

EFFECTS OF DIETARY ENERGY DENSITY AND INTAKE ON MAINTENANCE  
REQUIREMENTS IN BEEF COWS

A Thesis

by

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## ABSTRACT

A variety of issues concerning the sustainability of beef production systems, including alternative land use decisions and liquidation in cow inventory, have magnified the need to enhance system efficiency. One approach to increasing production efficiency is through the intensification of cow-calf systems. In intensified systems cows will be housed in a controlled environment (i.e. drylot) for at least a portion of their reproductive cycle, subsequently offering the opportunity to develop nutritional manipulation strategies to optimize cow efficiency. An experiment was conducted to analyze the effects of dietary energy density and intake on maintenance energy requirements in beef cows. In a  $2 \times 2$  factorial treatment arrangement, thirty-two crossbred cows were fed either a high- (**H**, 2.54 Mcal ME/kg) or a low-energy (**L**, 1.96 Mcal ME/kg) diet at one of two levels of intake (**80**; 80% NRC NE requirements, **120**; 120% NRC NE requirements). Several methods using empirical equations were used to estimate body energy on d 0 and 56 as a proxy for RE. HE was calculated as the difference between ME and RE. Body weight gain tended to be greater ( $P = 0.08$ ) in H than L, but was not different ( $P = 0.12$ ) between 120 than 80. Retained energy tended to be greater ( $P \leq 0.10$ ) in H than L and greater ( $P \leq 0.08$ ) in 120 than 80. Heat energy per  $EBW^{0.75}$  was greater ( $P < 0.01$ ) in L than H and greater ( $P < 0.01$ ) in 120 than 80, with no interaction ( $P = 0.29$ ). Birth weight and adjusted 205-d weaning weight of the calves from treated cows were not affected by diet ( $P > 0.22$ ) or level of intake ( $P > 0.56$ ). Feed requirement for maintenance was calculated to be 92.54 and 168.06 kcal ME/ $EBW^{0.75}$

for H and L, respectively. Fasting heat production was estimated to be 54.60 and 74.78 kcal/EBW<sup>0.75</sup> for H and L, respectively. Overall, increasing dietary energy density resulted in a decrease in maintenance requirements of approximately 28% and intake restriction decreased HE by approximately 28%, with no interaction, suggesting additive effects. Limit feeding high-energy diets to beef cows has the potential to increase the efficiency of production and land use in U.S. cow-calf systems.

## DEDICATION

To Mr. and Mrs. Anthony John Trubenbach, Jr.,

I have attempted to write this section multiple times; each time, I have found myself sitting silently in reflection of the glowing love that you have shown our family. Quite literally, the only thing I can think to say to you is, “Thank you.”

Thank you for the opportunity to pursue the career that I am so passionate about. Thank you for being the center of our family, and for the unconditional love that you have shown us. Most importantly, thank you for being the most perfect example of Christ that I can possibly imagine.

I can only pray that I become the man of character that I see in Tony and that I marry a woman who shows me the unwavering dignity and affection for life that Thelma has shown us all.

Mark 10: 6-9

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# CHAPTER I

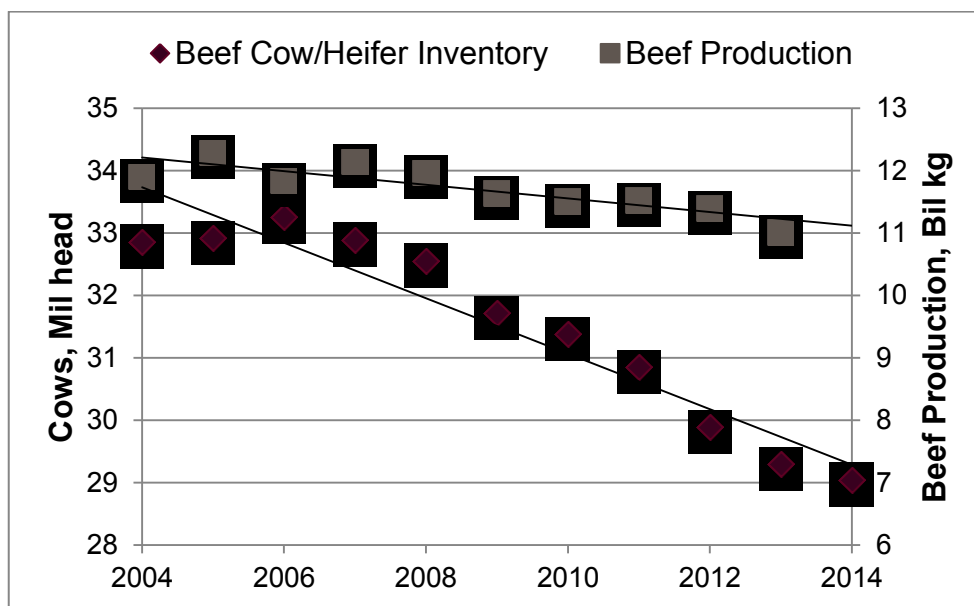
## INTRODUCTION AND REVIEW OF LITERATURE

### *Introduction*

Current economic signals, such as historically high positive cash margins, suggest that expansion should be occurring in cow-calf production systems; however the cow herd has been in a liquidation phase since its peak in 1978 (Trubenbach et al., 2014; NASS, 2014). Since 2003, average pastureland value in the US increased by over 98% (NASS). The US beef supply has also declined in recent years, although at a slower rate than that of cow liquidation (NASS, 2014; Figure 1.1). Divergence in the trend lines suggest increased production per cow; however, this divergence will reach limits, in terms of production capacity per cow, and cannot be depended upon as a solitary source of future gains in production capacity. The overall decline in these parameters indicates constraints in the production system, which are challenging the sustainability of its supply. There exists a real need to increase production efficiency to relieve pressures currently restraining beef production capacity in the US.

Bioenergetic efficiency in animal production has been researched since the 19<sup>th</sup> century and additional research has the potential to advance system efficiency via nutritional manipulation. Beef cattle bioenergetics incorporates an energy accounting system that utilizes empirical equations to account for biological uses of energy, ultimately resulting in NE values. The NRC (2000) defines metabolizable energy (ME) as gross energy less fecal energy, urinary energy, and gaseous energy losses; more

directly, ME is the energy available to the animal for metabolism. Metabolizable energy has two possible fates: retention in the form of tissue energy (RE) or conversion into heat energy (HE). Retained energy represents ME that is stored biochemically and incorporated into a biological product. Heat energy is ME that is not retained, a loss of energy from the production system.



**Figure 1.1** Current trend of beef cow inventory and beef production (NASS, 2014)

Partial efficiency is the proportion of ME that is accumulated as RE.

Mathematically, partial efficiency of production is described as the slope ( $k_p$ ) of the linear function of the dependent variable RE relative to the increase in the independent variable metabolizable energy intake (MEI) for  $RE > 0$ . When  $RE < 0$ ,  $k_m$  represents the partial efficiency (slope) of ME use to support maintenance metabolism. Overall, the

focus of nutritional strategies for cow-calf systems is to optimize products of RE (i.e. fetus and milk) per unit of ME consumed. One strategy to enhance bioenergetic efficiency in an intensified cow-calf system is to reduce maintenance energy costs in the cow.

Armsby and Fries (1919) were the first to create distinction between energy use for maintenance and production, stating that feedstuffs are described by two energy or “starch” values, one maintenance and the other production. They suggested that feed energy values for maintenance were most likely greater than those for production. Once this partitioning was put forth, research efforts focused on factors affecting the efficiency of ME use: ruminal VFA production and utilization, level of intake relative to maintenance, and product formation (protein vs. fat). Heat production can be divided into two categories: fasting heat production (FHP) and heat increment (HI), each representing one pathway for diet to affect energetic efficiency. Alterations in FHP are associated with effects on total body tissue metabolism, while HI is used to describe the heat associated with feed consumption, digestion and absorption. In other words, there are two components of heat production: one truly related to maintenance, and the other representing the cost of acquisition. Because of this perplexing issue, the effects of dietary energy on all sources of heat production must be examined in order to understand total efficiency of energy use.

Energy density (forage:concentrate ratio) of a diet has an effect on both FHP and HI (Ferrell and Oltjen, 2008) Total MEI also affects maintenance equilibrium, in terms of both FHP and HI (Freetly and Nienaber, 1998). The current discussion will examine

the effects of dietary ME density and MEI on maintenance requirements of beef cows, with the intent of using this understanding to identify opportunities to improve cow-calf production efficiency.

*Effects of energy density on production and energy utilization*

Swingle, et al. (1979) demonstrated the effects of feeding high- and moderate-energy density rations *ad libitum* on composition and efficiency of gain in compensating beef cows. Rate and efficiency of gain were increased with energy density, while composition of gain was not affected, in accordance with Garrett et al., (1987) and Guenther et al., (1965). Using their data and the NRC model to estimate ME intake, moderate- and high-energy density groups consumed 38.9 and 34.3 Mcal ME per day, respectively. Using the NRC to calculate energy content of lipid and protein gain, yielded daily RE of 177 and 248 kcal/Mcal ME for moderate- and high- energy density groups, respectively. Subtracting calculated RE values from ME results in HE, which was 24.0 % greater in cows consuming the moderate- energy density diet (32.0 Mcal/d) than the high- energy density diet (25.8 Mcal/d). Their data suggests that the differences in efficiency of ME use resulted in greater energetic efficiency in cows fed the high-energy ration.

Sawyer et al. (2004) reported similar effects in a short-term feeding trial, using compensating cows, fed an *ad libitum* diet using one of three strategies: conservative (30% roughage throughout); standard (decreased roughage from 30 to 10% over 20 d); and aggressive, decreased roughage from (30 to 10% over 10 d). Increasing energy density from conservative to standard or aggressive increased ADG and decreased DMI,

such that G:F was lower for conservative than standard and aggressive. There was no difference in overall ADG, DMI or G:F between standard and aggressive, indicating the actual shift from a low- to high-energy diet (regardless of the rate of transition) was the most significant driver of efficiency.

Sainz *et al.* (1995) reported similar results in production efficiency in growing calves fed either a low-energy diet *ad libitum*, or limit-fed a high concentrate ration designed to achieve similar rates of gain. Low-energy calves consumed more feed per day, but daily gains were similar and EBW gain:feed was decreased compared to limit-fed calves. Fatness was measured in several locations on the carcass, including backfat, KPH, abdominal fat, marbling score and carcass fat (based on density) and was less in low-energy calves than high-energy calves. Carcass density was greater in low-energy calves, indicating a smaller proportion of RE was partitioned toward lipogenesis, even though BW gains were similar. Calves consuming the low-energy diet reportedly consumed 11.9% more ME ( $253 \text{ kcal} \cdot \text{EBW}^{-0.75}$ ) than calves consuming the high-energy ( $226 \text{ kcal} \cdot \text{EBW}^{-0.75}$ ) diet, but RE was not different. Accordingly, calves on the low-energy diet produced more heat ( $218 \text{ kcal} \cdot \text{EBW}^{-0.75}$ ) than calves consuming the high-energy diet ( $177 \text{ kcal} \cdot \text{EBW}^{-0.75}$ ). This suggests greater ME use efficiency in calves limit-fed the high-energy diet.

Results presented by McLeod and Baldwin (2000) when growing lambs were fed similar amounts of ME as either a high- or low-energy diet were similar. High-energy lambs had greater ADG and gain:feed, indicating that a greater amount of ME was partitioned for gain, relative to lambs consuming the low-energy ration. This also

indicated that, in high-energy lambs, a smaller proportion of ME was lost as heat in the form of FHP and HI.

Reynolds et al., (1991b) evaluated the effects of feeding heifers similar amounts of ME from diets differing in ME density. Direct calorimetric measures of heat expenditure indicated that heifers consuming a high-energy ration tended to produce 7% less heat than heifers consuming a high forage diet. This difference is smaller than suggested by other studies, which was likely due to the pelleting of the diets. Pelleting has been shown to decrease HI; HI could represent a major portion of ME use in low-energy diets (Bull et al., 1970). Reducing HI by pelleting could explain the relatively smaller difference in HE in the Reynolds et al. (1991b) results.

In a trial conducted by McCurdy et al. (2010), growing calves were fed either a sorghum silage-based ration *ad libitum* or a high-energy ration (program-fed) at a level to promote similar gain as the silage-fed calves. Total RE was greater in program-fed calves than silage-fed calves. Program-fed calves retained more fat than silage-fed calves. Results were similar to those presented by Geay (1984), who concluded that efficiency of ME use for tissue deposition (RE/MEI) decreases in a curvilinear manner as proportion of protein in RE increases. In McCurdy et al. (2010), energetic efficiency (ME per unit of RE) of protein deposition is less than lipid deposition, partially because the proportion of energy used for protein turnover is higher. However, production efficiency (gain:feed) is inversely related to proportion of fat deposition, as protein deposition results in greater carcass weight than fat deposition. Protein contains a greater amount of water weight, which contains no energy, resulting in a smaller energy value

per unit of mass in protein than in fat deposition. It is also difficult in this study to separate the confounding effects of MEI and DMI, which is an issue that will be further discussed in this article.

Growing animals have not yet reached maturity, and are therefore increasing skeletal mass. (Randel and Welsh, 2013). Composition of gain in growing animals varies with diet energy density, possibly due to differences in signals controlling energy partitioning. Protein accretion increases protein turnover and associated energy requirements (Johnson, 1987). Although dietary energy density appears to affect energy partitioning between protein and fat accretion in growing cattle, the same is not always true in mature cows near a BCS 5 (Garrett et al., 1987; Guenther et al., 1965; Swingle et al., 1979). Theoretically, mature cows have achieved a stable skeletal size, but BW can be altered by changes in total body fat and protein. Replenishment of lost tissue during realimentation is efficient from a gain:feed standpoint; however, efficiency of gain falls severely as energy begins to be partitioned toward body reserves. Energy efficiency (RE/MEI) of tissue deposition in cows is similar to that in growing animals; however, proportion of tissue deposited as fat and protein differs considerably, especially above BCS 5.

#### *Effects of energy density on visceral organ mass*

McLeod and Baldwin (2000) conducted a trial where lambs were fed rations containing either 75% forage or 75% concentrate at isocaloric levels of ME to demonstrate the effects of dietary energy density on visceral organ mass. Digestive tract, small intestine and liver weights were greater in lambs fed forage than lambs fed

concentrate. Similarly, when expressed as a percentage of body weight, kidneys, digestive tract mass and mass of all individual segments thereof were greater or tended to be greater in lambs fed forage vs. concentrate. Liver weight per unit of total and empty body weight was not different between treatments, indicating that liver growth was related to overall body growth and not tissue-specific growth. Observations that VOM is affected by forage:concentrate ratio was contradicted by Johnson, et al. (1987) who showed that the percentage of forage:concentrate in the diet of sheep had no effect on total digestive tract weight. In the study by McLeod and Baldwin (2000), epithelial mass was greater in lambs consuming forage than in lambs consuming concentrate, which is consistent with an increase in energy metabolism and heat production. Dietary energy density is most often manipulated by increasing the percentage grain (concentrate) in the diet, meaning that low energy density diets usually possess greater forage inclusion. Much like results from McCurdy et al. (2010), it is often difficult to avoid confounding effects of energy density with dry matter intake and bulk density. For the purpose of this discussion, energy density and concentrate:forage ratio will be discussed as similar concepts, even if the two descriptions are not completely analogous. There are no studies reported in which the effects of both energy density and energy intake are isolated without confounding with DMI.

McCurdy et al. (2010) reported data that supports Johnson et al. (1987), but is in contrast to McLeod and Baldwin (2000). Organ mass change was determined by comparing carcasses slaughtered at the end of the project and prior to being placed on the study. When calves were fed either a high- or low-energy ration, there were no



differences reported in any internal organ mass, either expressed per metabolic body weight or on a total weight basis. It is possible that HI accounted for the increased amount of MEI in low-energy calves. Holmes et al. (1978) demonstrated that eating energy expenditure is greater per kg DM in younger animals than older animals.

Rompala et al. (1988) reported that energetic efficiency of lambs was affected by DMI, separate from effects of energy consumption. In this trial, lambs were fed isocaloric amounts of either a control diet or a diet containing 10% polyethylene, a chemically inert additive, to demonstrate the effects of dietary bulk on energy metabolism. Adding polyethylene to the diet increased DMI by 10% without affecting energy intake. Lambs consuming the polyethylene diet had heavier large intestine, stomach, heart, lung and kidney weights, indicating a sensitivity of these organs to total luminal contents. Liver and small intestine mass was not affected by polyethylene consumption. Rompala and Hoagland (1987) reported a similar lack of sensitivity in the liver and small intestine to increases in DMI. When lambs were subjected to a 48 h fast, there was no difference in FHP. Results from this study suggest that a change in heat production associated with bulk intake may be more related to HI than an increase in FHP; however, it was noted that it is possible that variance in measuring FHP resulted in the lack of a difference in this study.

Energy density affects DMI in ruminants, which impacts heat production (Fluharty et al., 1994; Jenkins and Ferrell, 1997). Because diets of differing forage:concentrate ratios frequently contain differing amounts of  $\text{ME} \cdot \text{kg}^{-1}$ , adjusted levels of dry matter intake are necessary to establish isocaloric trial designs, as discussed

by Rompala et al. (1988). Because DMI and MEI were not simultaneously at equilibrium in the presented data, the distinction between effects of chemical attributes and physical form are difficult to differentiate; however, it does appear that DMI has an effect on heat production, separate from MEI (Rompala et al., 1988).

#### *Effects of energy density on oxygen consumption*

In the previously described trial by McLeod and Baldwin (2000), *in vitro* oxygen consumption by isolated rumen epithelial samples tended to be greater in lambs fed the low-energy ration than the high-energy ration, but oxygen consumption in cells from the small intestine were not affected by energy density.

Oxygen-depleted blood is transported from the visceral organs to the liver in the portal vein. Arterial blood is used to measure blood oxygen concentration before tissue consumption. The difference between portal and arterial blood oxygen concentration represents oxygen consumption by the portal drained viscera. Hepatic veins transport blood from the liver to the inferior vena cava, containing oxygen-depleted blood from both the liver and most abdominal organs. In blood samples collected by Reynolds et al., (1991a) the portal-arterial difference was greater (more negative) in heifers fed a low-energy diet than heifers fed a high-energy ration, indicating greater portal-drained viscera oxygen consumption by heifers fed a low-energy diet. The hepatic-portal difference in oxygen concentration was not different between treatment groups, indicating that liver oxygen consumption was not different. Their data suggests that increases in heat production are explained in part by increases in tissue metabolism in portal drained viscera. However, oxygen consumption, and consequently energy use in

the liver is not affected by energy density of the diet, but rather is most affected by MEI, not ME density. This is consistent with data presented by Rompala et al. (1988), who stated that increased DMI at isocaloric levels of MEI yielded no difference in liver mass. In Reynolds et al. (1991b), total body oxygen consumption was greater in heifers consuming the low-energy ration than those consuming the high-energy ration, indicating that a greater proportion of ME was retained in heifers consuming the high-energy ration. Portal-drained viscera oxygen use as a percentage of whole body oxygen use tended to be greater with the low-energy ration (27%) than the high-energy ration (23%).

The rate of oxygen consumption of colon mucosa per g protein tended to be greater in lambs fed the polyethylene ration than those fed the control diet, but total body oxygen consumption was not found to be different (Rompala et al., 1988). This is most likely a result of the increase in GIT mass that was reported simultaneously. This suggests that simply adding dietary bulk produces different effects than increasing actual forage concentration in the diet. In this particular experiment, tissue mass was affected, but FHP remained the same, verifying issues with confounding results relative to DMI and MEI. Because MEI was comparable between treatments, it is possible that increased organ heat production was related to intake, resulting in less energy made available for deposition in the periphery, supporting their findings that FHP was not affected.

In the previously described trial by, McCurdy et al. (2010), *in vitro* oxygen consumption in isolated cells from the duodenum were not affected by dietary energy density, which is consistent with the results presented by McLeod and Baldwin (2000).

Similarly, *in vitro* oxygen consumption in liver cells was similar between silage-fed calves and program-fed calves. Although oxygen consumption in the liver and hindgut was not affected by dietary energy density, the difference in heat production could have been related to the increased HI associated with protein deposition in growing cattle, as previously discussed, rather than FHP.

Oxygen consumption, when properly isolated, is indicative of tissue-specific heat production. The experiments presented above resulted in relatively consistent results regarding the effects of dietary energy density on oxygen consumption. Hindgut tissue appears to consistently increase with an increased level of forage included in the diet, but increased FHP does not always observed. Rompala et al. (1988) and McLeod and Baldwin (2000) also suggested that liver mass is not affected by dietary energy density, assuming an isocaloric level of MEI, while the mass and subsequent oxygen consumption of portal drained viscera is typically increased by decreased dietary energy density.

#### *Eating energy*

The energetic cost of eating is highly variable (Richardson and Herd, 2004), especially across a variety of feed sources. Susenbeth et al., (1998) estimated that 10% to 30% of ME supply is used as eating or rumination energy, which represents a portion of HI. Although heat production associated with eating is not directly associated with energy density, per se, when energy density is changed, the dietary fraction of structural carbohydrates is subsequently altered as well. Increase in structural carbohydrates

increases the amount of energy expenditure associated with eating (Susenbeth et al., 1998).

Susenbeth et al. (1998) conducted a trial in which total body gas exchange was measured via direct calorimetry to demonstrate how it was affected by feed consumption. Heat production was measured for 3h while steers had no access to feed and then compared to heat production during the feeding period. Heat production was not affected by metabolism of absorbed nutrients ingested during the feeding period. They observed that the amount of time spent eating increased as straw concentration increased. Time spent ruminating was similar between periods of fasting and eating. Heat production increased by 19% when feed was offered, indicating a significant amount of HE was associated with chewing. Chewing increased heat production by 0.067 kcal per chew. Straw intake ultimately increased total heat production by 0.110 kcal per g diet DM consumed. Their data suggests that reducing dietary bulk increases the efficiency (k) of ME utilization by reducing amount of time spent chewing.

To demonstrate the effects of physical form on eating energy, Adam et al., (1984) conducted a trial to compare heat production in diets of pelleted concentrate, pelleted alfalfa, alfalfa hay and chopped grass hay. On both as fed and dry matter basis, rate of consumption of both pelleted diets was less than that of the hay diets. When expressed as kcal/kg DM consumed, heat production was lower in both of the pelleted diets than in the hay diets, but did not differ between chemical compositions. However, when heat was expressed as J/min spent eating, there was no difference between pelleted and hay diets, indicating that overall heat expenditure of a diet is more closely associated

with time spent chewing than chemical composition. The article also supported and further expanded data presented by Holmes et al., (1978) who demonstrated similar effects on heat production and also concluded that heat production associated with eating is related to animal BW. Data from both trials suggests that the rate of ingestion is inversely related to total body heat production. Because rate of ingestion is lower in younger animals than in older animals (Holmes et al., 1978), overall eating energy per kg DM is expected to be greater in younger animals. Data suggests that heat production increases 15 to 70% while actually eating the pelleted or hay diets, respectively. This increase in heat production is estimated to account for 1.0 and 3.8% of the ME concentration in the pelleted and hay diets, respectively, which is different from results that Susenbeth (1998) reported, which were almost 10-fold higher. Based on the assumption that rate of ingestion is inversely related with BW, eating energy may account for up to 16% of ME in low quality diets when fed to light-weight calves (Adam et al., 1984). The correlation between time spent eating and heat expenditure demonstrates the need to account for energy expenditure associated with eating in net energy systems, especially if energy usage associated with eating accounts for a relatively large proportion of ME.

#### *End products of digestion*

The products of rumen fermentation are known to affect energy utilization. Armstrong and Blaxter (1957) suggested that the efficiency of conversion of butyric and propionic acids are greater than the efficiency of acetic acid as glucose precursors. Sheep receiving a high acetic acid mixture experienced higher heat increment and

reduced energy retention compared to those receiving the low acetic acid mixture. In a trial using ruminally fistulated adult castrated male sheep, Armstrong et al. (1958) further analyzed the effects of volatile fatty acid (VFA) molar proportions on energy efficiency. When dilute salt solutions of different VFA mixtures were fed directly into the rumen, it was determined that the molar concentration of acetate relative to that of propionate and butyrate had a negative effect on the absorption of dietary energy. They also summarized results from previous work in their article, summarizing 33 trials to illustrate the relative value of ME from hay and maize meal. The summary concluded that ME utilization for both maintenance and fattening was decreased in fibrous diets, which are known to produce a higher ruminal acetate:propionate ratio, compared to low-fiber diets. Their data indicated that ME from diets high in fiber was used less efficiently than ME from diets low in fiber and high in starch. They suggested that ruminal fermentation of diets high in forage yielded greater proportions of acetic acid than diets low in forage and high in grain. Blaxter and Wainman (1964) supported this data, by demonstrating a direct relationship between energy density and efficiency of ME use for gain.

When Armstrong and Blaxter (1961) infused glucose into the abomasum and jugular vein of sheep consuming a maintenance diet of hay, they concluded that energetic efficiency was not different between jugular and abomasal infusion, but that both were greater than when it was infused into the rumen. These results first established a difference in efficiency resulting from site of glucose availability, specifically that post-ruminal absorption increased energy efficiency.

The ratio of VFA concentrations does not always have an apparent effect on energetic efficiency or maintenance Bull et al. (1970). When triacetin, a source of acetic acid, was added to a finely ground and pelleted ration of hay or hay and corn, there was no difference in either net utilization of ME for gain or maintenance requirements. It is hypothesized that no differences were found because the both triacetin and the control diet contained a glycerol additive, which serves as a readily available source of glucose. The physical nature of the rations also most likely resulted in greater rate of ruminal passage, resulting in greater small intestine glucose absorption or diminishing ruminal production of acetate.

#### *Conclusions about energy density*

Dietary energy density has a significant effect on the efficiency of ME use (RE/MEI). Because it is often difficult to measure both FHP and HI independently, it is often challenging to determine which of the two are affected by individual biological events. Energy required for maintenance appears to be related primarily to overall cellular or tissue workload. Thus, when organ mass is affected by dietary contents, the metabolic workload associated with maintaining the altered amount of tissue is also affected. Energy density does not appear to effect liver energy metabolism to the degree of the effects of MEI. The effects of energy density on HI appear to be embedded within several pathways related to intake, digestion, absorption and product formation. The proportion of ME used as eating energy is a highly variable source of heat production; however, it has no effect on FHP and, therefore, is directly associated with  $k$ . The end products of digestion, also affect the efficiency of energy utilization for maintenance.



The ratio of acetate:propionate has been shown to influence energetic efficiency; however, when glycerol or other sources of glucose are made available postruminally, this effect on efficiency is reduced. While eating energy and digestion end products do not affect FHP, they undoubtedly alter MEM, or the ME required to yield no net change in RE. In conclusion, diets consisting of higher energy density are more energetically efficient, as they result in reduced HI or k and generally result in decreased FHP, relative to a low energy density diet.

#### *Effects of metabolizable energy intake*

Like the effects of dietary energy density, shifts in energy metabolism occur as a result of anatomical changes associated with energy intake. Also similar to previous results from the energy density section, both FHP and HI can be affected by MEI. The following section will discuss the physiological origin of events known to influence heat production based on MEI.

#### *Effects of ME intake on performance and ME utilization*

Blaxter (1962) and Blaxter and Wainman (1964) summarized historical suggestions by Kellner and Armsby about ME utilization. The concept that ME use efficiency (RE/MEI) was greater below maintenance than above maintenance was applied to a graphic illustration of ME efficiency. Their illustration assumes a linear relationship between energy retention and MEI, which is not biologically accurate (Ferrell and Oltjen, 2008), but has merit in describing experimental relationships.

The linear regression of RE on MEI has been used to estimate ME requirement to support maintenance ( $ME_m$ ; Byers, 1980). This method of estimating maintenance

requires measures of MEI and RE at two levels of intake per diet. An alternate form of estimating energy requirements utilizes a semi-logarithmic function of HE on MEI (Lofgreen and Garrett, 1968). This method allows for estimation of  $ME_m$ , with only one measurement of intake, but assumes a standard level of FHP to be used in solving for energy equilibrium (Byers, 1980). A similar method of semi-logarithmic transformation can be used to estimate FHP, when HE and MEI is measured at two levels of intake (Garrett, 1987).

Freetly and Nienaber (1998), subjected cows to one of two treatments: control, fed fixed amount of chopped brome hay near the estimated maintenance level of intake; treated, fed restricted (65% of control intake) amount of chopped brome hay for 112 d and sequentially realimented to consume the same chopped hay above maintenance (135% of control intake). Treatments were designed so that the total amount of feed consumed during the 224-d period was the same between control and treated cows. As expected, body weight in treated cows decreased during phase 1, and increased during phase 2. Treated cows produced less total heat than control cows during phase 1 and more total heat than control cows during phase 2. Although there were differences in heat production within collection periods, total heat production over the 224 d was not different between control and treated cows. Treated cows were in negative energy balance from d 28 to d 84, but were not different from zero by d 112, suggesting that physiological adaptation resulted in either greater dietary energy efficiency or reduced energy requirements. Although treated cows were at maintenance (zero energy balance) on both d 0 and d 112, heat production was higher on d 0 than d 112. These results

suggest that cows achieve new equilibrium maintenance requirements with altered levels of intake, which was consistent with a previous report by Jenkins and Ferrell (1997). It should also be noted that digestibility of the diet was not found to be different between phase 1 and phase 2, indicating that energy availability was not altered by intake. This supports that changes in maintenance requirements (FHP) (not dietary energy availability) caused the differences in heat production. After realimentation on d 112, treated cows were in positive energy balance. Because energy balance never returned to zero during phase 2, it was suggested that adaptation to new equilibrium requirements resulting from restriction may occur more rapidly than adaptation to increased intake.

McLeod and Baldwin (2000) fed lambs rations of differing energy density at two levels of ME intake in a  $2 \times 2$  factorial design. Lambs fed a higher ME intake experienced greater final empty body weight (EBW), ADG and feed efficiency than low ME intake lambs, regardless of dietary energy density. Because a greater amount of ME was available for absorption, a greater amount of energy was retained. However, heat production was not reported or calculated in this study, nor could it be calculated due to a lack of report on RE or HE. Increased EBW gain most likely increased energy demand. It is well documented that the proportion of ME lost in the form of heat increases as MEI increases above maintenance (Ferrell & Oltjen, 2008). It is also noteworthy that there were no interactions relative to MEI, ADG or efficiency of gain in this experiment, suggesting that the effects of dietary energy density and intake were independent of one another.

Sainz et al. (1995) found that increasing MEI resulted in greater empty body weight (EBW), backfat, abdominal fat, kidney, pelvic and heart fat (KPH), marbling scores, carcass fat and empty body fat in growing steer calves. High intake calves had less carcass density and experienced greater rate and efficiency of gain than low intake calves. Although high intake calves retained more energy, they also produced more total heat (247 vs. 177 kcal\*kg EBW<sup>-0.75</sup> for high and low intake, respectively) due to greater MEI when compared to low intake calves. The increased gain in high intake calves represents a dilution of maintenance requirements by production. However, the concept of maintenance dilution is likely impractical to cow-calf systems, as maximizing cow intake would likely not generate a response in lactation great enough to offset the cost of additional feed consumption.

Reynolds et al. (1991a,b) fed heifers in a factorial arrangement consisting of 2 diets fed at 2 levels of intake. Increasing MEI resulted in greater energy loss in the form of feces, methane, urine and heat, but still resulted in greater digested, metabolized, tissue and heat energy, although retained energy represented a greater proportion of ME. There were no interactions relative to energy efficiency in this study, again confirming that the effects of dietary energy density and intake promoted independent forms of heat expenditure.

Camacho et al. (2014) demonstrated the effects of limiting MEI on gestating beef cows. Cows were fed individually either at maintenance (CON) or at a restricted (RES) rate of 60% of maintenance energy requirements for a period of 55 d, followed by either a continued control (CC) maintenance diet, continued restriction (RR) or realimentation

to control diet (RC). Following another period of 55 d, cows were either left on control diet (CCC;RCC) or realimented to the control diet (RRC) for the remaining 114 d.

During the first period of energy restriction, restricted cows had a larger percentage of maternal BW loss than control cows. Throughout most of the second period, RR and RC cows had greater percentage of maternal BW loss than CC cows, and by the end of the period, all three treatments had different percent losses, with RR being the greatest, followed by RC and CC, respectively. Following realimentation of all restricted cows, by d 254 of gestation (d 224 of the trial), percent increase in BW was greatest in RCC cows, with CCC being the lowest and RRC cows intermediate, but not different than CCC. The efficiency of gain (gain:feed) was greater in restricted cows, possibly because of metabolic alterations. Their results supported data presented by Freetly and Nienaber (1998), who suggested feed restriction increases efficiency of gain in mature cows during the compensating period.

#### *Effects of ME intake on splanchnic tissue mass*

McLeod and Baldwin (2000) reported that MEI affects splanchnic tissue mass. Total digestive tract (TDT), rumen, omasum, abomasum, large intestine, liver, heart, kidneys and lung weights were all greater in high intake lambs than in restricted lambs. Similarly, when expressed as a percentage of empty body weight, TDT, rumen, reticulum, small intestine and liver weights were greater in high intake lambs than in low intake lambs, indicating that tissue specific growth was achieved at a greater rate than carcass growth. This increase in organ mass per unit of total BW ultimately results in

greater energy requirements associated with additional cell maintenance, relative to body size.

Energy restriction has been shown to have no effects on organ mass in pregnant cows. In a trial by Wood et al. (2013) the effects of moderately limiting net energy (NE) consumption of gestating beef cows were evaluated. Cows that were fed 85% (Low) of energy requirements experienced no difference in total or mass specific fetal weight, fat weight or weight of any splanchnic tissue, excluding rumen weight, compared to cows fed 140% (High) of requirements. The results of this trial indicate that minimal decreases or substantial increases in intake may not result in differences in organ mass, but that severe restriction may be necessary for such degradation to occur in pregnant females. It is also possible that the effect of pregnancy confounded these results, as open cows were shown to have greater liver mass per kg BW than pregnant cows in this study.

Camacho et al. (2014) showed that while energy restriction had no effect on body condition score (BCS) or gravid uterine weight, on d 110 of the trial (d 140 of gestation) restricted cows had decreased liver and rumen weight compared to control cows. The decrease in organ weight may have resulted from gestation status or a combination thereof in a physiological attempt to conserve energy. Liver mass as a percentage of total BW is smaller in pregnant cows relative to open cows (Wood et al., 2013). It is possible that the feed restriction exacerbated the effects of pregnancy, increasing the rate of liver mass degradation. Following realimentation of all restricted cows in the Camacho et al. (2014) experiment, viscera, EBW and ultrasonography measurements of backfat and

ribeye area (REA) were not found to be different between treatments groups, indicating that organ mass corrects rapidly with realimentation.

#### *Effects of ME intake on gas exchange*

Arterial oxygen concentration was found by Reynolds et al. (1991b) to be lower in high MEI heifers than in low intake heifers. As previously discussed, the differences in portal-arterial, hepatic-portal and hepatic-arterial oxygen concentrations are indicative of oxygen consumption in the respective organ from which blood is flowing. The portal-arterial difference was found to be smaller (less negative) and the hepatic-arterial difference tended to be smaller in high intake heifers than in low intake heifers. MEI did not affect the hepatic-portal difference. Whole body, along with total splanchnic, PDV and liver oxygen use was found to be greater in high intake heifers than in low intake heifers. The percentage of oxygen extraction was greater in total splanchnic and liver tissues, but was not significantly different in PDV. Percentage of total body oxygen consumption was found to be greater in the liver of high intake heifers than in low intake heifers, indicating a disproportional increase in liver oxygen use, relative to body weight change, as a result of increasing MEI. This data suggests that increasing energy intake causes liver metabolic rate to increase, resulting in greater total oxygen consumption.

In the trial by Wood et al. (2013), cows fed above maintenance consumed more oxygen per unit of body protein than limited cows. Limited intake cows displayed decreased rate of total liver oxygen consumption and liver oxygen consumption per BW, indicating a decrease in overall metabolic rate with restricted intake. This supports data presented by Reynolds et al. (1991b) and Freetly and Nienaber (1998), reinforcing a

major pathway through which maintenance energy equilibrium shifts during intake restriction.

In summary, the decrease in liver and PDV mass resulting from restricted MEI cause a decrease in total cellular activity. This decrease in oxygen consumption indicates decreased FHP, primarily resulting from a physiological attempt to minimize peripheral body tissue mobilization. The effect of pregnancy on liver mass is also noteworthy. Interactions between intake and pregnancy status may lead to interesting insight relative to pathways affecting energy use.

#### *Blood flow*

When MEI was increased in growing heifers, Reynolds et al. (1991a) demonstrated that heart rate and rectal temperature increased compared to low intake heifers. Blood flow was measured, and found to be greater in the portal-drained viscera (PDV), liver and kidneys of high intake heifers than in low intake heifers. Arterial packed cell volume was lower in high intake heifers, most likely a result of an increase in blood flow volume, and subsequent dilution of cell concentration. The increased blood flow is representative of oxygen transport, indicating a larger volume of oxygen consumption when MEI is increased, supporting the elevated level of HE documented.

#### *Metabolites*

Wood et al. (2013) demonstrated the effects of limiting NE intake on circulating serum metabolites in beef cows. Serum non-esterified fatty acid (NEFA) concentration was found to be greater in cows fed below maintenance than in cows fed above maintenance. This difference represents a catabolic state, ultimately causing the



breakdown of fat stores for energy supply. Also, serum thyroid hormone (T3) concentration was found to be lower in limited cows compared to cows consuming above maintenance. T3 is correlated with resting metabolic rate, which means that cows below maintenance consumption could have decreased FHP and energy requirements.

#### *Conclusions about energy intake*

Data reported in the above articles discuss several generalities about ruminant bioenergetics. The extent to which the chemical nature of a diet affects energy metabolism remains disputed, but some support that differences in energy expenditure associated with energy density are strongly due to the physical characteristics (such as bulk mass) of a diet. It remains clear that energy expenditure associated with eating is positively correlated with time spent chewing, which is influenced by fiber concentration and overall intake. Because energy density is typically inversely related to fiber composition, dietary fiber content of a ration may be the largest source of dissimilarities in heat production.

The end products of digestion affect the efficiency of energetic use. The acetate:propionate ratio is known to have negative effects on heat production. However, in the presence of adequate glucose availability, the ratio has no effect on heat production. Efficiency of ME use for maintenance and gain can be altered by this inefficiency in precursor utilization. The increase in acetate utilization could potentially lead to increased use of feed resources that are not in direct competition with human consumption, such as residues, straw and other low quality forages.

It is clear that energy density and intake affect energy use for maintenance and gain. The differences in consumption-related heat expenditure associated with both factors result from changes in overall metabolism of molecules containing chemically combustible components. Fasting heat production is a measure of total resting metabolic rate, and is influenced by the both mass and intensity of cell maintenance workloads. Oxygen consumption measurements are used to represent metabolic rate, and are influenced by energy density and intake. Data suggests that increasing dietary energy density decreases VOM, while leaving liver mass unaffected. Decreasing intake results in decreased overall metabolism by reducing splanchnic tissue mass and subsequent metabolic rate. Total MEI effects total splanchnic tissue mass and heat production directly. Energy density, however, appears to only affect portal drained viscera, excluding metabolism in the liver. The effects have been shown to be additive in experiments where factorial treatment arrangements were used.

Protein turnover is also energetically expensive. As protein anabolism occurs, rate of turnover increases. The energetic cost of synthesis, degradation and maintenance of protein represents up to 8.9% of total body heat production (McBride and Kelly, 1990). Increasing energy density and decreasing intake tend to decrease protein turnover, ultimately resulting in decreased HE.

The summation of the above listed factors affecting energy metabolism are central to understanding the physiological events that occur in response to dietary manipulation. Ultimately, it appears that energetic efficiency can be enhanced by limit feeding high-energy rations. However, more data is needed to verify such assumptions,

specifically examining the effects and their interactions on cows in productive environments.

CHAPTER II  
EFFECTS OF DIETARY ENERGY DENSITY AND INTAKE ON MAINTENANCE  
ENERGY REQUIREMENTS IN BEEF COWS

*Synopsis*

Alternative land use decisions in the US and increasing land costs have strengthened the need for greater land use efficiency in cow-calf production. Intensified systems including the delivery of concentrated diets to cows during periods of low nutrient requirements or throughout the production cycle are one strategy to increase productivity on given area of land. Accordingly, an experiment was designed to evaluate the effects of dietary energy density and intake on maintenance energy requirements in beef cows. Thirty-two crossbred cows in early- to mid-gestation were stratified by weight and randomly assigned to treatment in a  $2 \times 2$  factorial arrangement. Cows were fed either a high-(**H**; 2.54 Mcal ME/kg) or low-energy (**L**; 1.94 Mcal ME/kg) diet at one of two levels of intake (**80**; 80% NRC NE requirements, **120**; 120% NRC NE requirements) once daily using the Calan gate system. A series of measurements were taken on d 0 and d 56 to estimate body energy. The difference between body energy on d 0 and d 56 was calculated and is RE over the 56 d period. Heat energy was calculated as the difference in ME intake and total RE and was used to calculate  $NE_m$  requirements. Energy digestibility was not affected ( $P = 0.29$ ) by level of intake. Body weight gain tended to be greater ( $P = 0.08$ ) in H than L and was numerically greater ( $P = 0.12$ ) in 120 than 80. Retained energy tended to be greater ( $P = 0.10$ ) in H than L and greater ( $P$

= 0.08) in 120 than 80. Heat energy per  $EBW^{0.75}$  was greater ( $P < 0.01$ ) in L than H and greater ( $P < 0.01$ ) in 120 than 80, with no interaction ( $P = 0.29$ ). Birth weight and adjusted 205-d weaning weight of the calves from treated cows were not affected by diet ( $P > 0.22$ ) or level of intake ( $P > 0.56$ ). Metabolizable energy for maintenance was calculated to be 92.54 and 168.06 kcal/ $EBW^{0.75}$  for H and L, respectively. Net energy for maintenance was calculated to be 54.60 and 74.78 kcal/ $EBW^{0.75}$  for H and L, respectively. Overall, increasing dietary energy density resulted in a decrease in maintenance requirements of approximately 28% and intake restriction decreased HE by approximately 28%, with no interaction, suggesting additive effects. Limit feeding high-energy diets has the potential to increase the efficiency of production and land use in U.S. cow-calf systems.

## *Introduction*

Since its peak in 1978, the US beef cow inventory has been in decline, despite positive cash margins in recent years (Thompson, 2013; Trubenbach et al., 2014). A multitude of factors accumulating competition for land resources, including urban sprawl and recreational use, have increased grazing land prices significantly (NASS, 2014). Capital requirement for expansion efforts, particularly in terms of land investment, is high relative to rate of return (Bevers, 2013) Production intensification, as described in the current article, refers to housing productive beef cows in an intensive setting (drylot, feedlot, etc.) for at least a portion of their reproductive cycle. While variable costs of production (i.e., feed, labor, etc.) perceivably increase in intensified systems, they are currently being strategically implemented to mitigate the effect of land prices on expansion capitalization by increasing production capacity per unit of land.

In one manifestation of intensified systems, cows are housed in a feedlot or drylot setting and fed a total mixed ration for at least a portion of the production cycle. Accessibility of cattle in confinement could make data collection and cattle handling more practical and increase the cost-effectiveness of reproduction technologies. In addition, nutritional manipulation may be enhanced in intensified systems relative to more extensive grazing systems.

Limit-feeding a high-energy diet has the potential to increase the efficiency of cow-calf production. Increasing energy density of the diet increases the efficiency of realimentation in mature cows (Swingle et al., 1979; Sawyer et al., 2004), potentially resulting from a decrease in maintenance energy requirements. Continuous intake

restriction shifts requirements for energy stasis to a lower equilibrium in beef cows (Freetly and Nienaber, 1998). Similar outcomes have been observed in growing cattle (Sainz et al., 1995; McCurdy et al., 2010) and sheep (Reynolds et al., 1991b; McLeod and Baldwin, 2000), but research analyzing the effects of dietary energy density and intake simultaneously is limited in mature cows. This experiment was designed to test the hypotheses that increasing dietary energy density and restricting intake decrease maintenance energy costs in beef cows.

#### *Materials and methods*

The experimental protocol was approved by the Institutional Animal Care and Use Committee at Texas A&M Agrilife Research.

Thirty-two mature, crossbred ( $3/4$  Angus X  $1/4$  Nellore) cows were used in an experiment designed to examine the effects of dietary energy concentration and intake on energy metabolism. Cows were stratified by day of gestation and BW and randomly assigned into pens of 4 head ( $n = 8$ ). A  $2 \times 2$  factorial arrangement of treatments was applied, with two levels of energy density (Table 2.1): high-energy (**H**; 1.54 Mcal NE/kg) and low-energy (**L**; 1.08 Mcal NE/kg), each provided to supply two levels of NE intake: 80% NRC requirements (**80**) and 120% NRC requirements (**120**).

**Table 2.1** Formulated ingredient and nutrient composition of treatment diets<sup>a</sup>

Ingredient	High	Low
	Energy	Energy
	% As fed	
Wheat straw	34.52	64.08
Corn	29.46	0.00
Distillers grain	27.46	27.36
Urea	1.10	1.10
Molasses	5.00	5.00
Mineral	2.46	2.46
Diet components	DM basis <sup>b</sup>	
Crude protein, %	16.30	14.40
Total digestible nutrients, %	68.00	54.00
Metabolizable energy, Mcal	2.45	1.94
Net energy (NE <sub>m</sub> ), Mcal	1.54	1.08
Net energy (NE <sub>g</sub> ), Mcal	0.95	0.53

<sup>a</sup>According to NRC model estimates

<sup>b</sup>Dry matter contents: high energy, 89.8%; low energy, 90.8%.

Energy requirements were calculated using the mean BW of cows within a treatment combination prior to treatment application, and cows within a given treatment combination were each offered the same amount of feed (Table 2.2). Maintenance was estimated per NRC model estimates. Cows were fed individually at approximately 0700 h daily using a Calan gate system, with orts (if present) collected once per week. Cows had *ad libitum* access to fresh water throughout the experiment.

At the beginning and end of the feeding period (56 d), animals were subjected to a series of measurements including: weight, hip height, heart girth, body condition (BC) score and ultrasound measurements of rib fat thickness (between 12<sup>th</sup> and 13<sup>th</sup> rib) and



rump fat thickness, intramuscular fat and ribeye area for both direct comparison and use in an analysis of body energy reserves via selected regression models. In addition to BW measurements at the beginning and end of the feeding period, BW was measured daily for the first 7 d to elucidate changes in fill associated with treatment. Body weights were also collected on d 14, 28, 42 and 56.

**Table 2.2** Treatment intake of dietary components

Intake <sup>a</sup>	High energy diet		Low energy diet	
	Low intake	High intake	Low intake	High intake
As fed, kg	4.40	6.39	6.49	9.52
Dry matter, kg	3.90	5.67	5.80	8.48
Digestible energy, Mcal	11.67	16.96	13.79	20.15
Metabolizable energy, Mcal	11.17	16.24	12.71	18.67
Net energy <sup>b</sup> , Mcal	6.79	9.87	7.01	10.29

<sup>a</sup>Intake / d

<sup>b</sup>Designed to deliver 80 and 120% total NE requirements; not isocaloric due to differences in NE<sub>g</sub> for gestation

Fecal grab samples (2 per day) were collected and immediately frozen on d 14, 28, 42, and 56 to determine fecal production using acid detergent insoluble ash as an internal marker. Samples of the TMR were taken daily and equal daily amounts were composited weekly for subsequent analysis.

*Laboratory analysis*

Feed and fecal samples were processed and analyzed using the same techniques. Samples were dried in a forced-air oven for at least 96 h at 55°C and allowed to air

equilibrate for determination of partial DM. Samples were ground through a 1-mm screen using a Wiley mill and dried at 105°C for determination of DM. Organic matter was determined as the loss in dry weight upon combustion in a muffle furnace for 8 h at 450°C. Acid detergent fiber analysis was performed using an Ankom Fiber Analyzer (Ankom Technology Corp., Macedon, NY), and acid detergent insoluble ash (ADIA) was determined by loss in ADF DM weight upon combustion in a muffle furnace at 450°C.

Gross Energy (GE; Mcal/kg DM) was determined by direct calorimetry using a Parr 6300 Calorimeter (Parr Instrument Company, Moline, IL).

#### *Calculations*

Metabolic BW was calculated as  $BW \times 0.96 \times 0.891$  per NRC (2000).

Fecal production was calculated by dividing ADIA consumption by fecal ADIA concentration:

$$\text{Fecal production, kg} = \frac{DMI \times ADIA_d}{ADIA_f}$$

where:

DMI, kg

$ADIA_d$  = Dietary ADIA concentration (%DM)

$ADIA_f$  = Fecal ADIA concentration (%DM)

Digestibility of DM, OM, ADF and GE were all calculated using the same method:

$$\text{Digestibility}_n, \% = \frac{\text{Intake}_n - \text{Fecal}_n}{\text{Intake}_n} \times 100\%$$

where:

$$\text{Intake}_n = \text{DMI (kg)} \times \text{dietary nutrient concentration (\%DM)}$$

$$\text{Fecal}_n = \text{Fecal production (kg)} \times \text{fecal nutrient concentration (\%DM)}$$

Measures of digestible energy (DE) and metabolizable energy (ME) were calculated by the following equations:

$$\text{DE (Mcal/kg DM)} = \text{GE} \times \text{Digestibility}_{\text{GE}}$$

$$\text{ME (Mcal/kg DM)} = \text{DE} \times 0.82$$

Maintenance requirement for metabolizable energy ( $\text{ME}_m$ ) was calculated for both H and L using a linear regression of the means of RE on MEI. The linear functions representing each diet were solved for RE = zero; the solution of which represented the  $\text{ME}_m$  value for each respective diet.

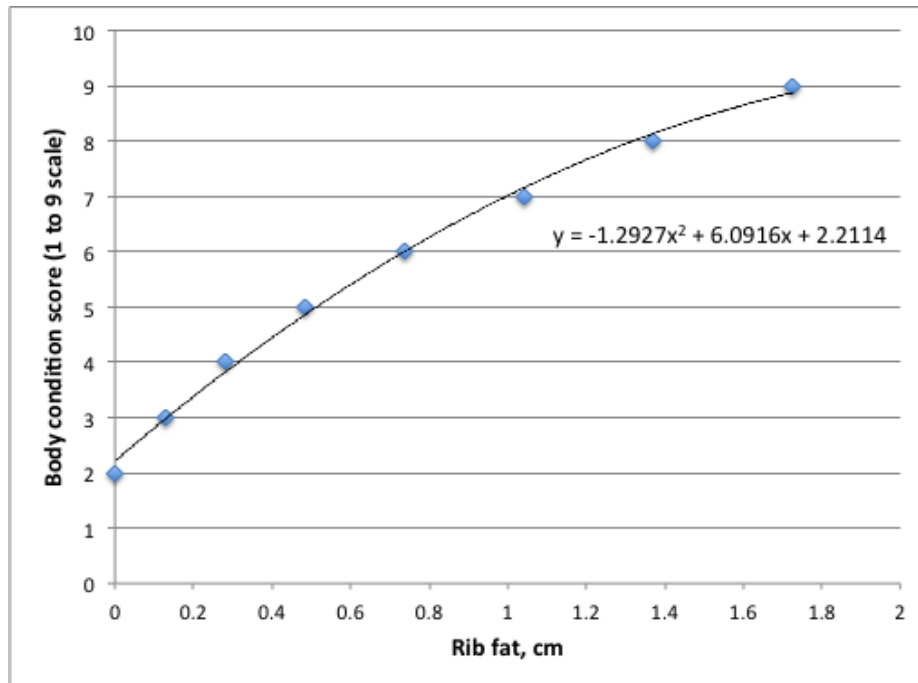
Fasting heat production was estimated for H and L using the linear regression of the means of log (HE) on MEI. The linear functions representing each diet were solved for MEI = zero; the solution of which represented the estimate of FHP for each respective diet.

Body condition score (BCS) was calculated at both the beginning and end of the trial using the regression equation (Figure 2.1) presented by Herd and Sprott (1998).

$$\text{BCS} = -1.2927x^2 + 6.0916x + 2.2114$$

where:

$$x, \text{ cm} = \text{Rib fat}$$



**Figure 2.1** Direct measurements of rib fat thickness used to estimate the body condition score of treatment cows (Herd and Sprott, 1998).

Equations published in Nutrient Requirements of Beef Cattle (2000; NRC) were used to calculate empty body energy.

1. Body composition was estimated using the following equations:

$$AF = 3.768 \times CS$$

$$AP = 20.09 - 0.668 \times CS$$

where:

AF = proportion of empty body fat

AP = proportion of empty body protein

CS = body condition score

2. Body components were calculated as:

$$TF = AF \times EBW$$

$$TP = AP \times EBW$$

$$EBW = BW - FL$$

$$FL = SBW * \alpha$$

$$SBW = BW \times 0.96$$

where:

TF = total fat, kg

TP = total protein, kg

FL = fill, kg

$\alpha$  (% SBW) was estimated for each treatment using unpublished data in which ruminal contents were measured from cannulated steers fed the diets used in this study at equivalent rates ( $\text{g/kg EBW}^{0.75}$ ) via rumen evacuation.

3. Total body energy was calculated as:

$$TBE \text{ (Mcal)} = 9.4 \times TF + 5.7 \times T$$

4. RE and HE were calculated as:

$$RE = TBE_f - TBE_i$$

$$HE = ME - RE$$

where:

$TBE_f$  = total body energy on d 0, Mcal

$TBE_i$  = total body energy on d 56, Mcal

RE = retained energy, Mcal

HE = heat energy, Mcal

ME = metabolizable energy, Mcal.

In addition to NRC estimates of body energy, published regression equations (Table 2.3) were used to estimate body energy for calculation of RE and ME. An equation presented by Ferrell and Jenkins (1984) was used to estimate energy content of the empty body of mature beef cows, which is consistent with calculations based on NRC equations. Equations from articles by Gresham et al. (1986), Wagner et al. (1988) and Bullock et al. (1991) were used to estimate energy in the carcass of mature beef cows; however, calculations for empty body and carcass were used synonymously with empty body energy in the current article.

The regression equations presented by Bullock et al. (1991) appear to be incorrect and results from those particular equations are impractical. Estimates for RE and HE were calculated using the formerly described methodology. RE was calculated as the difference in TBE on d 0 and 56, and HE was estimated to be the difference between ME and RE.

#### *Statistical analysis*

All data analyses were analyzed using PROC MIXED procedures in SAS 9.2 (SAS Inst. Inc., Cary, NC). The model effects included diet, intake and diet  $\times$  intake. A block effect of sex was used in the analysis of post-experimental calf performance.

**Table 2.3** Multiple regression coefficients of selected models used for estimating energy contained in the empty body or carcass of beef cows

Model	Type	Independent variables <sup>b</sup>										R <sup>2</sup>
		$\beta_0$	BW	BF <sub>c</sub>	BF <sub>m</sub>	BF <sub>m</sub> <sup>2</sup>	HH	WH	WT:HH	BCS	EBW	
Ferrell and Jenkins (1984, 1)	Empty Body	73.3	2.9	422.0			-2.7					0.87
Ferrell and Jenkins (1984, 2)	Empty Body	-333.0									4.6	0.69
Gresham et al. (1986)	Carcass	-733.7	1.8		77.7	-1.8		2.5				0.87
Wagner et al. (1988, 1)	Carcass	-487.2	1.3								78.4	0.90
Wagner et al. (1988, 2)	Carcass	-661.5	2.7									0.81
Wagner et al. (1988, 3)	Carcass	-756.7							361.5			0.83
Wagner et al. (1988, 4)	Carcass	-221.5								128.2		0.85
Bullock et al. (1991, 1)	Carcass	-35709.4	109.6	20031.0							4612.4	0.93
Bullock et al. (1991, 2)	Carcass	20658.4	152.0	13983.6			531.3					0.92
Bullock et al. (1991, 3)	Carcass	-58602.6									5764.7	0.91

<sup>a</sup>Mcal

<sup>b</sup>BW = live body weight (kg); BF<sub>c</sub> = back fat (cm); BF<sub>m</sub> = back fat (mm); HH = hip height (cm); WH = wither height (cm, estimated as HH - 5); BCS = body condition score (1 to 9 scale, 1 = emaciated and 9 = very obese); WT:HH = ratio of WT:HH, kg/cm; EBW = empty body weight (kg)

## *Results*

One cow from L120 was completely removed from the experiment and subsequent statistical analysis due to illness unrelated to treatment.

There were no interactions between energy density and intake level ( $P > 0.23$ ) for estimates of digestibility or dietary energy availability (Table 2.4). By design, DMI, digestible organic matter intake, GE intake, DE intake and MEI were greater ( $P < 0.01$ ) in L than in H, and greater ( $P < 0.01$ ) in 120 than in 80. Digestibility of DM, OM and GE was greater ( $P < 0.01$ ) in cows fed H than those fed L, but ADF digestibility was greater ( $P < 0.01$ ) in L (56.84%) than in H (52.10%). Dry matter digestibility was greater ( $P = 0.04$ ) for cows fed at 80 compared to those fed at 120 % of NRC requirements, but digestibility of OM, ADF and GE were not affected ( $P > 0.17$ ) by level of intake. As expected, observed values of DE and ME per unit of feed DM were both greater ( $P < 0.01$ ) in cows fed H than in those fed L, but were not affected ( $P = 0.29$ ) by level of intake.

Cows consuming L had greater ( $P = 0.03$ ) BW (Table 2.5) than cows consuming H before treatments were applied, but BW was not different ( $P = 0.37$ ) at trial completion. Body weight was not different ( $P > 0.29$ ) between 80 and 120 at either the beginning or completion of the feeding trial. Body weight gain tended ( $P = 0.08$ ) to be greater in cows consuming H (25.7 Mcal) than those consuming L (13.8 Mcal) and was numerically greater ( $P = 0.12$ ) in 120 (25.0 Mcal) than 80 (14.5 Mcal).



**Table 2.4** Observed nutrient digestibility and energy availability of treatment diets<sup>a</sup>

Item	High energy diet		Low energy diet		SEM	Probability		
	Low intake	High intake	Low intake	High intake		Diet	Intake	Diet × intake
Dry matter intake, kg/d	4.39	6.38	6.44	9.19	0.135	< 0.01	< 0.01	< 0.01
Dry matter digestibility, %	63.72	62.66	58.15	56.06	0.008	< 0.01	0.04	0.50
Organic matter digestibility, %	66.65	66.14	62.86	61.13	0.009	< 0.01	0.17	0.45
Acid detergent fiber digestibility, %	51.34	52.85	57.22	56.45	0.010	< 0.01	0.69	0.23
Gross energy digestibility, %	65.84	65.45	62.36	60.69	0.011	< 0.01	0.29	0.50
Energy availability <sup>b</sup>								
Digestible energy	2.83	2.82	2.66	2.59	0.047	< 0.01	0.29	0.51
Metabolizable energy	2.32	2.31	2.18	2.12	0.039	< 0.01	0.29	0.51
Digestible organic matter intake, kg/d	2.40	3.42	3.32	4.73	0.055	< 0.01	< 0.01	< 0.01
Gross energy intake, Mcal/d	17.00	24.70	25.12	36.89	0.000	< 0.01	< 0.01	< 0.01
Digestible energy intake, Mcal/d	11.28	16.08	15.68	22.21	0.309	< 0.01	< 0.01	< 0.01
Metabolizable energy intake, Mcal/d	9.25	13.19	12.86	18.21	0.253	< 0.01	< 0.01	< 0.01

<sup>a</sup>Observed via feed and fecal nutrient analysis<sup>b</sup>Mcal/kg DM**Table 2.5** Body measurements of cows fed high- and low-energy rations at two levels of intake

Item	High energy diet		Low energy diet		SEM	Probability		
	Low intake	High intake	Low intake	High intake		Diet	Intake	Diet × intake
Initial measurements								
Body weight, kg	424.55	419.67	440.25	449.30	10.593	0.03	0.83	0.49
Metabolic body weight, kg	84.41	82.58	87.61	88.47	1.563	< 0.01	0.74	0.37
Hip fat, mm	4.19	3.24	6.19	5.27	1.067	0.05	0.34	0.99
Back fat, mm	2.64	3.05	4.79	5.27	0.976	0.02	0.62	0.97
Intramuscular fat, %	2.91	2.47	2.94	2.90	0.262	0.35	0.33	0.43
Ribeye area, cm <sup>2</sup>	57.44	64.52	64.52	67.58	3.570	0.08	0.08	0.48
Final measurements								
Body weight, kg	441.33	454.25	452.44	464.72	12.485	0.37	0.29	0.97
Metabolic body weight, kg	87.25	88.45	89.65	91.04	1.900	0.17	0.48	0.96
Hip fat, mm	2.79	3.18	5.08	4.89	0.931	0.03	0.91	0.75
Back fat, mm	2.48	2.98	4.16	5.21	1.029	0.04	0.39	0.76
Intramuscular fat, %	2.92	2.54	2.70	3.05	0.246	0.52	0.93	0.12
Ribeye area, cm <sup>2</sup>	57.67	66.37	62.82	67.11	3.483	0.32	0.04	0.45
Change in measurements								
Body weight, kg	16.78	34.58	12.18	15.41	6.908	0.08	0.12	0.27
Metabolic body weight, kg	2.83	5.87	2.04	2.57	1.164	0.07	0.11	0.26
Hip fat, mm	-1.40	-0.06	-1.11	-0.39	0.580	0.97	0.06	0.56
Back fat, mm	-0.16	-0.06	-0.06	-0.02	0.356	0.48	0.25	0.39
Intramuscular fat, %	0.02	0.07	-0.24	-0.14	0.150	0.55	0.15	0.26
Ribeye area, cm <sup>2</sup>	-3.44	1.85	-1.69	-1.20	2.215	0.77	0.20	0.29

No interactions between diet energy density and level of intake ( $P > 0.12$ ) were observed for ultrasound measurements taken at the initiation or termination of the trial. Change in hip fat at least tended to be negative in both H ( $P = 0.06$ ) and L ( $P = 0.05$ ), but was not different from zero in 80 or 120. At trial initiation, hip fat and rib fat were greater ( $P < 0.05$ ) and REA tended ( $P = 0.08$ ) to be greater in L than in H. This is possibly related to greater initial BW observed in L. Intramuscular fat was not different ( $P = 0.35$ ) between H and L. Cows fed 120 tended ( $P = 0.08$ ) to have greater REA than cows fed at 80, but IMF, rib fat and hip fat were not different ( $P > 0.33$ ). At trial termination, hip fat and rib fat were greater ( $P < 0.04$ ) in L than in H, but IMF and REA were not different ( $P > 0.32$ ). Ribeye area was greater ( $P = 0.04$ ) for 120 than 80, but there was not a significant difference ( $P > 0.39$ ) in rib fat, hip fat or IMF. Change in rib fat, REA and IMF was not different from zero for any treatment. Despite the differences observed prior to application of treatments, the changes in rib fat, hip fat, IMF or REA were not different ( $P > 0.48$ ) between H-fed and L-fed fed cows. Change in hip fat tended ( $P = 0.06$ ) to be greater (more negative) for 80 (-1.25 cm) than for 120 (-0.45 cm), but change in rib fat, IMF and REA were not significantly affected ( $P > 0.15$ ) by level of intake.

Because estimates of RE and HE from equations by Bullock et al. (1991) are believed to be nonsensical, they will not be further discussed in the text. No significant ( $P > 0.25$ ) interactions between diet energy density and level of intake were observed for RE ( $\text{Mcal} \cdot \text{EBW}^{-0.75}$ ), regardless of which equation was used to estimate RE. Retained energy estimates calculated from NRC equations (2000) tended to be greater (Table 2.6)

in cows fed H than in those fed L ( $P = 0.10$ ), and for those fed at 120 versus 80 percent of NRC predicted energy requirement. Similarly, the equations from Ferrell and Jenkins, (1984), Gresham et al., (1986) and Wagner et al., (1988) to calculate RE (Mcal·EBW<sup>0.75</sup>) resulted in a tendency for H to be greater than L ( $P < 0.10$ ). In one equation from Wagner et al. (1988 Equation 4) no differences ( $P > 0.40$ ) in estimated RE were observed due to diet or intake effects. One equation (Ferrell and Jenkins, 1984 Equation 1) to estimate RE produced estimates of greater ( $P = 0.05$ ) RE for 120 than 80. Equations from the NRC also produced estimates that tended to be greater ( $P = 0.08$ ) for 120 than 80. All other equations, with the exception of Wagner et al. (1988 Equation 4) predicted estimates of RE that were numerically greater ( $P < 0.15$ ) in 120 than in 80.

**Table 2.6** Estimates of retained energy per metabolic body weight<sup>a</sup> in cows fed high- and low-energy rations at two levels of intake

Model	High energy diet		Low energy diet		SEM	Probability		
	Low intake	High intake	Low intake	High intake		Diet	Intake	Diet × intake
NRC	5.76	17.00	-1.43	6.33	5.59	0.10	0.08	0.74
Ferrell and Jenkins (1984, 1)	9.20	21.30	1.73	8.16	4.95	0.03	0.05	0.55
Ferrell and Jenkins (1984, 2)	16.75	34.94	11.80	14.75	6.84	0.06	0.11	0.25
Gresham et al. (1986)	4.61	12.79	2.92	3.13	5.03	0.08	0.14	0.82
Wagner et al. (1988, 1)	3.49	9.27	-1.46	2.56	3.25	0.07	0.12	0.77
Wagner et al. (1988, 2)	9.92	20.69	6.99	8.73	4.05	0.06	0.11	0.25
Wagner et al. (1988, 3)	10.08	20.64	6.81	8.68	4.05	0.05	0.11	0.26
Wagner et al. (1988, 4)	-2.01	-0.95	-7.83	-2.62	4.87	0.42	0.50	0.65
Bullock et al. (1991, 1)	269.00	778.40	-266.80	209.10	341.14	0.10	0.14	0.95
Bullock et al. (1991, 2)	512.60	1139.40	203.80	453.30	235.52	0.03	0.06	0.40
Bullock et al. (1991, 3)	502.80	1172.20	48.41	393.20	297.47	0.03	0.08	0.57

<sup>a</sup>kcal/d/EBW<sup>0.75</sup>, Calculated as RE / d / EBW<sup>0.75</sup>, where d = 53 days

No significant ( $P > 0.25$ ) interactions between diet energy density and level of intake were observed regarding HE (Mcal·EBW<sup>-0.75</sup>). Heat energy calculated from estimates of RE based on NRC equations (2000; Table 2.7) was greater ( $P < 0.01$ ) for L than H and greater ( $P < 0.01$ ) for 120 than 80. Calculations of HE from all regression equations were greater ( $P < 0.01$ ) for H than L and greater ( $P < 0.01$ ) for 120 than 80.

**Table 2.7** Estimates of heat production per metabolic body weight<sup>a</sup> in cows fed high- and low-energy rations at two levels of intake

Model	High energy diet		Low energy diet		SEM	Probability		
	Low intake	High intake	Low intake	High intake		Diet	Intake	Diet × intake
NRC	113.37	156.56	157.95	213.86	6.21	< 0.01	< 0.01	0.29
Ferrell and Jenkins (1984, 1)	109.94	152.26	154.79	212.03	6.06	< 0.01	< 0.01	0.20
Ferrell and Jenkins (1984, 2)	102.38	138.62	144.71	205.44	8.54	< 0.01	< 0.01	0.14
Gresham et al. (1986)	114.52	160.77	159.43	217.06	5.42	< 0.01	< 0.01	0.28
Wagner et al. (1988, 1)	115.64	164.29	157.98	217.63	4.31	< 0.01	< 0.01	0.19
Wagner et al. (1988, 2)	109.22	152.87	149.53	211.45	6.11	< 0.01	< 0.01	0.12
Wagner et al. (1988, 3)	109.05	152.92	149.71	211.51	6.09	< 0.01	< 0.01	0.13
Wagner et al. (1988, 4)	121.15	174.51	164.35	222.81	4.73	< 0.01	< 0.01	0.57
Bullock et al. (1991, 1)	-149.85	-604.88	423.30	11.05	340.22	0.07	0.19	0.94
Bullock et al. (1991, 2)	-393.51	-965.82	-47.29	-233.13	235.83	0.02	0.10	0.39
Bullock et al. (1991, 3)	-383.68	-998.60	108.10	-172.98	297.13	0.02	0.12	0.56

<sup>a</sup>kcal/d/EBW<sup>0.75</sup>, Calculated as (ME - RE) / d / EBW<sup>0.75</sup>, where d = 53 days

After termination of the trial, all cows were placed into a common pasture and allowed to graze while being fed a protein supplement; i.e., all were managed similarly following the termination of the trial. Calf birth weight from treated cows (Table 2.8) was not affected by diet ( $P = 0.22$ ) or level of intake ( $P = 0.81$ ). Calf age (190± 12 d) at pre-weaning was not different between diet energy density ( $P = 0.89$ ) or level of intake ( $P = 0.19$ ). Calf BW, adjusted 205d BW and ADG were not affected by diet ( $P > 0.85$ )

or level of intake ( $P > 0.24$ ). Cow BW and BCS were not different between diets ( $P > 0.14$ ) or levels of intake ( $P > 0.36$ ) at the time of pre-weaning (approximately 200 d postpartum, and 252 days following trial termination).

**Table 2.8** Pre-weaning performance of cows and offspring<sup>a</sup> from cows fed high- and low-energy rations at two levels of intake

Item	High energy diet		Low energy diet		SEM	Probability		
	Low intake	High intake	Low intake	High intake		Diet	Intake	Diet × intake
Birth weight, kg	30.63	30.29	32.53	32.15	1.755	0.22	0.81	0.98
Age, d	194.36	188.87	194.99	186.86	6.489	0.89	0.19	0.79
Body weight, kg	198.32	184.28	193.94	185.33	15.256	0.85	0.24	0.76
Adjusted 205 day weight, kg	205.17	196.02	201.65	200.21	12.537	0.96	0.56	0.66
Average daily gain, kg	0.84	0.80	0.82	0.82	0.055	0.88	0.56	0.65
Cow performance data								
Body weight, kg	480.99	487.86	495.00	511.37	14.504	0.14	0.36	0.70
Body condition score	5.68	5.62	5.50	5.71	0.204	0.79	0.68	0.46

<sup>a</sup>Random effect of sex was applied in the statistical analysis

## Discussion

Our objective was to quantify the effects of dietary energy density and intake on energy utilization to further interpret maintenance energy requirements in beef cows. Our design resulted in a difference in both DMI and MEI. Digestibility of DM, OM and GE was greater in H than L, which is consistent with the literature (Garrett, 1987; Reynolds et al., 1991b; Fluharty et al., 1994; Ferrell and Oltjen, 2008). Digestibility of ADF was greater in L than H, potentially due to excessive rate of consumption and ruminal passage in H. Gorocica-Buenfil and Loerch (2005) described similar effects of energy density on ADF digestibility. Because DE and ME were calculated from measures of digestibility, it makes sense that they were greater for H than L, as the NRC

(2000) predicts. However, calculated ME (Mcal/kg DM) was lower than NRC (2000) predicted values for H (2.32 versus 2.45 Mcal/kg, respectively), but greater than predicted for L (2.15 versus 1.94 Mcal/kg, respectively). This is most likely related to the digestibility of wheat straw relative to NRC model estimates. If wheat straw digestibility was greater than expected, its greater fraction in L would incrementally increase digestibility of L more than H, narrowing the difference in DE between the two. This is also consistent with increased ADF digestibility in L than in H, possibly because decreased rumen pH resulting from corn inclusion decreased fiber digestibility in H (Horn and McCollum, 1987).

Because energy density of the diets was different than predicted, ME intake was higher than expected in L and lower than expected in H. Our estimates are predicated upon the assumption that  $ME = 0.82 \times DE$  (NRC, 2000). Energy losses (as a proportion of DE intake) associated with increase with acetate:propionate (Johnson and Johnson, 1995). If this occurred in the present study, dietary ME density values may have been greater than 0.82 of DE for the H diets, and less than 0.82 DE for the L diets. Energy lost in the form of methane is typically approximately 6% GE intake, ranging between 2 and 12% Johnson and Johnson (1995) estimated methane production to be related to dietary energy digestibility by the following equation):

$$\text{Methane, \% GE intake} = 10.21 - 0.05 * \text{GE Digestibility}$$

This equation actually assumes a negative correlation between energy digestibility and methane energy expenditure; however, the small  $r^2$  value (0.052) indicates minimal correlation. According to this data, the range of methane production

(% GE intake) for the diets in the current study is likely very minimal (6 to 8%) and similar between diets, suggesting that energy losses in the form of methane were possibly insignificant between diets. Even if differences could have been detected, the magnitude of energy expenditure was most likely very minimal.

Conversely, the proportion of ingested energy lost as methane has been predicted to increase as intake is restricted (Mills et al., 2001), which may result in overestimated dietary ME values in feed restricted animals. In the present study, all treatments were feed restricted. Using the general relationship described by Mills et al. (2001), the difference in this study would have been approximately 0.1 % of GE intake greater energy loss as methane in 80 vs. 120 diets. Although the difference is minimal within this range of intakes, it is worth noting that ME of 80 was potentially smaller than predicted by the model, thus decreasing estimates FHP in limit fed cattle. This further supports suggestions of decreased NE requirement equilibrium with intake restriction (Jenkins and Ferrell, 1997; Freetly and Nienaber, 1998)

Although the diets were designed to deliver isocaloric amounts of  $NE_m$  at both levels of intake, total weight gain, either on a BW or metabolic BW basis, tended to be greater in H than in L. Based on the previously discussed lab results, ME delivery was less than expected for H and greater than expected for L, meaning that the partial efficiency of ME use for maintenance increased with energy density by a margin greater than expected. Although 80 was designed to deliver less NE than required to support maintenance, the cows achieved positive RE across all equations used in its estimation. Increases in NE availability are most likely explained by reduced FHP and HI. Energy

restriction decreases splanchnic tissue mass (McLeod and Baldwin, 2000; Camacho et al., 2014) and subsequent heat production (Reynolds et al., 1991b). Rate of consumption is inversely related to energy expenditure associated with eating (Holmes et al., 1978). Feed restriction in the current trial anecdotally decreased time spent eating, while increasing rate of meal consumption, potentially decreasing HI, further supporting our evidence that intake restriction decreased heat expenditure, and most likely decreased FHP.

There were minimal treatment effects on ultrasound measurements of rib fat, IMF and REA. The tendency for the higher level of intake to have less loss in fat thickness, although most were not different from zero, is not surprising, as the increased energy delivery of 120 relative to 80 should reasonably result in greater RE and subsequent fat deposition. On the contrary, because changes in ultrasound measurements of fat were not different from zero in most cases, the suggestion that intake restriction allows a shift in equilibrium FHP (Freetly and Nienaber, 2008) is further supported. Cows in 80 were fed below NE requirements, and did not lose weight or body condition, specifically in cows fed H. The inherent variance in collecting ultrasound data, coupled with the minimal amount of fat detectable in these cows makes a small absolute error a large amount of variance, reducing the capability to detect differences. Because the change in most ultrasound measurements were not different from zero, the ability to detect differences is likely insignificant. However, regression equations that utilized some measurement of fat as a predictor variable yielded smaller estimates of RE than those that did not (4.6 vs. 14.2 Mcal, respectively, across all treatments). Similar effects



of dietary energy density on RE were reported by Armstrong and Blaxter (1961), Swingle et al. (1979), Garrett (1987), Reynolds et al. (1991), and Sawyer et al., (2004). Energy intake was shown to produce similar patterns by Reynolds et al. (1991) and Freetly and Nienaber (1998). Regardless of the probability of differences, the objective of the study was to utilize the measures of fat in equations to estimate RE. Subsequently, the actual differences in least square means are not of primary interest because they were measured consistently across all treatments.

Although not statistically significant, the numerical difference in mean RE between H and L is noteworthy. With the exception of one (Wagner et al., 1988, Equation 4), the prediction equations from literature at least tended to support the numerical difference in NRC estimates of RE between H and L. This tendency supports our estimates of HE, indicating increased ME use for RE, which is consistent with data from Swingle et al. (1979), which suggested increase efficiency of ME use for gain (RE/MEI). The tendency for RE to be greater in 120 than in 80 is expected, as the increased MEI results in increased nutrient balance and energy deposition. This pattern is consistent with studies on cows (Freetly and Nienaber, 1998; Freetly et al., 2006) and growing cattle (Birkelo et al., 1991), in which FHP was shown to increase by 7 % and  $ME_m$  by 14% with increased intake from 1.2 to 2.2 times maintenance. Although only one Ferrell and Jenkins (1984, Equation 1) equation from literature yielded statistically significant results, the numerical differences are similar to those observed in NRC estimates, and are relatively consistent across all equations (Table 2.9). It is also worth

making note that across all equations, the order of calculated means remains almost completely constant across treatments.

**Table 2.9** Effect of increasing dietary energy density and restricting intake on retained energy

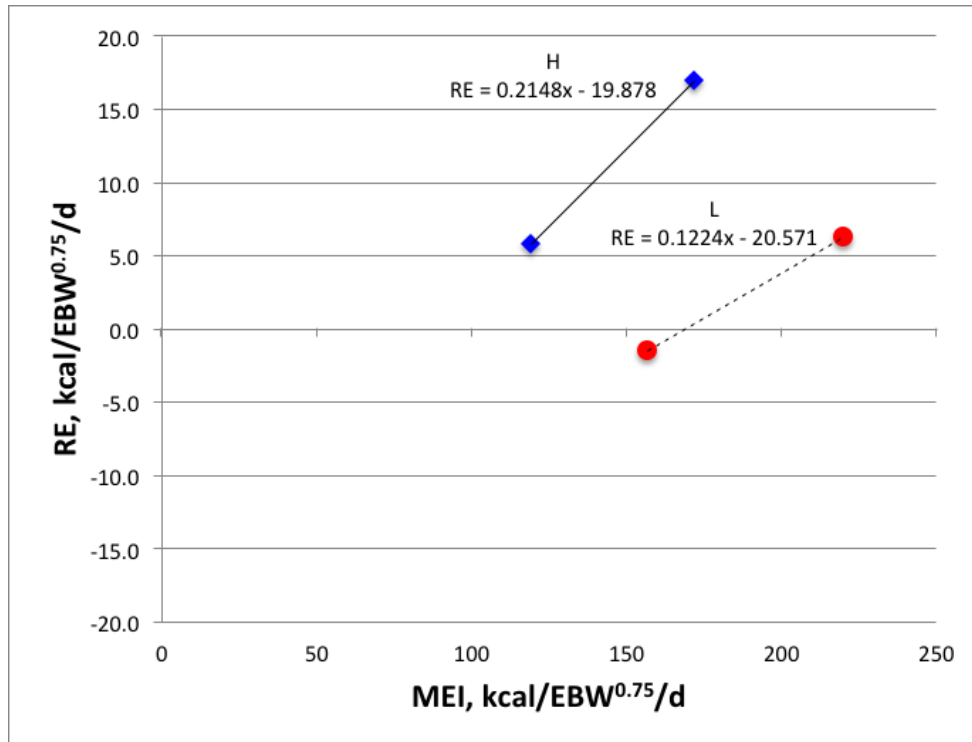
	Factor Means				Difference	
	H	L	80	120	Diet <sup>a</sup>	Intake <sup>b</sup>
NRC	11.38	2.45	2.17	11.66	8.93	9.50
Ferrell and Jenkins (1984, 1)	15.25	4.94	5.46	14.73	10.31	9.27
Ferrell and Jenkins (1984, 2)	25.85	13.28	14.28	24.85	12.57	10.57
Gresham et al. (1986)	8.70	3.02	3.77	7.96	5.68	4.19
Wagner et al. (1988, 1)	6.38	0.55	1.02	5.92	5.83	4.90
Wagner et al. (1988, 2)	15.31	7.86	8.46	14.71	7.44	6.26
Wagner et al. (1988, 3)	15.36	7.75	8.44	14.66	7.62	6.22
Means	14.03	5.69	6.23	13.50	8.34	7.27

<sup>a</sup>Calculated as H - L

<sup>b</sup>Calculated as 120 - 80

Using mean MEI and RE data, estimates  $ME_m$  were made by regressing RE on MEI, and solving for RE = 0 (Figure 2.2). The resulting  $ME_m$  values were estimated to be 92.54 and 168.06 kcal\*EBW<sup>-0.75</sup> for H and L, respectively. Estimates of  $ME_m$  based on the NRC model (2000) were 160.0 and 175.9 kcal\*EBW<sup>-0.75</sup>. The fact that  $ME_m$  is greater for L than H is reasonable, as NE values are greater in high-energy diets than in low-energy diets (Garrett and Jonson, 1983); however, the degree by which  $ME_m$  of H was shifted (-42.2%) according to estimates made using equations from the NRC (2000) is remarkable. This suggests a gross overestimation of  $ME_m$  requirements in cows consuming a high-energy diet by the NRC model (2000). The effects of energy density are well supported by data presented in the current article, and also by data reported by

Swingle et al. (1979) and Sawyer et al. (2004), although the current reduction is substantially larger than the literature suggests.



**Figure 2.2** The effect of MEI on RE in cows fed either a high- or low-energy diet

The fact that HE was greater in L than H is not surprising, as MEI was greater in L, by design; however, RE was no less in H than in L. The proportion of ME lost as heat was greater in L (99.1%) than in H (93.1%). This is supported by Swingle et al. (1979) and Reynolds et al. (1991), who reported greater proportion of ME lost as heat in cattle consuming a low-energy diet than heifers consuming a high-energy diet. However, the magnitude of difference was not as great in these studies, Freetly and Nienaber (1998)

reported a 22% decrease in  $ME_m$  requirements when intake was restricted by 65% in mature cows. potentially due to the degree of feed restriction on the current study. This degree of difference is very similar to the decrease observed in the current study. Maintenance requirements ( $ME_m$ ) reported by Freetly and Nienaber (1998) were slightly greater ( $103.7 \text{ kcal} \cdot \text{EBW}^{-0.75}$ ) than in our cows consuming H ( $92.5 \text{ kcal} \cdot \text{EBW}^{-0.75}$ ) and lower than in our cows consuming L ( $168.0 \text{ kcal} \cdot \text{EBW}^{-0.75}$ ).

Their diet consisted of Bromegrass hay, which is lower than H and higher than L, in terms of energy density. This disparity between reported  $ME_m$  requirements in these trials further supports our suggestions that increasing energy density decreases maintenance energy requirements. Order of mean HE across treatments changed very minimally across all equations, suggesting that the particular equation used for estimation of body energy is not necessarily of abundant importance; regardless of equation, percent change in heat production associated with increasing dietary energy density (Table 2.10) is between the range of -31.2 and -25.5%. Similarly, the percent change in heat energy associated with intake restriction is similar across equations (-29.0 to -26.8%). The minimal variance in percent change across equations validates the importance of expressing energy savings on a relative basis. Because energy requirements in beef cows vary dramatically across weights and breed types (Jenkins and Ferrell, 1997), making a recommendation based on a percent reduction in requirement per metabolic body weight makes sense. This allows for relative adjustments to previous assumptions about requirements, which is more applicable than estimating a total reduction (Mcal), which may not necessarily be accurate across cow

body types. Because there were no interactions relative to estimates of heat expenditure, the effects of increasing energy density and restricting intake are assumed to be additive. This is verified by the decrease in HE by approximately 46.9% from L120 to H80 across all equations.

**Table 2.10** Effect of increasing dietary energy density and restricting intake on daily heat production

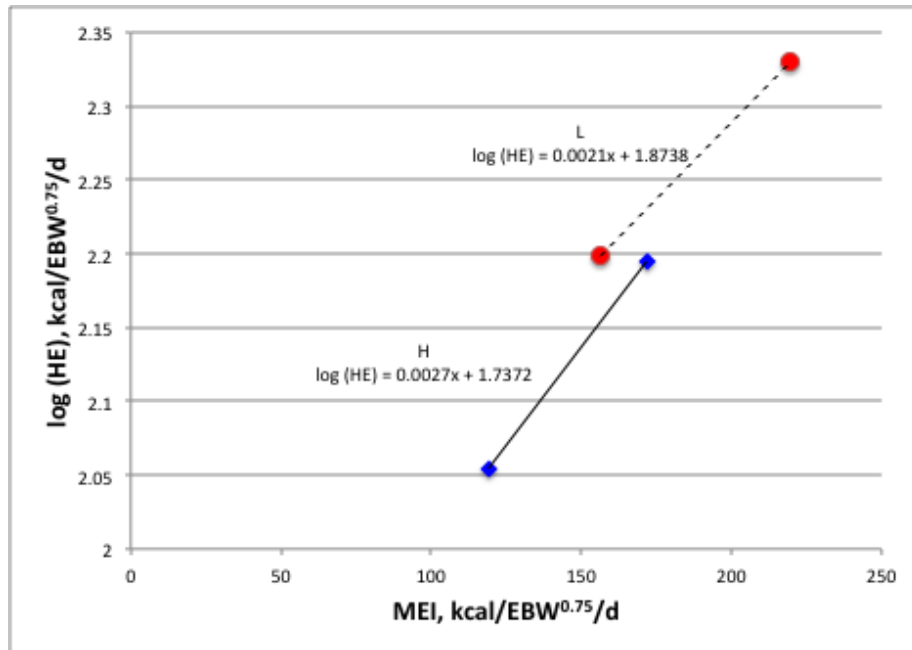
	Factor Means				Percentage change	
	H	L	80	120	Diet <sup>a</sup>	Intake <sup>b</sup>
NRC	134.97	185.91	135.66	185.21	-27.4%	-26.8%
Ferrell and Jenkins (1984, 1)	131.10	183.41	132.37	182.15	-28.5%	-27.3%
Ferrell and Jenkins (1984, 2)	120.50	175.08	123.55	172.03	-31.2%	-28.2%
Gresham et al. (1986)	137.65	188.25	136.98	188.92	-26.9%	-27.5%
Wagner et al. (1988, 1)	139.97	187.81	136.81	190.96	-25.5%	-28.4%
Wagner et al. (1988, 2)	131.05	180.49	129.38	182.16	-27.4%	-29.0%
Wagner et al. (1988, 3)	130.99	180.61	129.38	182.22	-27.5%	-29.0%
Means	132.32	183.08	132.02	183.38	-27.8%	-28.0%

<sup>a</sup>Calculated as  $100\% \times [(H - L) / L]$

<sup>b</sup>Calculated as  $100\% \times [(80 - 120) / 120]$

Fasting heat production was estimated by regressing log (HE) on MEI (Figure 2.4). Because heat production occurs in a nonlinear function as MEI approaches infinity, log transformation of heat production allows for a meaningful linear regression of HE on MEI (Garrett, 1987; Figure 2.3). The y-intercept of these equations represents log(FHP). After taking the inverse (inverse log,  $10^x$ ) of the intercepts, FHP of H and L were estimated to be 54.6 and 74.8 kcal·EBW<sup>-0.75</sup>·d<sup>-1</sup>, respectively. This effect of dietary energy density on FHP is supported by Blaxter (1972), who stated that FHP decreases as

energy density increases in the diet; however, the magnitude of decrease from L to H is remarkably greater than the literature suggests.

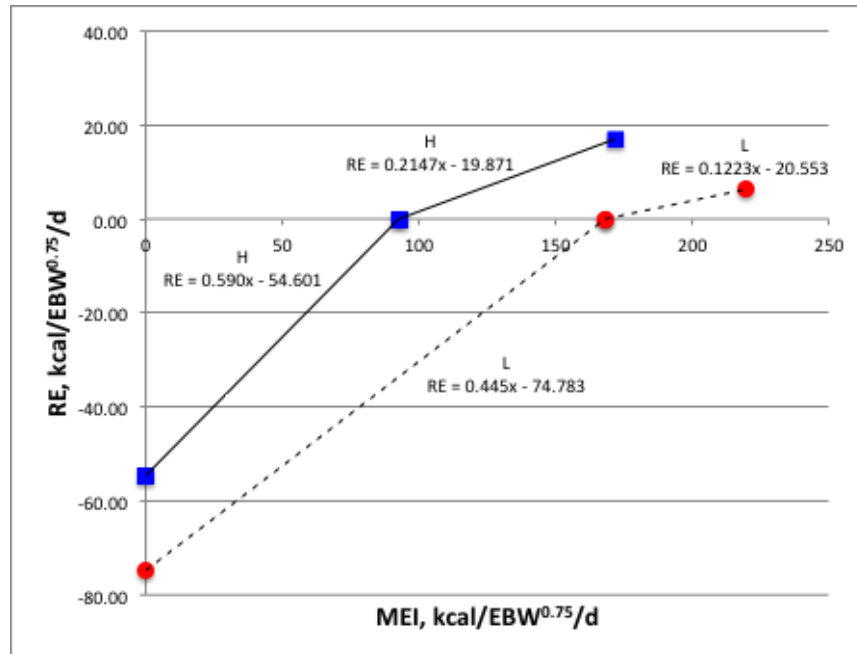


**Figure 2.3** Logarithmic transformation of the effect of MEI on HE in cows fed either a high- or low-energy diet

Using these estimates of FHP and  $ME_m$ , a graphic illustration of NE was designed (Figure 2.4). This design is useful in promoting visual assessment of the energetic requirements resulting from diet, and also for assessing the energetic efficiency of the diet. As predicted, maintenance energy requirements, expressed as both  $NE_m$  and  $ME_m$  (as calculated) were reduced when dietary energy density increased. The illustration successfully depicts both the decrease in FHP and the increased efficiency with which ME is utilized in H relative to L. The slope of RE on MEI represents the

efficiency of ME use for energy retention below ( $k_m$ ) and above ( $k_g$ ) maintenance intake.

This method of analysis is consistent with Garrett (1987).



**Figure 2.4** Calculated NE values of the high- and low- energy diets

This method of analysis expresses the difference in energy requirements associated with altering dietary energy density; however, it does not address the effects of intake restriction on maintenance requirements. When intake is restricted, metabolism decreases as a result of the physiological alterations (Jenkins and Ferrell, 1997; Freetly and Nienaber, 1998), resulting in equilibrium requirements lower than the previously established requirements. The reduction in HE of 80 relative to 120 supported these suggestions.

## CHAPTER III

### SUMMARY

The results from this study successfully displayed the effects of dietary energy density and intake on maintenance requirements and heat production. This data suggests that NRC model estimates of  $NE_m$  requirements are grossly overestimated for cows consuming a high-energy diet. Furthermore, additional evidence from this experiment supported previous suggestions that intake restriction resulted in a shift in equilibrium maintenance energy requirements; however, because an energy balance was not conducted before and after treatment application, direct statements regarding the effect of energy intake on  $NE_m$  requirements cannot be verified by this dataset.

Cow efficiency is not only measured by calf weaning weight, but also by the minimization of dietary inputs. These data suggest promising ideas about the future of intensified cow-calf production. Through nutritional optimization, there exists opportunity to increase not only the efficiency of production and land use, but also the sustainability of beef production. Further investigation warrants the use of energy balance to verify previously ideas about equilibrium shifts in maintenance requirements (in high-energy diets). Additionally, both the minimal and optimal level energy intake required for long-term maintenance should be evaluated in cows.



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