.

[2] Maintenance energy requirement of cows were classified as low (less than 0.5 SD from yearly mean MR) or high (greater than 0.5 SD from yearly mean MR).

Table 8. Pearson correlation for cows in yr 1, 2, and 3, corrected for year, for plasma concentrations of triiodothyronine (T_3), thyroxine (T_4), and insulin-like growth factor I (IGF-I) and the ratio of T_3 to T_4 (T_3:T_4) with body weight, body condition score, metabolic body weight, NRC estimated MR, and MR of beef cows maintaining constant body weight (obs = 45)

Item	**T_3**	**T_4**	**T_3:T_4**	**IGF-I**
BW, kg				
Maintenance	0.12	0.06	0.22	0.12
Early lactation	0.09	-0.01	0.17	0.21
Weaning	-0.02	-0.10	0.19	0.13
BCS				
Maintenance	0.18	0.07	0.13	0.10
Early lactation	-0.08	0.03	-0.15	0.29**
Weaning	0.07	0.12	-0.09	0.29**
Metabolic BW, $kg^{-0.75}$	0.12	-0.07	0.22	0.12
NRC MR, Kcal•kg $BW^{-.075}$•d^{-1}	0.20	0.13	0.03	-0.07
MR, Kcal•kg $BW^{-.075}$•d^{-1}	0.02	0.01	0.10	0.05

** $P \leq 0.10$

Table 9. Effect of low (LMR), moderate (MMR) and high (HMR) maintenance energy requirement of beef cows during mid- to late gestation on birth weight, 205 d weaning weight (WW), and average daily gain (ADG) of calves[1] in yr 1, 2, and 3

	Maintenance energy requirement[2]				
	LMR	**MMR**	**HMR**	**MR**	**Sex**
Overall					
Calves, no.	21	23	16		
Birth weight, kg	39.1 ± 1.1	38.5 ± 1.1	38.2 ± 1.3	0.87	0.09
WW, kg	243.7 ± 12.3	252.9 ± 12.0	248.0 ± 14.0	0.56	0.21
ADG, kg/d	1.39 ± 0.06	1.45 ± 0.06	1.40 ± 0.06	0.35	0.10

[1] Calves were born during 63 d, 47 d, and 26 d in yr 1, 2, and 3, respectively.

[2] Maintenance energy requirement was classified as low (LMR; > 0.5 SD less than yearly mean MR), moderate (MMR; ± 0.5 SD of yearly mean MR), or high (HMR; > 0.5 SD greater than yearly mean MR).

Table 10. Pearson correlations, corrected for year, between plasma concentrations of triiodothyronine (T_3), thyroxine (T_4), and insulin-like growth factor I (IGF-I) and the ratio of T_3 to T_4 in beef cows maintaining constant body weight and in early lactation with birth weight, 205 d weaning weight (WW), and ADG of calves in yr 1, 2, and 3

	Maintenance				Early lactation			
Item	T_3	T_4	T_3:T_4	IGF-I	T_3	T_4	T_3:T_4	IGF-I
Observations, no.	44				37			
Birth weight, kg	-0.11	-0.19	0.17	-0.31*	-0.30**	-0.31**	-0.30**	-0.31**
WW, kg	-0.23	-0.35*	0.26**	-0.07	0.56*	0.53*	0.56*	0.55*
ADG, kg/d	-0.08	-0.23	0.29**	0.14	0.37*	0.33*	0.37*	0.36*

* $P \leq 0.05$
** $P \leq 0.10$

FIGURES

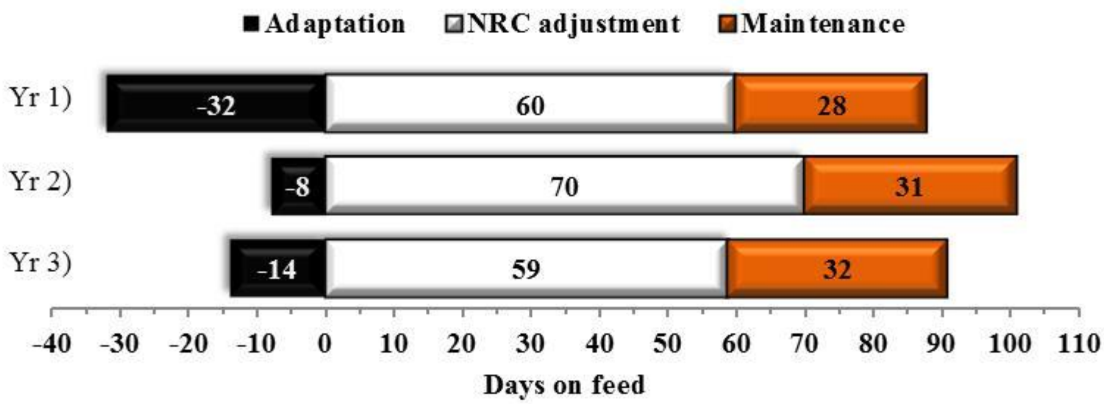

Figure 1. Adaptation, adjustment, and maintenance periods of beef cows fed to maintain constant body weight during yr 1, yr 2, and yr 3.

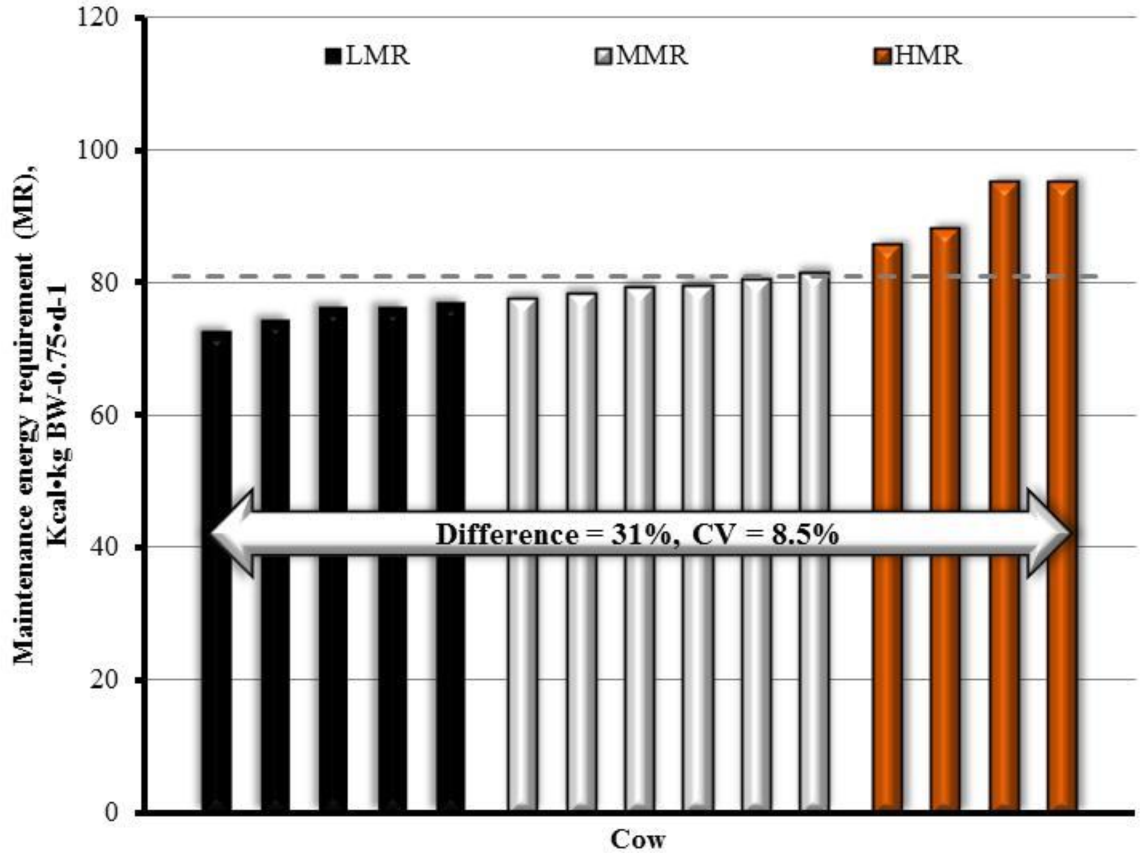

Figure 2. Maintenance energy requirement (MR; Kcal•kg $BW^{0.75}$•d^{-1}) of nonlactating, pregnant beef cows (n = 15) maintaining constant body weight for 28 d in yr 1.
Percent difference represents the difference in MR between cows with the greatest and least MR.

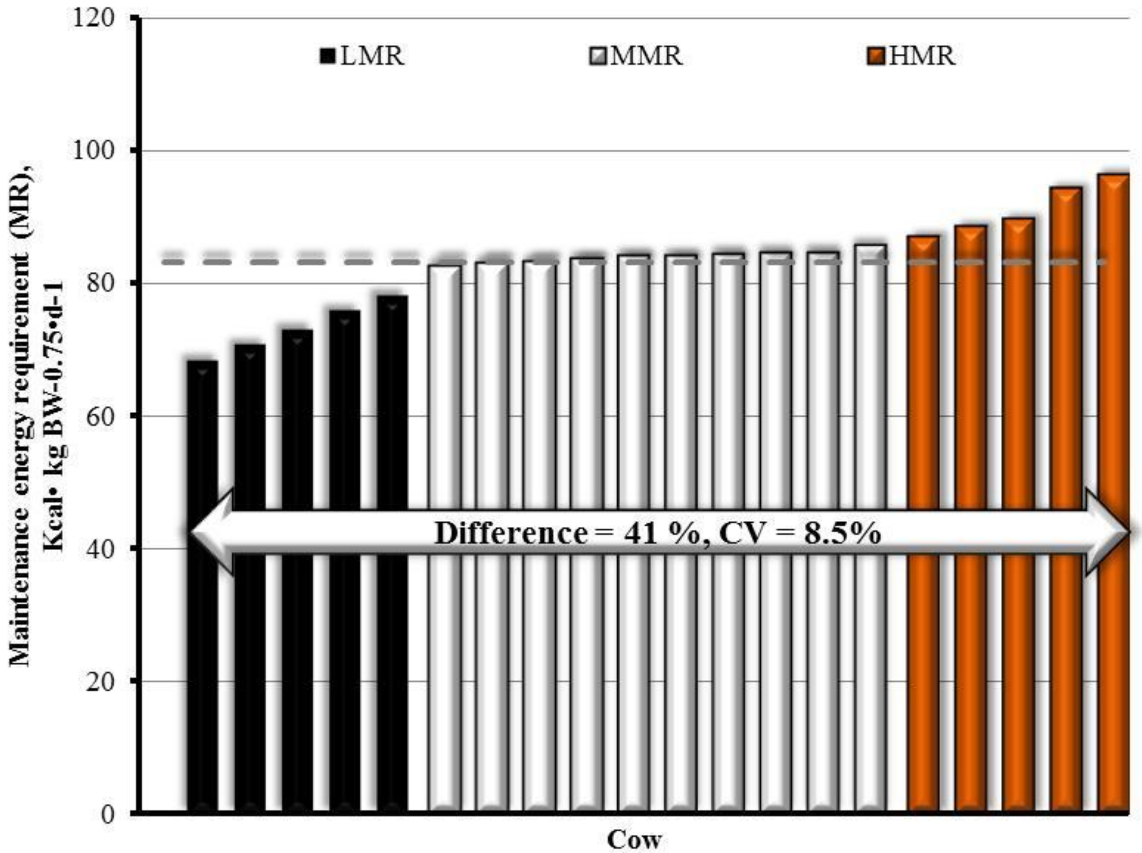

Figure 3. Maintenance energy requirement (MR; Kcal•kg $BW^{0.75}$•d^{-1}) of nonlactating, pregnant beef cows (n = 20) maintaining constant body weight for 31 d in yr 2.
Percent difference represents the difference in MR between cows with the greatest and least MR.

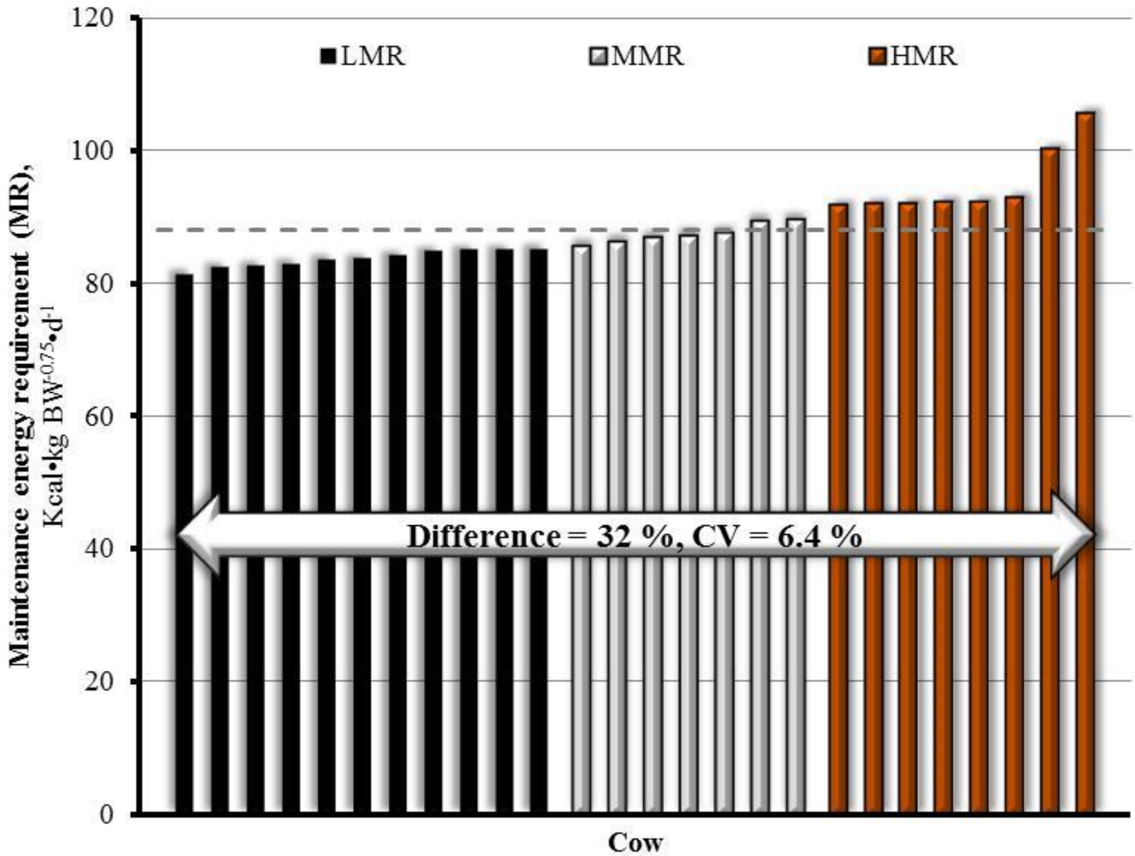

Figure 4. Maintenance energy requirement (MR; Kcal•kg $BW^{0.75}$•d^{-1}) of nonlactating, pregnant beef cows (n = 26) maintaining constant body weight for 32 d in yr 3.
Percent difference represents the difference in MR between cows with the greatest and least MR.

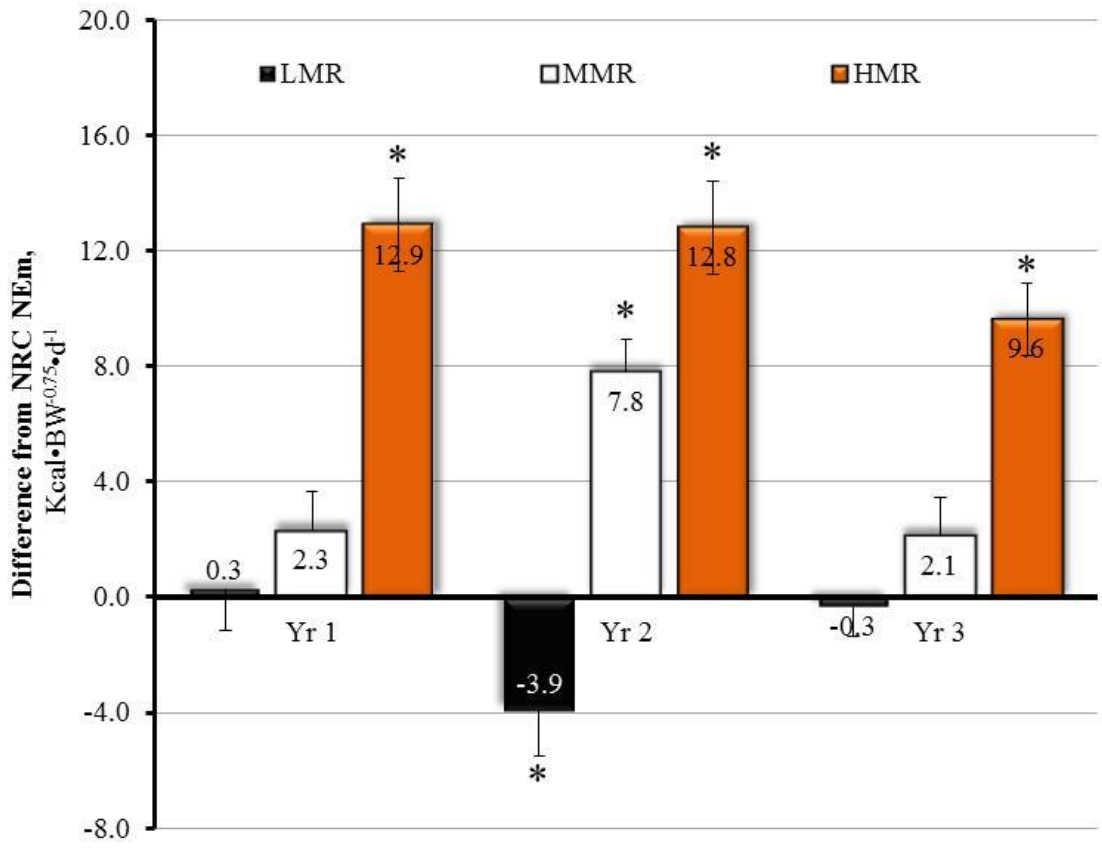

Figure 5. Energy requirement difference from NRC estimated NE_m when beef cows with low (LMR), moderate (MMR) and high (HMR) maintenance energy requirements were fed to maintain constant body weight[1] during mid- to late gestation in yr 1[2], yr 2[3], and yr 3[4].
Pooled S.E. = 1.4.

[1] Cows maintained constant BW for 28, 31, and 32 d in yr 1, yr 2, and yr 3, respectively.

[2] LMR: n = 5; MMR: n = 6; HMR: n = 4

[3] LMR: n = 5; MMR: n = 10; HMR: n = 5

[4] LMR: n = 11; MMR: n = 7; HMR: n = 8

[*] Means within year differ from NRC estimated NE_m ($P \leq 0.03$).

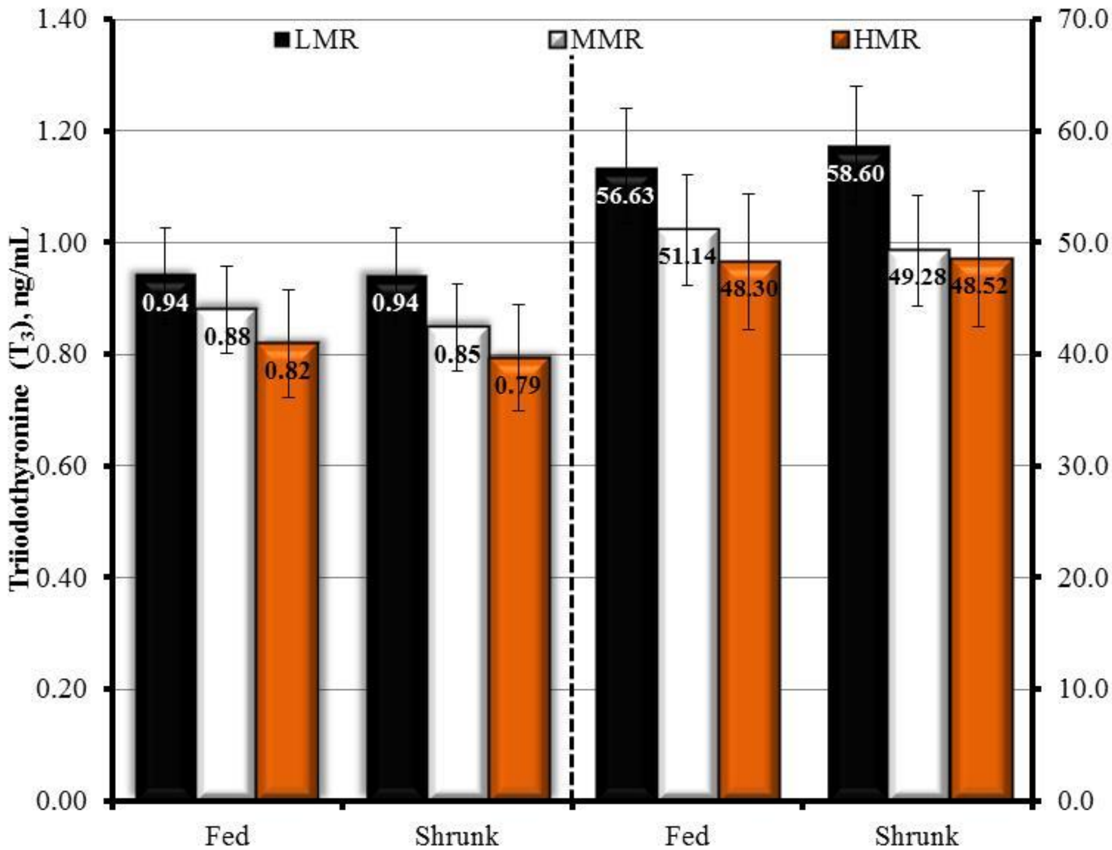

Figure 6. Lack of effect of low (LMR), moderate (MMR), and high (HMR) maintenance energy requirement on plasma concentrations of triiodothyronine (T_3) and thyroxine (T_4) in beef cows (n = 15) maintaining constant body weight within 1 h of feed consumption and ad libitum water (Fed) or 6 h after feed and water restriction (Shrunk) in yr 1.
Pooled S.E. for T_3 = 0.09, T_4 = 5.50.

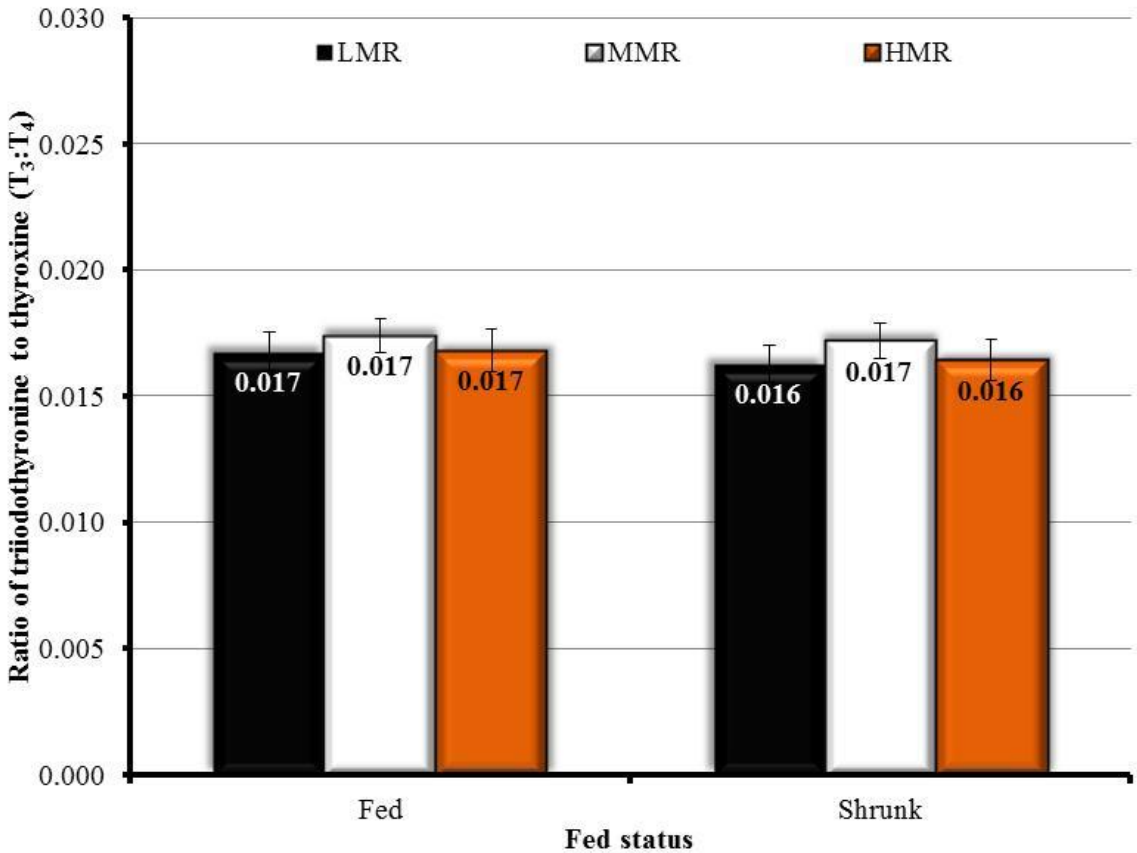

Figure 7. Lack of effect of low (LMR), moderate, (MMR), and high (HMR) maintenance energy requirement on the ratio of triiodothyronine to thyroxine (T_3:T_4) in beef cows (n = 15) maintaining constant body weight within 1 h of feed consumption and ad libitum water (Fed) or 6 h after feed and water restriction (Shrunk) in yr 1.
Pooled S.E. for T_3:T_4 = 0.001.

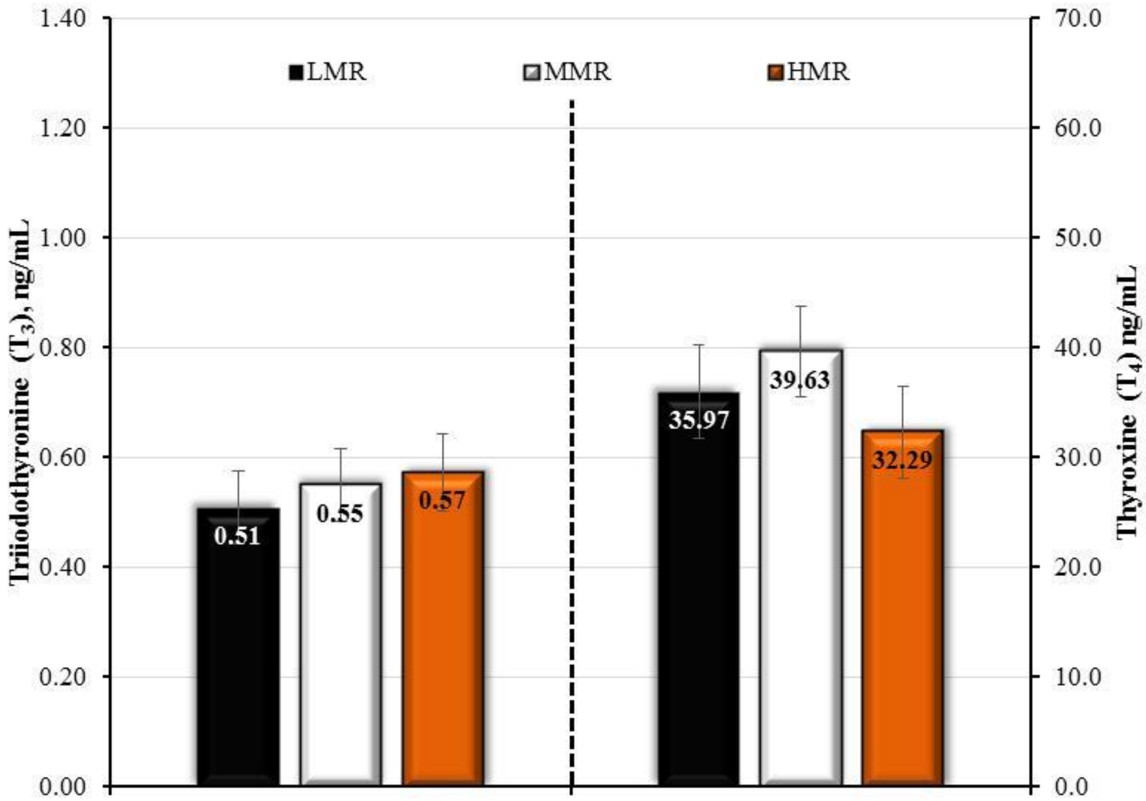

Figure 8. Lack of effect of low (LMR), moderate (MMR), and high (HMR) maintenance energy requirement on plasma concentrations of triiodothyronine (T_3) and thyroxine (T_4) in beef cows (n = 20) maintaining constant body weight after 6 h of feed and water restriction in yr 2.
Pooled S.E. for T_3 = 0.07, T_4 = 4.18.

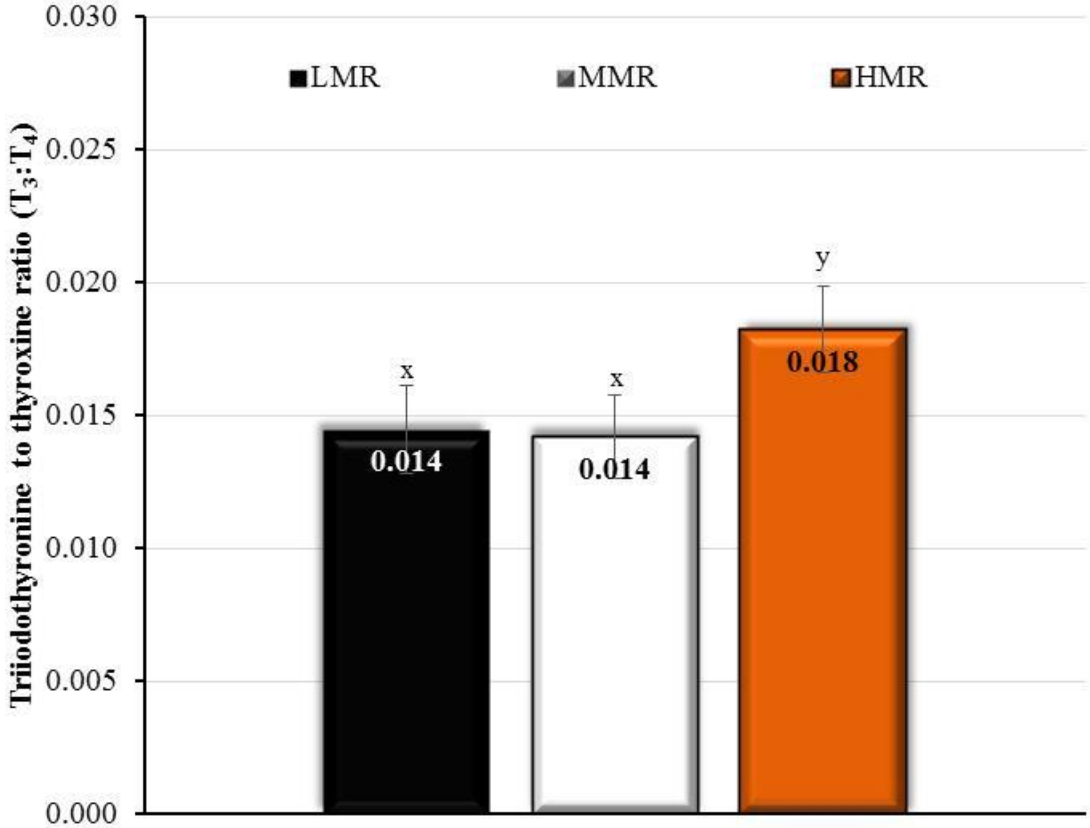

Figure 9. Effects of low (LMR), moderate (MMR), and high (HMR) maintenance energy requirement on the ratio of triiodothyronine to thyroxine (T_3:T_4) in beef cows (n = 20) maintaining constant body weight after 6 h of feed and water restriction in yr 2.
Pooled S.E. = 0.002.
$^{x, y}$ Means differed (*P* = 0.06).

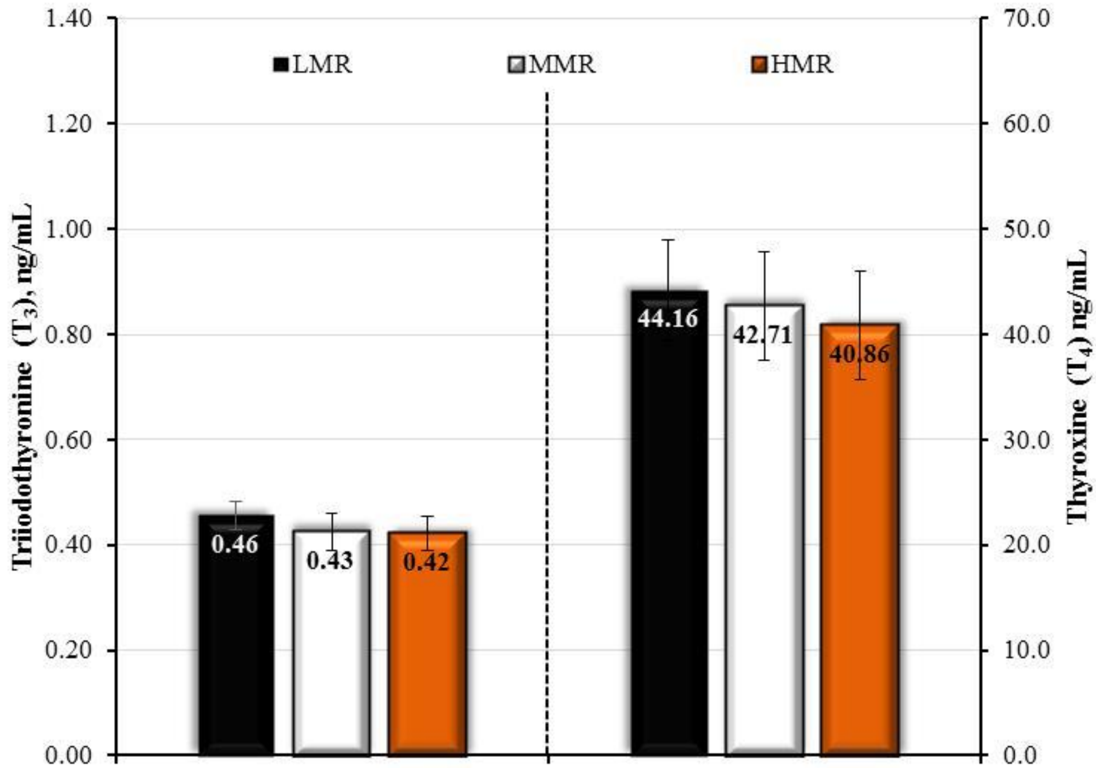

Figure 10. Lack of effect of low (LMR), moderate (MMR), and high (HMR) maintenance energy requirement on plasma concentrations of triiodothyronine (T_3) and thyroxine (T_4) in beef cows (n = 26) maintaining constant body weight after 6 h of feed and water restriction in yr 3.
Pooled S.E. for T_3 = 0.03, T_4 = 5.07.

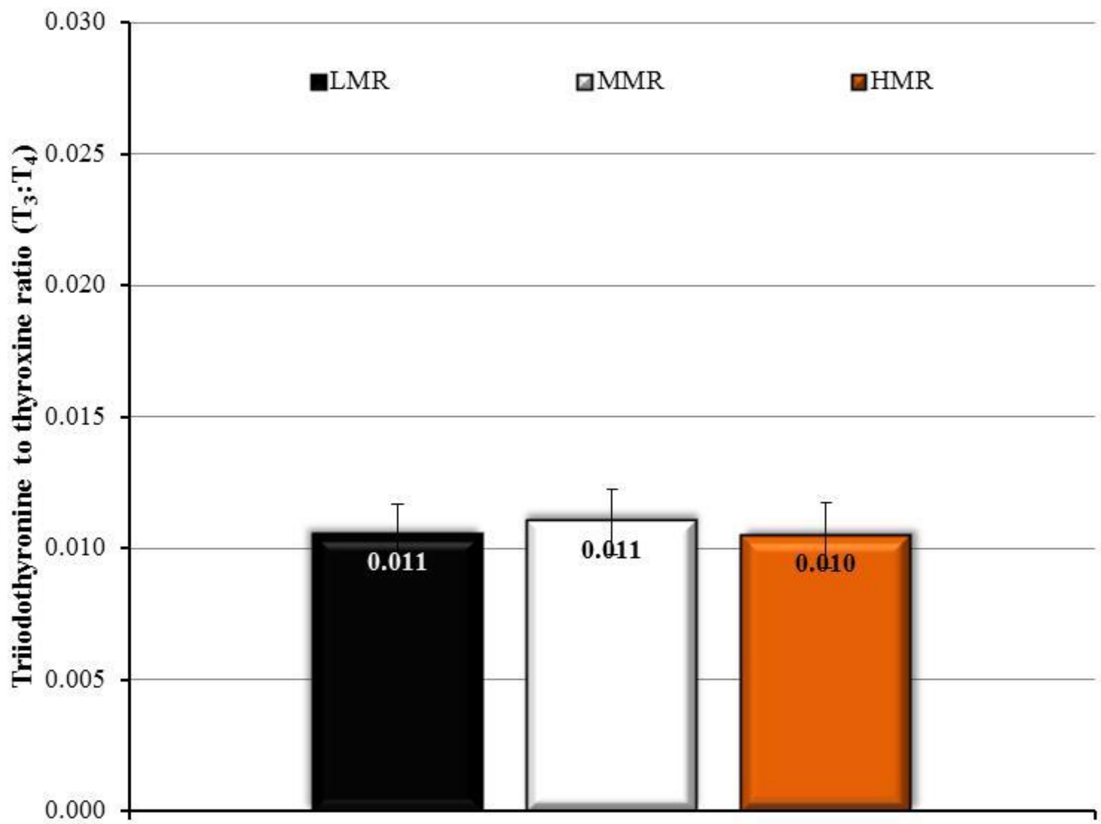

Figure 11. Lack of effect of low (LMR), moderate (MMR), and high (HMR) maintenance energy requirement on the ratio of triiodothyronine to thyroxine (T_3:T_4) in beef cows (n = 26) maintaining constant body weight 6 h after feed and water restriction in yr 3.
Pooled S.E. = 0.001.

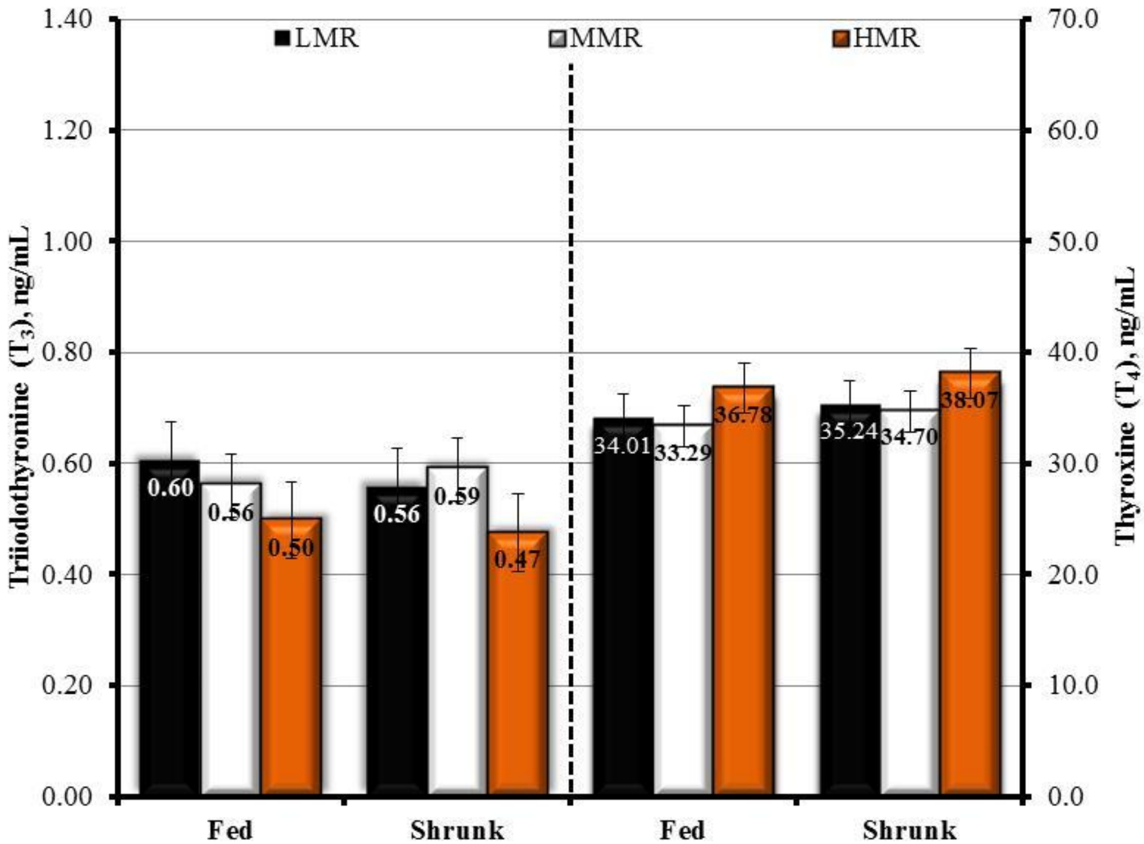

Figure 12. Lack of effect of low (LMR), moderate (MMR), and high (HMR) maintenance energy requirement, on plasma concentrations of triiodothyronine (T_3) and thyroxine (T_4) in beef cows (n = 15) during early lactation within 1 h of feed consumption and ad libitum water (Fed) or 6 h after feed and water restriction (Shrunk) in yr 1.

Pooled S.E. for T_3 = 0.06, T_4 = 2.12.

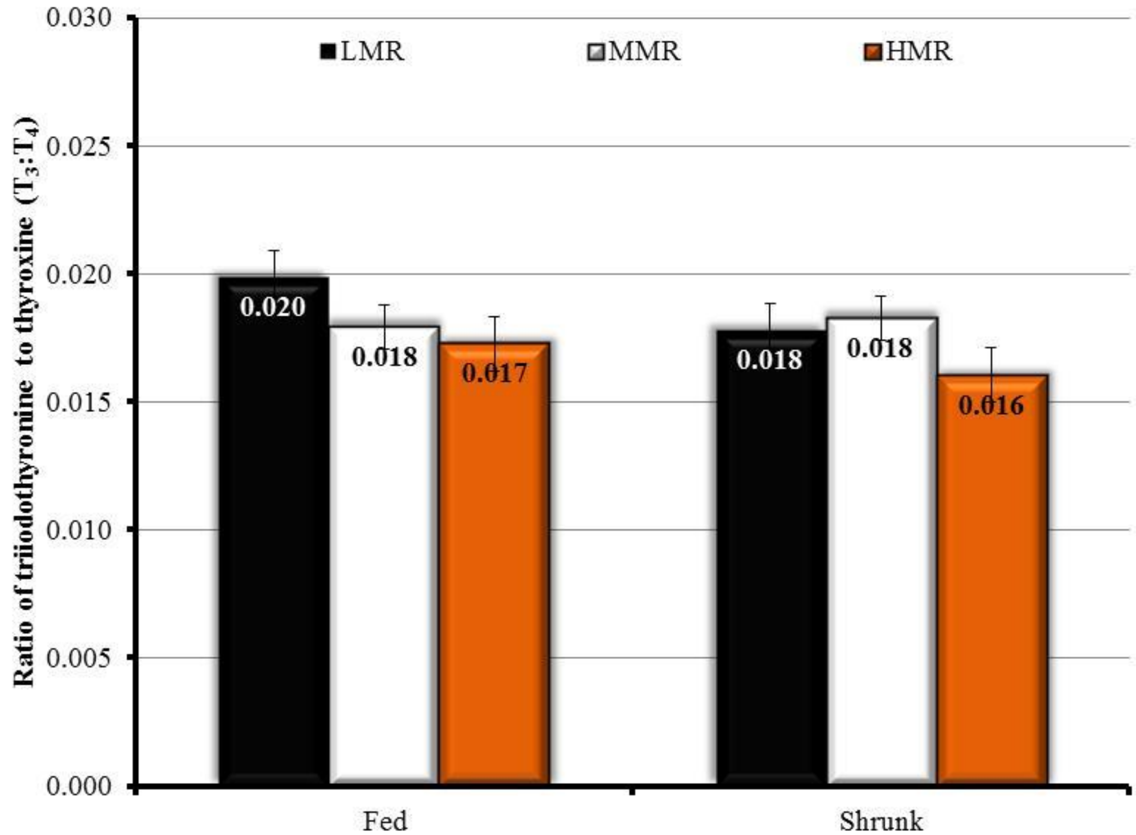

Figure 13. Lack of effect of low (LMR), moderate (MMR), and high (HMR) maintenance energy requirement, and fed status, on ratio of triiodothyronine to thyroxine (T_3:T_4) in beef cows (n = 15) during early lactation within 1 h of feed consumption and ad libitum water (Fed) or 6 h after feed and water restriction (Shrunk) in yr 1.
Pooled S.E. = 0.001.

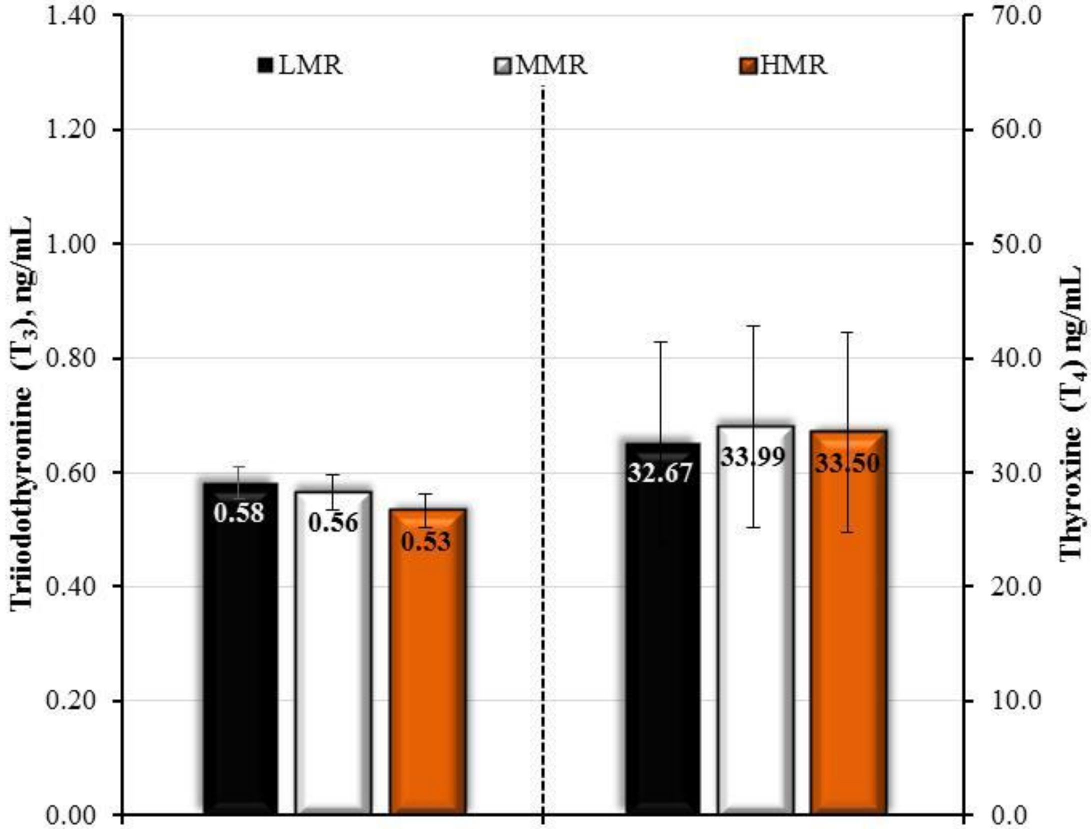

Figure 14. Lack of effect of low (LMR), moderate (MMR), and high (HMR) maintenance energy requirement on plasma concentrations of triiodothyronine (T_3) and thyroxine (T_4) in beef cows (n = 26) during early lactation 6 h after feed and water restriction in yr 3.
Pooled S.E. for T_3 = 0.03, T_4 = 8.78.

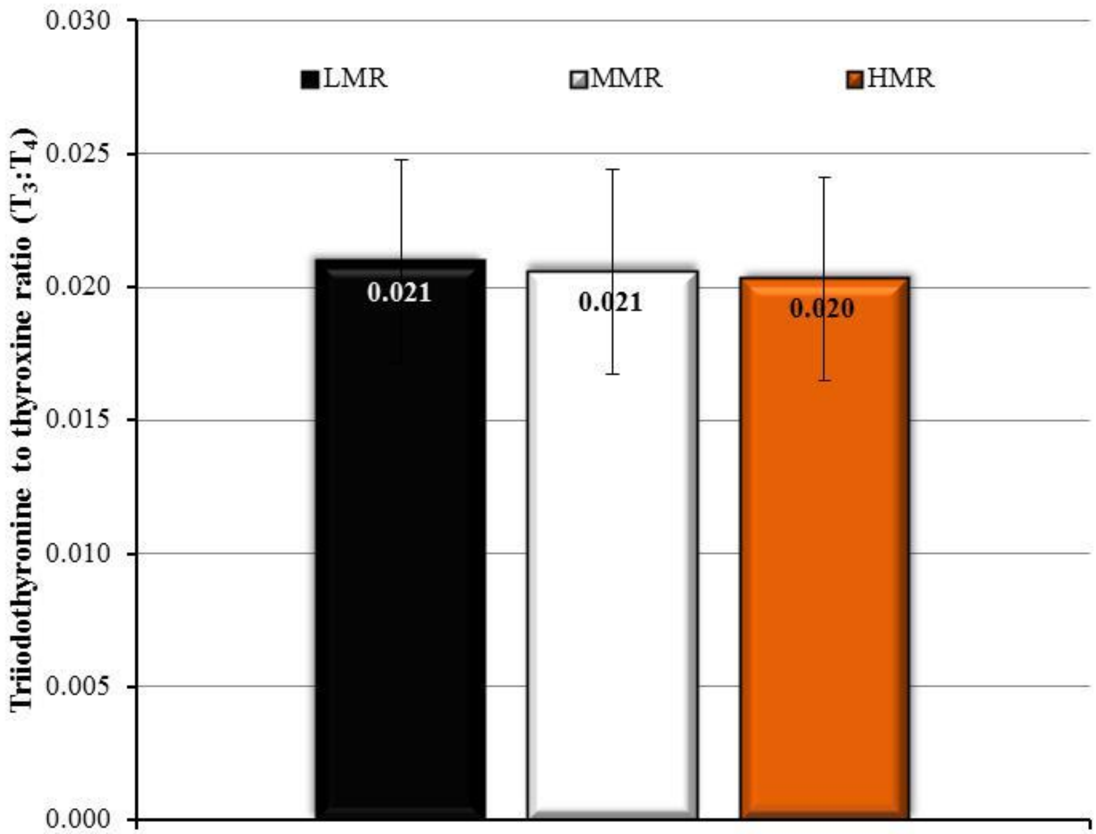

Figure 15. Lack of effect of low (LMR), moderate (MMR), and high (HMR) maintenance energy requirement on the ratio of triiodothyronine to thyroxine (T_3:T_4) in beef cows (n = 26) during early lactation 6 h after feed and water restriction in yr 3.
Pooled S.E. = 0.004.

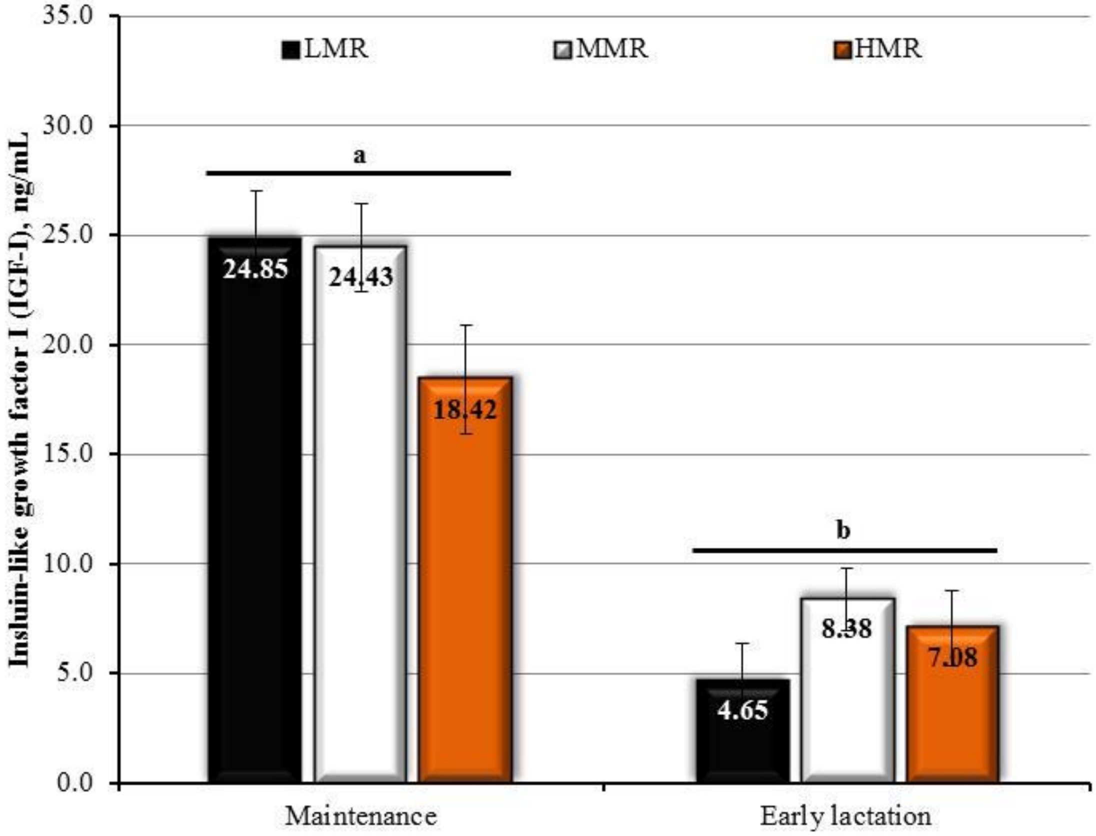

Figure 16. The effects of low (LMR), moderate (MMR), and high (HMR) maintenance energy requirement on plasma concentrations of insulin-like growth factor I (IGF-I) in beef cows (n = 15) at maintenance and early lactation 6 h after feed and water restriction in yr 1.
Pooled S.E. during maintenance = 2.23; during early lactation = 1.64.
[a, b] Means with different letters differ ($P < 0.001$)

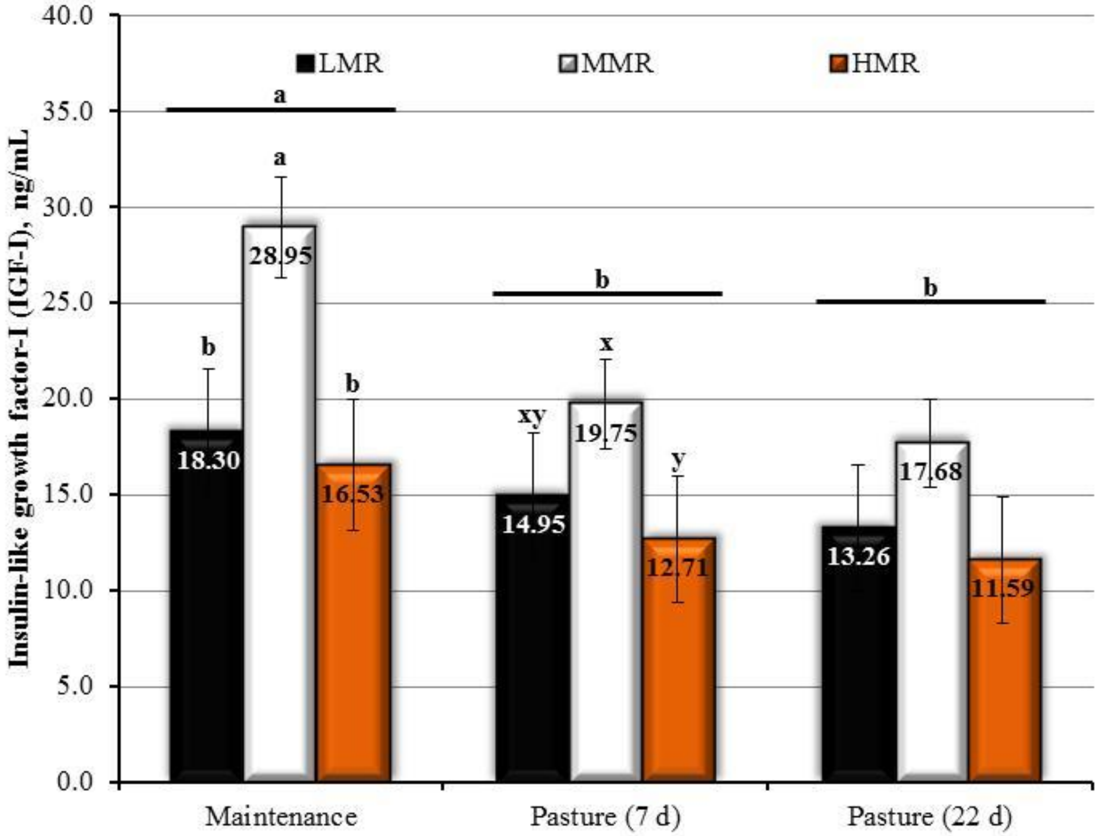

Figure 17. The effects of low (LMR), moderate (MMR), and high (HMR) maintenance energy requirement on plasma concentrations of insulin-like growth factor I (IGF-I) in beef cows (n = 20), 6 h after feed and water restriction, during maintenance and 7 and 22 d after realimentation to pasture in yr 2.

Main effects: MR, $P = 0.07$; Day, $P < 0.001$; MR x Day, $P = 0.16$. Pooled S.E. = 3.02.

[a, b] Means within period differ ($P = 0.01$)

[x, y] Means within period differ ($P = 0.08$)

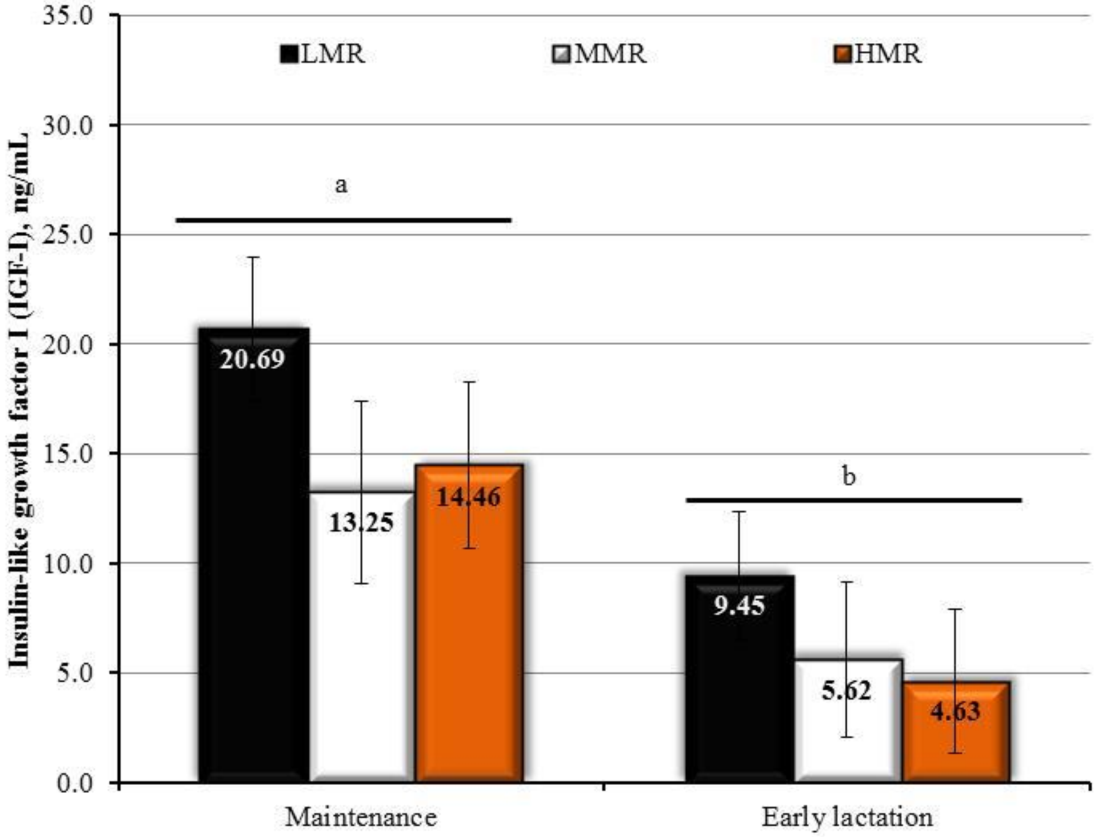

Figure 18. The effects of low (LMR), moderate (HMR) and high (HMR) maintenance energy requirement on plasma concentrations of insulin-like growth factor I (IGF-I) in beef cows (n = 26), 6 h after feed and water restriction, during maintenance of body weight and early lactation in yr 3.

Pooled S.E. during maintenance = 3.75; during early lactation = 3.25

[a, b] Means with different letters differ (*P* = 0.002)

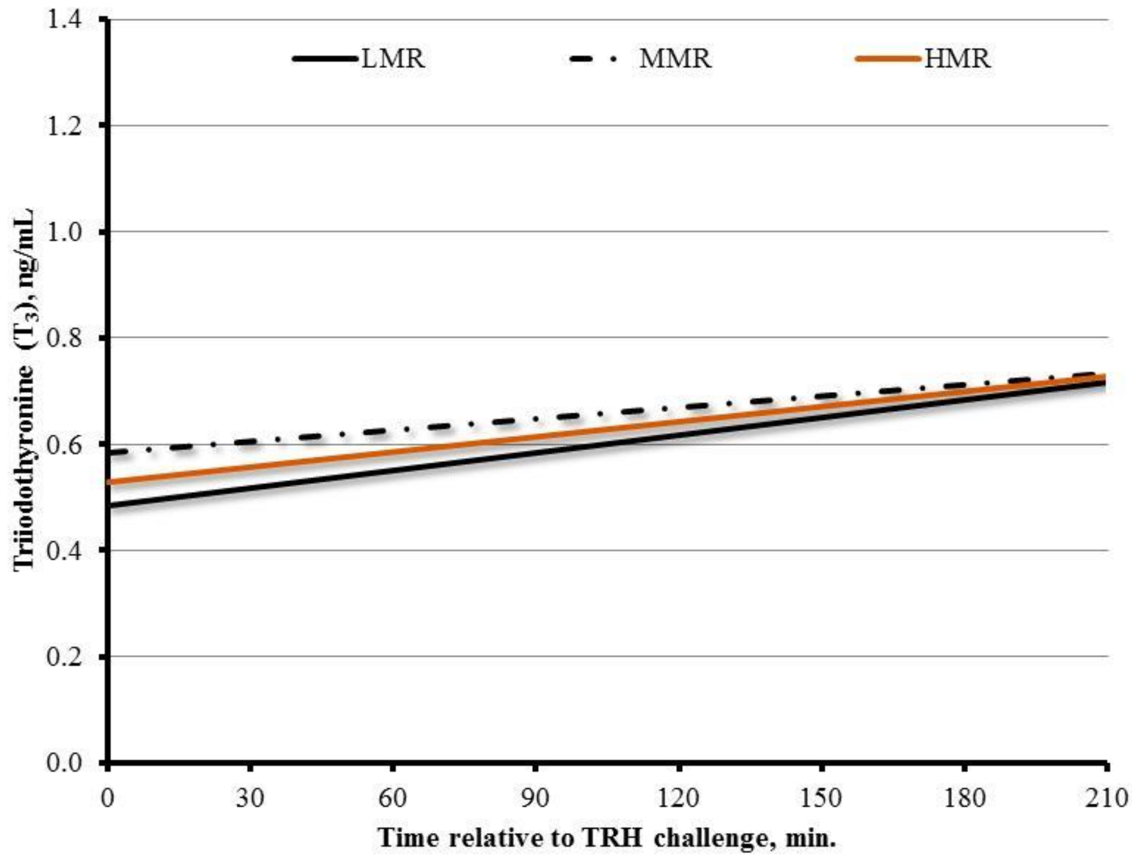

Figure 19. Least squares regression lines for plasma concentrations of triiodothyronine (T_3) in beef cows with low (LMR; n = 5), moderate (MMR; n = 5), and high (HRM; n = 4) maintenance energy requirements during thyrotropin releasing hormone challenge in yr 2.
MR effect, $P = 0.08$. Time effect, $P < 0.001$. Time x MR effect, $P = 0.65$. Pooled SE = 0.06.

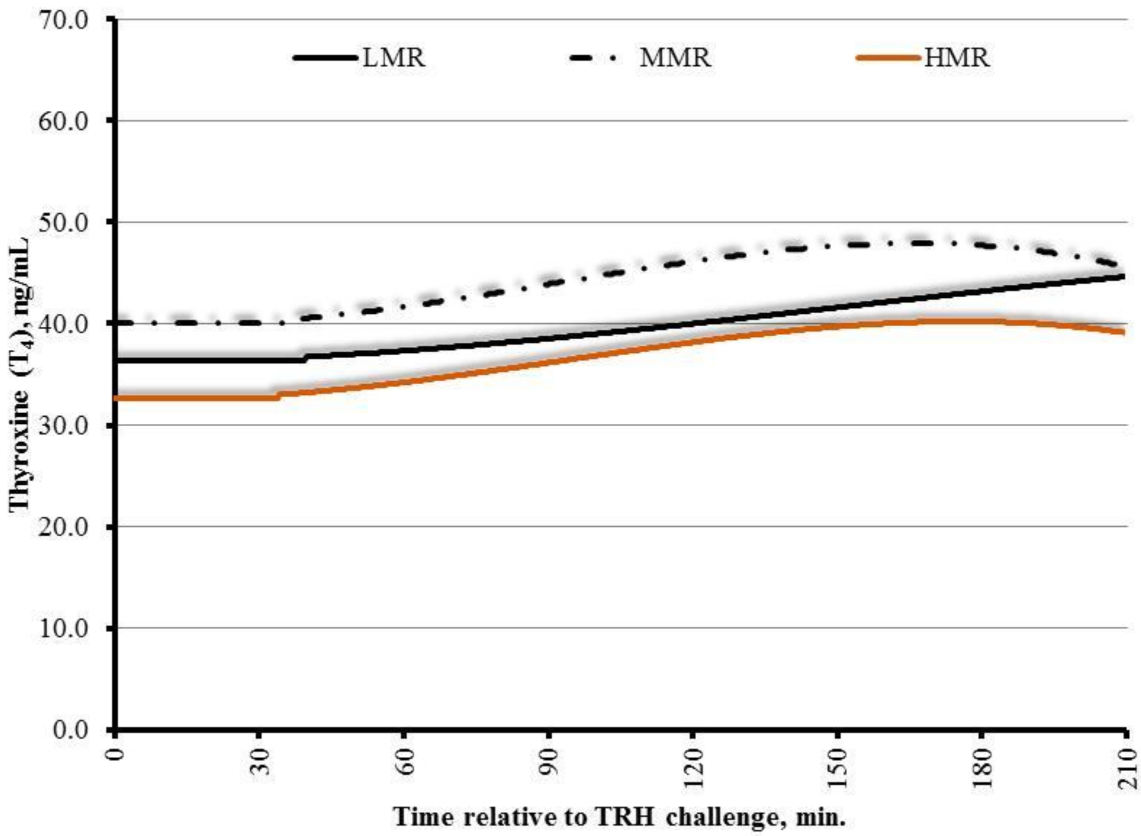

Figure 20. Least squares regression lines for plasma concentrations of thyroxine (T_4) in beef cows with low (LMR; n = 5), moderate (MMR; n = 5), and high (HRM; n = 4) maintenance energy requirements during thyrotropin releasing hormone challenge in yr 2.
MR effect, $P < 0.001$. Time effect, $P < 0.001$. Time x MR effect, $P = 0.83$. Pooled SE = 3.4.

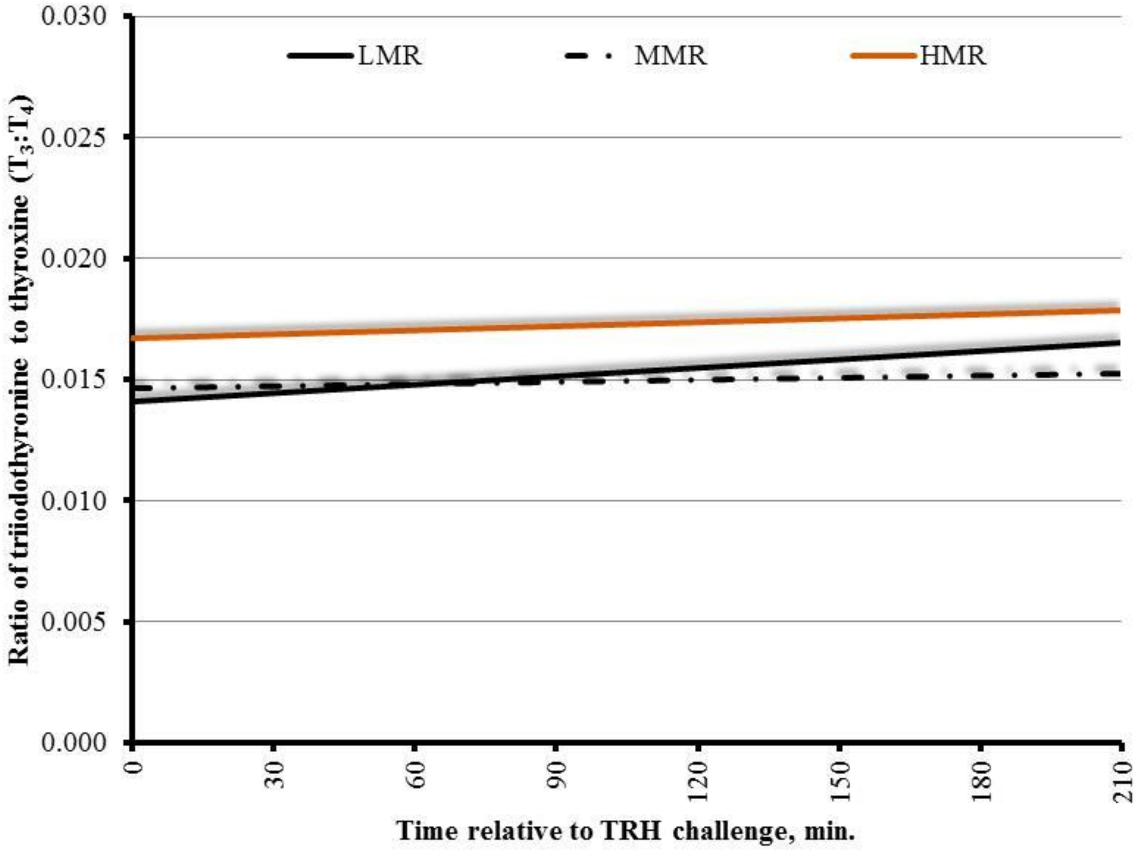

Figure 21. Least squares regression lines for the ratio of triiodothyronine to thyroxine (T_3:T_4) in beef cows with low (LMR; n = 5), moderate (MMR; n = 5), and high (HRM; n = 4) maintenance energy requirements during thyrotropin releasing hormone challenge in yr 2.
MR effect, $P < 0.001$. Time effect, $P = 0.65$. Time x MR effect, $P = 0.93$. Pooled SE = 0.001.

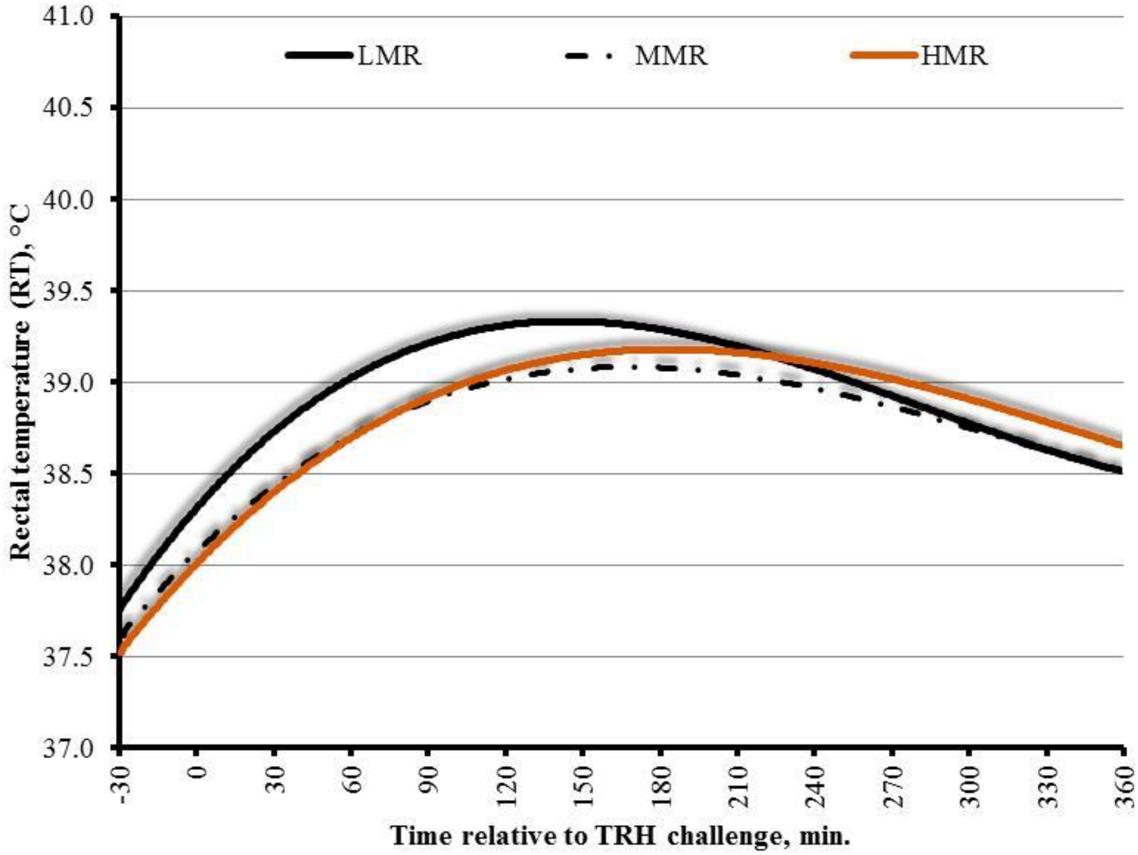

Figure 22. Least squares regression lines for rectal temperature (RT) in beef cows with low (LMR; n = 5), moderate (MMR; n = 5), and high (HMR; n = 4) maintenance energy requirements during thyrotropin releasing hormone challenge in yr 2.
MR effect, $P < 0.003$. Time effect, $P < 0.001$. Time x MR effect, $P = 0.85$. Pooled SE = 0.17.

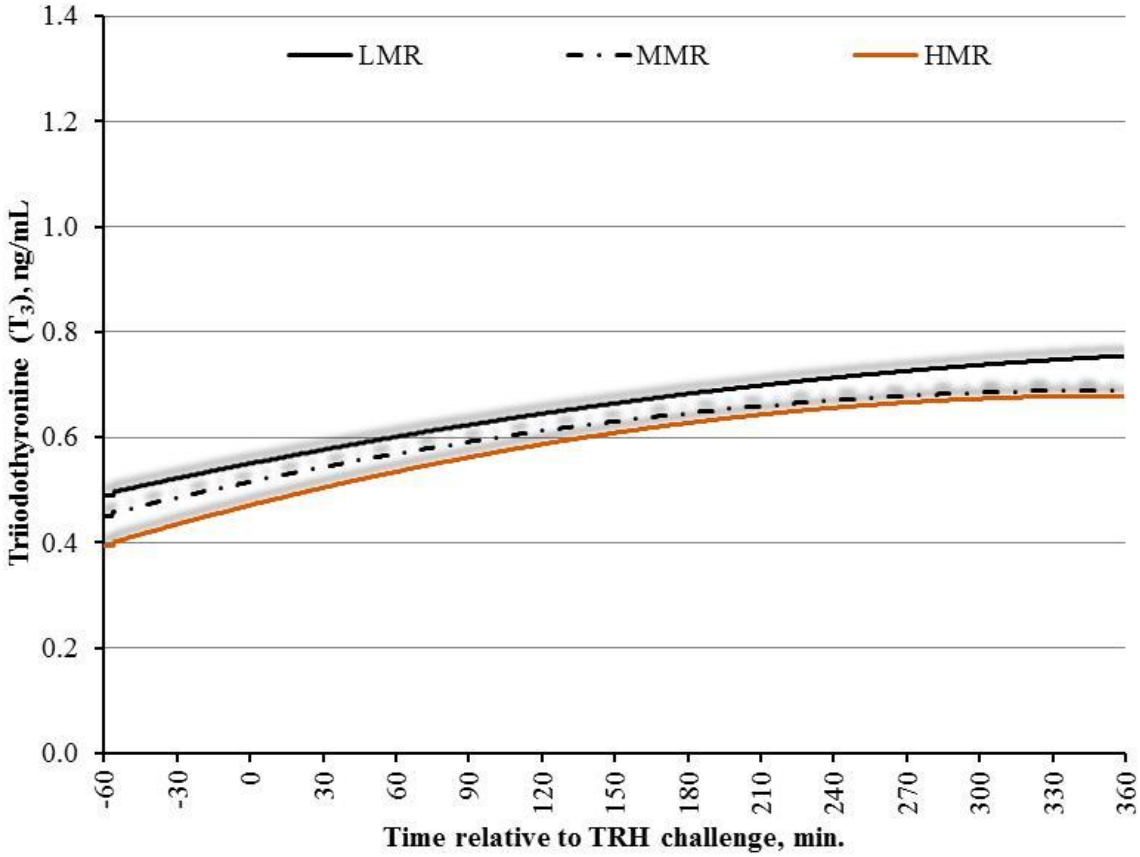

Figure 23. Least squares regression lines for plasma concentrations of triiodothyronine (T_3) in beef cows with low (LMR; n = 9), moderate (MMR; n = 5), and high (HMR; n = 6) maintenance energy requirements during thyrotropin releasing hormone challenge in yr 3.
MR effect, $P = 0.001$. Time effect, $P < 0.001$. Time x MR effect, $P = 0.99$. Pooled SE = 0.05.

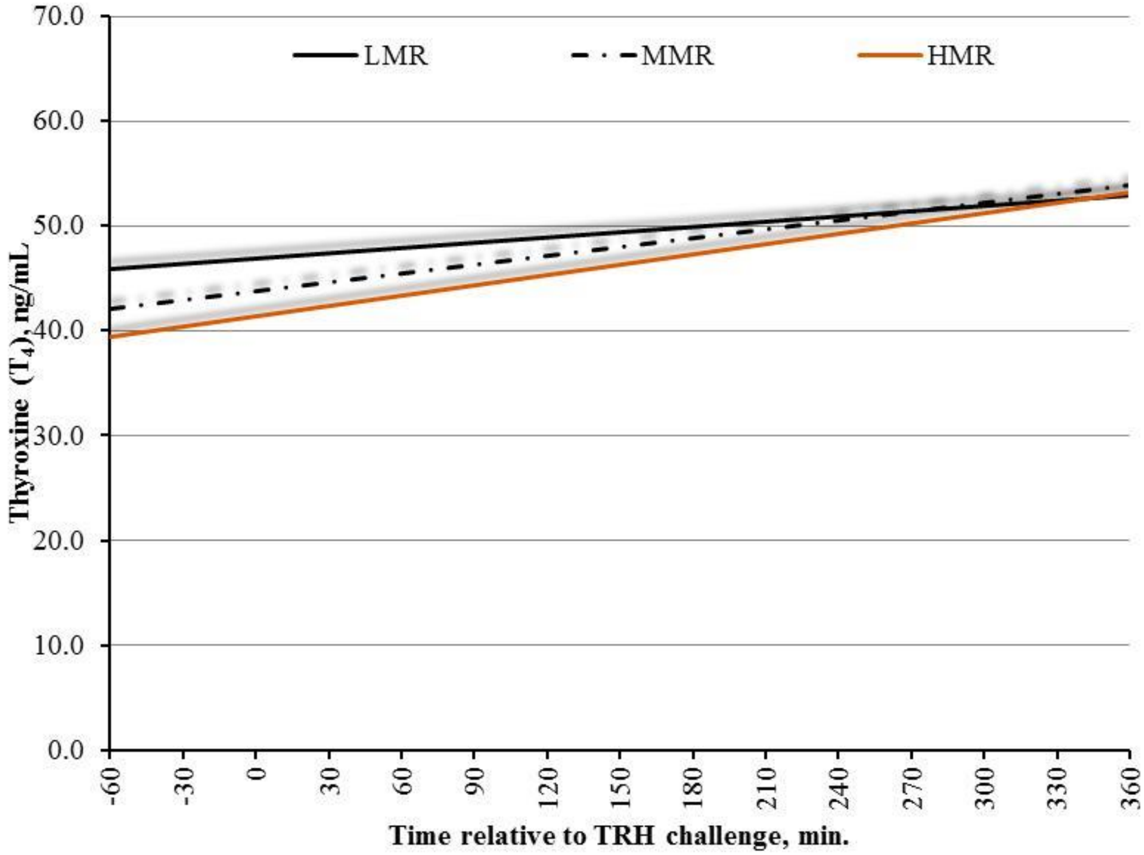

Figure 24. Least squares regression lines for plasma concentrations of thyroxine (T_4) in beef cows with low (LMR; n = 9), moderate (MMR; n = 5), and high (HMR; n = 6) maintenance energy requirements during thyrotropin releasing hormone challenge in yr 3.
MR effect, P = 0.06. Time effect, P < 0.001. Time x MR effect, P = 0.76. Pooled SE = 3.94.

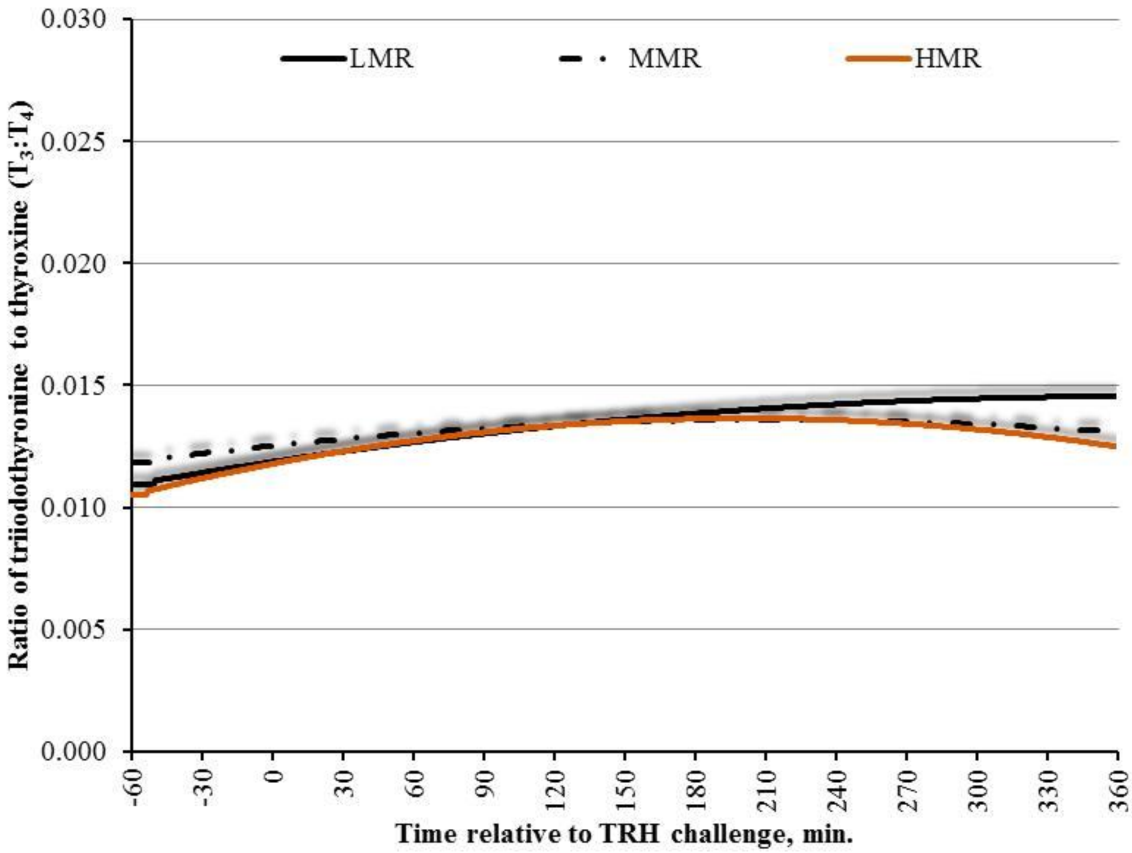

Figure 25. Least squares regression lines for the ratio of triiodothyronine to thyroxine (T_3:T_4) in beef cows with low (LMR; n = 9), moderate (MMR; n = 5), and high (HMR; n = 6) maintenance energy requirements during thyrotropin releasing hormone challenge in yr 3.
MR effect, P = 0.65. Time effect, P < 0.003. Time x MR effect, P = 0.79. Pooled SE = 0.001.

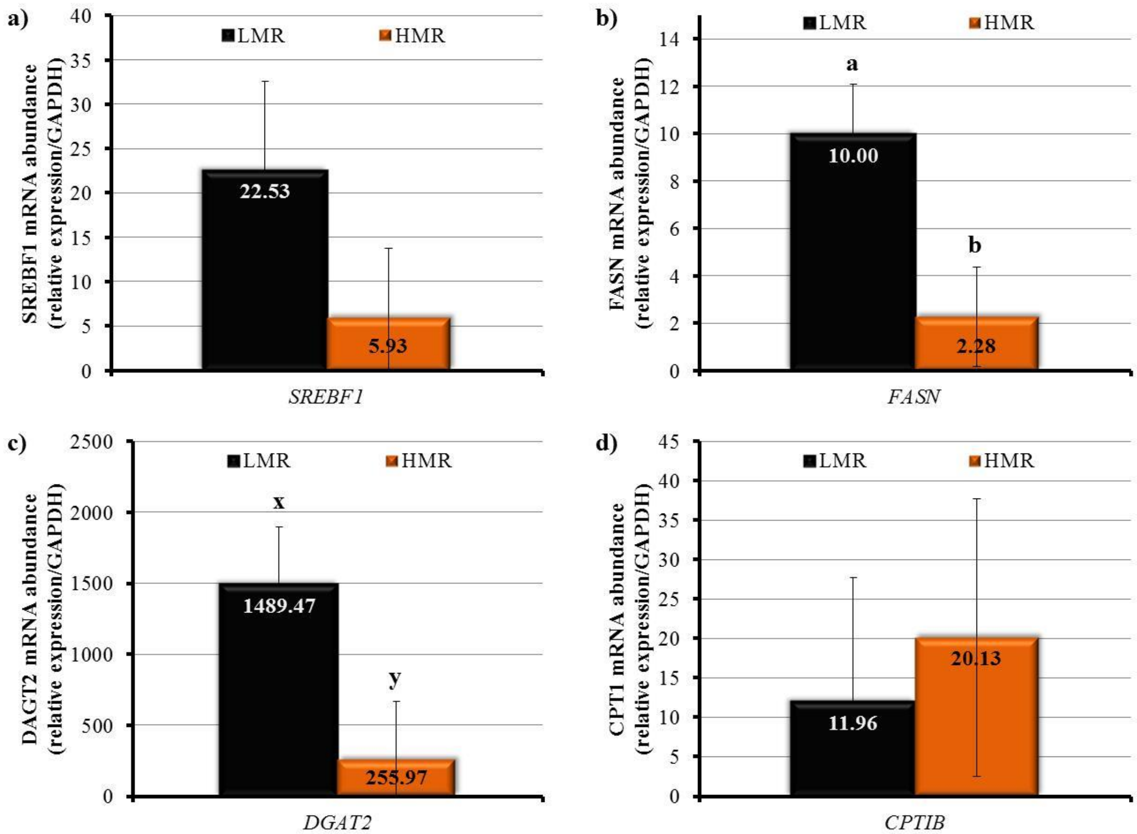

Figure 26. Expression of lipogenic and lipolytic genes[1] during maintenance of constant body weight in longissimus muscle of beef cows with low (LMR) and high (HMR) maintenance energy requirements in yr 3.

[1] *SREBF1* = sterol regulatory element binding factor 1; *FASN* = fatty acid synthase; *DGAT2* = diacylglycerol acyltransferase 2; *CPT1B* = carnitine palmitoyltransferase 1B

[a, b] Means differ ($P = 0.04$)

[x, y] Means differ ($P = 0.07$)

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VITA

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