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EFFECTS OF DIETARY FAT AND PROTEIN FROM CORN COPRODUCTS ON GROWTH, CARCASS CHARACTERISTICS, RUMINAL METABOLISM, AND GENOMIC REGULATION OF MARBLING DEVELOPMENT IN EARLY-WEANED BEEF CATTLE

BY

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DISSERTATION

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ABSTRACT

Four experiments were conducted to evaluate the effects of dietary fat and protein from corn coproducts on growth, carcass characteristics, ruminal metabolism, methane production, and transcriptional regulation of marbling. In Exp. 1, crossbred heifers (n = 150) and steers (n = 100) were used to evaluate 1 of 5 growing diets in a 2 × 2 + 1 factorial arrangement of treatments: 1) corn-based control; 2) low fat, low protein coproduct blend; 3) high fat, low protein coproduct blend; 4) low fat, high protein coproduct blend; 5) high fat, high protein coproduct blend. Low protein and low fat diets were formulated to be isonitrogenous with similar fat content to control (16.0% CP, 3.0% fat), and high protein and high fat diets were formulated to be 20.0% CP and 5.0% fat respectively. Calves were weaned at 90 d, blocked by sex and then by weight into 25 pens (10 hd/pen). The objective of this experiment was to determine if differing concentrations of protein and fat in coproduct-based growing diets of early-weaned calves affect feedlot performance and carcass composition. Calves were fed experimental diets for 112 d and then acclimated to a common feedlot diet for an additional 112 d. Body weight, hip height (HH), and ultrasound data were collected at the end of each 112d feeding phase. Carcass data included HCW, LM area (LMA), 12th rib back fat (BF), marbling score (MS), KPH, and USDA QG. No interactions ($P \geq 0.27$) of fat and protein concentration were detected; therefore, main effects are discussed. No effects ($P \geq 0.12$) of control, protein, or fat were detected for BW, or HH. Calves consuming increased dietary protein from coproducts had increased ($P = 0.04$) ADG in the growing phase. Feeding cattle control decreased ($P = 0.04$) DMI, and increased ($P < 0.01$) G:F during the growing phase and feeding phase. Ultrasound revealed increased ($P = 0.05$) BF in calves fed high fat at d 112. High protein diets decreased ($P = 0.02$) ultrasound MS at d 112. Carcasses from cattle fed high fat diets had greater ($P = 0.03$) MS compared to those from cattle fed low levels of dietary fat. Carcasses from cattle fed high protein diets had reduced ($P < 0.01$)

percentage of carcasses that graded Prime compared to carcasses from cattle fed increased concentrations of fat. No differences ($P \geq 0.15$) were observed for HCW, LMA, BF, KPH, or YG. Cattle fed high protein diets produced fewer ($P < 0.01$) carcasses that graded Prime than cattle fed low protein diets. These data indicate that growth was unaffected by protein and fat concentration in growing calf diets, but MS and QG were positively influenced by fat and protein concentration in early calf diets. In Exp. 2, *Longissimus lumborum* of thirty crossbred calves (Age = 95 ± 1.7 d; BW = 179 $\pm$ 18 kg) were fed diets from experiment 1. Biopsies were collected from the LM at 0, 112, and 224 d for transcriptional analysis via RT-qPCR of 14 genes associated with adipogenesis and lipogenesis within the muscle. The objective of this experiment was to examine the effect of dietary fat and protein concentration on serum concentrations of leptin, IgF1 and growth hormone, and gene expression of fourteen genes that regulate lipid metabolism and adipogenesis. Serum was collected at d 0, 112, and 224 and analyzed for leptin, insulin-like growth factor 1, and growth hormone concentration. Data were analyzed to ascertain the effects of protein level, fat level, time, and their interactions on gene expression and blood metabolite concentration. Increased protein and decreased fat in the growing diet resulted in a protein × fat × day interaction characterized by a carryover effect which increased ($P < 0.01$) gene expression of PPAR gamma, insulin induced gene 1, thyroid hormone responsive SPOT14 protein, ATP citrate lyase, adiponectin, diacylglycerol O-acyltransferase homologue 2, fatty acid binding protein 4, fatty acid synthase, phosphoenolpyruvate carboxykinase 1, and stearoyl-CoA desaturase, as well as, serum leptin concentrations during the finishing phase. Expression of sterol regulatory element binding transcription factor 1 was increased ($P < 0.01$) at d 112 in steers fed high protein, high fat diets compared to those fed high protein, low fat diets. A fat × day interaction ($P < 0.01$) occurred for

the expression of ADIPOR2 and CEBPA resulting in a carryover effect wherein low fat diets fed during the growing phase increased expression of both genes at the end of the finishing phase (d 224). Carcasses from cattle fed control during the growing phase tended ($P = 0.09$) to have higher marbling scores while other carcass parameters were not different ($P \geq 0.13$). These data indicate that feeding differing levels of dietary fat and protein during the growing phase does affect intramuscular adipogenesis at the transcriptional level, but differences in gene expression were not sufficient to affect carcass quality among cattle fed coproducts. In Exp. 3, 40 steers (age = 134 ± 3 d; BW = 185 ± 11 kg) were randomly allotted to 1 of 5 dietary treatments: 1) corn-based control (CNT), 2) 0% corn distillers solubles (CDS), 3) 10% CDS, 4) 19% CDS, or 5) 27% CDS. Diets 2–5 included coproducts (corn gluten feed and soybean hulls) and were formulated to achieve fat concentrations of 3, 5, 7, and 9%, respectively. Diets were fed once daily for 106 d growing phase. All steers were fed a corn-based diet from d 107 to 196 (finishing phase). Contrasts were used to examine a) the difference between CNT and 10% CDS; b) linear and quadratic effects of CDS inclusion. The objective of this experiment was to evaluate differences in growth and carcass traits associated with feeding either starch or increasing levels of CDS. During the growing phase, steers fed CNT had increased ($P \leq 0.03$) BW, G:F and ADG compared to those fed 10% CDS. Increasing CDS inclusion increased (linear; $P = 0.01$) ADG and G:F. At the conclusion of the growing phase, BF determined via ultrasound was greater ($P = 0.05$) in CNT-fed calves compared to 10% CDS. There were no treatment differences ($P \geq 0.14$) in finishing phase ADG, DMI, or G:F. Steers fed CNT had increased ($P = 0.02$) overall ADG compared to steers fed 10% CDS, and increasing CDS inclusion increased (linear; $P = 0.05$) overall ADG. Final BW, and overall DMI and G:F were not different ($P \geq 0.06$). There were no

effects ($P \geq 0.10$) of treatment on carcass traits. Feeding a coproduct diet with 10% CDS during the GP decreased overall ADG compared to feeding corn.

Finally, in Exp. 4, steers (n = 5; BW = 345 ± 22 kg) were fed Exp. 3 diets for ad libitum intakes in a 5x5 Latin square design. The objectives of this experiment were to evaluate rumen fermentation patterns, nutrient digestibility, and ruminal methane production associated with feeding either starch or increasing levels of CDS. Apparent dry matter digestibility (DMD) increased (linear; $P = 0.02$) with increasing dietary CDS inclusion. Steers fed CNT increased ($P = 0.01$) DMD compared to those fed 10% CDS. Fat digestibility increased (linear; $P < 0.01$) as CDS inclusion increased, but NDF and ADF digestibility were not affected ($P \geq 0.17$) by dietary treatment. Also, there was no difference ($P \geq 0.37$) in ruminal methane emissions with increasing dietary inclusion of CDS. Also, increasing CDS inclusion improved DM and fat digestibility as well as overall ADG. This research provides insight into the effects of elevated protein and fat from corn coproducts on the molecular regulation of intramuscular fat development. Feeding differing levels of dietary fat and protein during the growing phase does affect intramuscular adipogenesis at the transcriptional level, but differences in gene expression were not sufficient to affect carcass quality among cattle fed coproducts in our small subset. However, coproducts with no corn fed during the growing phase resulted in carcasses with similar marbling scores to those fed corn-based growing diets suggesting that starch may not be necessary to produce high quality carcasses from early-weaned calves. Additionally, These data indicate a difference in the behavior of fat from CDS in the rumen compared to other fat supplements such as corn oil. Increased performance with increased CDS inclusion and the lack of adverse effects on ruminal metabolism and carcass traits make CDS a viable option for beef cattle diets.

DEDICATION

For my parents. Without your faith and unconditional love, I would have been lost. You have both been the single guiding light, and the standard by which I measure the character and integrity of myself and everyone I meet.

For the children of the future. May this work mark the beginning of a lifetime of service that will hopefully enrich your lives and ensure that you are provided with the information necessary to feed an ever-growing and changing world.

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CHAPTER 1

INTRODUCTION

Early weaning is a management system used by beef producers to increase reproductive efficiency (Vaz and Lobato, 2010) and shorten the feeding phase needed for market animals to reach the choice grade (Loy et al., 1999). Early-weaned calf management has been extensively researched in comparison to traditional weaning practices (Harvey et al., 1975; Richardson et al., 1978; Myers et al., 1999; Schoonmaker et al., 2003, 2004a; Shike et al., 2007; Du et al., 2009; Du et al., 2010). Du et al. (2009) noted that nutritional manipulation of marbling is more effective in utrero, in neonates and in early-weaned calves because the abundance of multipotent stem cells (potential adipocytes) is greater in younger animals. In early-weaning systems, this gives producers' a window from 150 to 250 d of age in which marbling can be affected by nutritional management (Du et al., 2010).

Historically, it was believed that dietary starch was necessary for early-weaned calves to improve marbling (Schoonmaker et al., 2003, 2004a) and subsequent carcass quality (Myers et al., 1999; Shike et al., 2007). More recently, research has indicated that early-weaned calves fed growing diets that include distillers grains, corn bran, and other coproducts with varying levels of fat and protein produce carcasses with similar marbling scores to those fed starch-based diets (Bedwell et al., 2008; Retallick et al., 2010; Meteer et al., 2011). With the large amounts of coproduct feeds available and the relatively high concentrations of fat and protein in many of these ingredients, it may be possible to replace the dietary energy, previously provided as starch without adverse effects on meat quality.

Carcass traits (i.e. marbling) are extremely complex and fall under the control of not only environmental factors, but also of interconnected gene networks each exerting small effects that combine to produce physiological changes (Wu et al., 2006). Biochemical studies of adipose tissue (e.g., Smith and Crouse, 1984; Rhoades et al., 2007) and muscle protein (Gingras et al., 2007) metabolism have provided many insights into basic tissue development as it pertains to nutrition and growth. Enzyme activity in the energy metabolism and lipogenic pathways are largely a result of the rate at which the enzymes are synthesized (Salati et al., 2004; Freyssenet, 2007). Metabolic regulation relies heavily on transcriptional regulation as a long-term mechanism for determining the expression level of key enzymes (Desvergne et al., 2006). While several studies have evaluated performance and carcass characteristics of early-weaned calves (Harvey et al., 1975; Richardson et al., 1978; Loy et al., 1999; Myers et al., 1999; Schoonmaker et al., 2003, 2004b; Retallick et al., 2010; Meteer et al., 2011), little work has been done to compare coproduct diets with differing nutrient compositions and their impact, when fed early in life, on carcass quality at the transcriptional level.

Condensed distillers solubles (CDS) are a liquid coproduct from the ethanol industry, which may contain increased concentrations of fat dependent upon fractionation and deoiling protocols of the plant. Lardy (2007) reported fat concentrations in CDS ranging from 9 to 15%, but fat concentrations can exceed 18% dependent upon source (Pesta et al., 2012). The increased availability of CDS in the Midwest, and the elevated concentration of fat, makes them useful for inclusion in a variety of cattle feeding strategies. The ability of dietary fat to shift ruminal fermentation toward propionate production was hypothesized to be the mechanism that may help explain the similar marbling scores observed in carcasses from calves fed coproducts and those fed starch-based diets during the growing phase (112 d; Retallick et al., 2010; Meteer et al.,

2011; Segers et al., 2012). Diets with as little as 4% supplemental fat have been shown to increase propionate production in the rumen when compared to fat free diets without affecting fiber digestibility (Zinn, 1998). The extremely elevated fat concentrations in CDS reported by Lardy (2007) and Pesta et al. (2012) make it imperitive to understand the behavior of this ingredient in the rumen as well as how it impacts compositional development and subsequent carcass characteristics.

Additionally, stocker and feedlot operations in the beef industry are responsible for 19% of the methane emissions from beef and dairy cattle in the United States (EPA, 2011). The dairy industry accounts for an additional 23% of emission while cow/calf the operations account for the remaining 58% (EPA, 2011). Lipids have been shown to have a negative impact on methane production through several processes, including enhancing propionate production, biohydrogenation, and protozoal inhibition (Johnson and Johnson, 1995). Czerkawski et al. (1966) infused the rumen of sheep with oleic, linoleic, or linolenic acid. All animals displayed decreased methane production by at least 13.8% with infusion of polyunsaturated fatty acids (PUFA; Czerkawski et al., 1966). It was also noted that methanogenic populations were solely affected by the addition of lipid because general carbohydrate fermentation proceeded as expected even when methane levels were half their pre-infusion levels (Czerkawski et al., 1966). Other studies have revealed similar results when diets containing soybean oil and tallow were fed to cattle and compared with isocaloric controls (Swift et al., 1948; Haaland, 1978; Van der Honing et al., 1981), but there is no data illustrating the effect of fat from corn coproducts on ruminal methane production. With the growing interest in environmental sustainability, it is important to understand the effect of these diets on ruminal methane production.

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CHAPTER 2

THE REVIEW OF THE LITERATURE

Introduction

The economic instability of today's agricultural markets have caused input costs for cattle producers to rise and profit margins to narrow. This leaves beef producers looking for ways to increase production efficiency in an attempt to generate additional revenue. Research conducted on ways to adapt production practices has primarily focused on the post-weaning phase of calf development. For example, early weaning calves can improve reproductive efficiency in the cow (Vaz and Lobato, 2010) as well as carcass characteristics in the calf (Loy et al., 1999). Historically, feed costs have been prohibitive in the decision to wean early. The high protein and energy requirements of growing calves demand the use of concentrates in order to achieve necessary gains for profitability. However, currently in the Midwest, coproduct feeds are plentiful; this allows feed costs to be moderated by producers willing to use coproducts. Little research has been conducted to examine the impacts of these feeds in young calves; although, there is almost a half century of research indicating that calf nutrition has lasting impacts on carcass quality (Harvey et al., 1975; Hood, 1982).

Corn Coproduct Overview

Coproducts from ethanol and the corn milling industry may be an option to help producers alleviate feed costs, and include: dry or wet distillers grains (DG), wet or dry corn gluten feed (CGF), condensed distillers solubles (CDS), corn bran and soy hulls. In 2010, U.S. ethanol production reached 50.7 billion L per yr, and, with an expected growth to 56.8 billion L

per yr by 2015, it is only logical for producers to use these feed resources (Renewable Fuels Association, 2011).

Sources and Production

Grain alcohol has been manufactured for centuries, and distillers grains plus solubles (DGS) has been utilized as a feedstuff since the beginning of the 19th Century (Henry, 1900). Dried distillers grains plus solubles (DDGS) are a byproduct of the dry milling process of corn to produce ethanol. Outlined by Berger and Singh (2010), ethanol, and subsequently DDGS, is produced when the corn kernel is ground, mixed with water and cooked under pressure to gelatinize the starch. The starch is further broken down by the addition of alpha-amylase. This yields dextrins and the resulting substrate is referred to as mash. After a short tempering phase, the mash is fermented by adding yeast and glucoamylase. The glucoamylase breaks down dextrins into various sugars. Yeast then ferments the resulting sugars to produce ethanol. From the fermentation tank, the ethanol is distilled and the whole stillage (all non-ethanol material) is centrifuged to separate the solids from the thin stillage. Thin stillage is condensed, and added back to partially dried solids to produce WDGS, or the mixture can be dried to produce DDGS (Berger and Singh, 2010). Drying distillers grains may account for 40% of the energy costs incurred by the ethanol manufacturer and may decrease nutritional value (Ham et al., 1994). Currently, CDS is also available as a liquid supplement. Condensed distillers solubles is relatively high in CP (15-25%) and, in some cases, fat (EE 18- 25%) and has been investigated as a supplement for low quality forages (Gilbery et al., 2006). In growing cattle with high CP requirements, CDS may have some merit as a protein supplement (Lardy, 2007).

In the food processing industry, corn oil and high fructose corn syrup is produced by wet milling. The process begins with steeping corn in water with sulfur dioxide (Singh et al., 1997).

The corn germ is then removed and processed to produce corn oil. The starch and bran are separated and the starch is used to make sweeteners and chemicals or dried to produce corn starch. The remaining fiber and protein is termed corn gluten feed (CGF) and may be sold wet or as a dried product (Hoffman, 1989). Corn gluten feed and distillers grains with or without solubles are available as wet or dry products. Wet products make excellent feedstuffs, if producers have acceptable storage space, ability to transport, and a high enough feed-out rate to utilize products before they spoil (Klopfenstein, 1996). Wet CGF has been shown to be more rumen degradable than dry CGF. Firkins et al. (1985) hypothesized that the presence of water caused the cellulose in CGF to swell, and thereby increased its availability for degradation by rumen microbes.

Nutritional Value and Variation

Nutritional values of corn coproducts are highly variable. The National Research Council Guidelines for the Nutrient Requirements of Beef Cattle (NRC, 1996) reports nutritive values for DDGS as follows: 90.3% DM, 30.4% CP, 46.0% NDF, 10.3% Fat and 0.4% S. For CGF, nutrient values are 90.0% DM, 23.8 % CP, 37.0% NDF, 3.9% Fat and 0.5% S. Manufacturer estimates for nutrient values of corn bran are 89.0% DM, 14.0% CP, 38.1% NDF, 8.9% Fat, and 0.81% S (Dakota Gold®, 2011) and 39.1% DM, 21.0% CP, 6.5% NDF, 22.3% Fat, and 1.25% S for CDS (Dakota Gold®, 2011). It is important to note, that sulfuric acid and sulfur dioxide are used heavily in the processing of grains, as well as cleaning equipment used for fermentation, and, as a result S levels can reach unhealthy levels in corn coproducts.

Spiehs et al. (2002) surveyed 12 plants and reported S levels of 0.33 to 0.74% for DDGS. Holt et al. (2004) sampled 4 plants and found that S content ranged from 0.35 to 0.69% for DDGS; 0.36 to 0.39% for wet distillers grains; and from 0.25 to 1.15% for CDS. These data

indicate that predicted S content (NRC, 1996) for corn coproducts is grossly underestimated for modern production practices. In fact, S values will change between processors and even mills using the same distillation protocol (Berger and Good, 2007). Variation in nutrient content can be due to factors such as grain selection, batch vs. continuous fermentation, and drying temperature and duration (Carpenter, 1970; Olentine, 1986; Spiehs et al., 2002). Fractionation techniques for grain processing are advancing constantly and the nutrient value of coproducts change each time fractionation protocols are altered. Corn is approximately two-thirds starch, therefore, given an efficient fermentation/distillation process, the CP, fiber, and fat content of DG should be approximately 3 times that of corn (Stock et al., 2000). This system agrees with NRC (1996) values; however, nutrient content is not the only factor that makes coproduct feeds unique.

Rumen Digestibility of Coproduct Feeds

Rapid and extensive cell wall digestibility has been observed *in vitro* using CGF as a substrate (Abe and Horii, 1978). This illustrates that CGF is a readily fermentable feedstuff that can supply energy in the form of digestible fiber. Additionally, the protein component of CGF was degraded to a greater extent than that of soybean meal (SBM; Abe and Horii, 1978). These results were confirmed *in vivo* when ruminal NH_3 and propionate (5.8 and 13.0 mmol/ml, respectively) were recorded for CGF supplemented cows compared to NH_3 and propionate levels (4.1 and 11.6 mg/dl, respectively) for cows supplemented with SBM and cows consuming only native grass hay (0.5 and 11.7 mg/dl, respectively; Fleck et al., 1988). The germ protein of corn is removed for oil extraction in the manufacturing of CGF, so the protein content of CGF is lower than that of DG; however, steep liquor from the soaking process is condensed and may be added to CGF before drying (Hoffman, 1989). The steep liquor contains increased levels of

digestible nitrogen N which is likely responsible for elevating rumen NH_3 concentrations (18.9 mg/dl compared to 8.4 mg/dl only 1 h postfeeding; Wagner et al., 1983). Bowman and Patterson (1988) observed that after 1 h of *in vitro* incubation, NH_3 concentrations were greatest in cultures using CGF, as a substrate, compared to those using corn bran, corn gluten meal, and SBM. By 6 h, however, CGF produced the lowest NH_3 concentration among treatments, suggesting a more rapid rate of CP degradation. Bowman and Patterson (1988) also reported DM digestibility in the rumen was lower for lambs fed CGF than those fed corn plus urea, or corn plus SBM while N digestibility was higher. This apparent decrease was explained by reduced microbial efficiency resulting from the increased fiber in the CGF supplement and subsequent ruminal outflow of microbial DM (Owens and Issacson, 1977).

Rumen Metabolism: Protein

Coproduct feeds such as DG have been studied for almost 40 years with substantial interest in the increased level of RUP (Klopfenstein et al., 2007). Zein is the primary protein in corn and is approximately 40% degradable in the rumen (McDonald, 1954; Little et al., 1968). Aines et al. (1987) calculated average rumen escape values for DGS and determined that 2.6 times the amount of protein from DDGS would escape the rumen undegraded compared to that of SBM. Bypass protein is important for optimal growth in young growing ruminants (Nelson, 1997).

Protein requirements in growing cattle vary based on age, BW, and stage of development but are greater than in cattle that have reached physiological maturity. Amino acid (AA) requirements in growing cattle are determined largely by the AA composition of the rumen microbial crude protein (MCP; Merchen and Titgemeyer, 1992). The AA supply from MCP is

well-balanced and similar to that of SBM (Merchen and Titgemeyer, 1992). Individual AA can be experimentally determined to be first- or second-limiting, and may be co-limiting (e.g. S, AA, lysine, histidine, and perhaps threonine, valine, and isoleucine; Merchen and Titgemeyer, 1992). Quantity and quality of the postruminal AA supply can be altered by maximizing net microbial protein synthesis, manipulating supplemental protein source, or feeding ruminally protected AA (Merchen and Titgemeyer, 1992). Microbial crude protein production can be calculated based upon TDN of the diet using the equation (NRC, 1996):

$$MCP\ g/day = 6.25\ (-31.86 + 26.12\ TDN\ (kg\ intake/day))$$

Often, microbial protein synthesis will not meet the AA requirements for optimal growth without protein supplementation.

Gunn et al. (2009) measured plasma urea nitrogen levels in cattle fed 25 or 50% DDGS and compared those to isonitrogenous composites formulated to contain nutrient concentrations similar to DDGS. Composites were made from corn gluten meal, dry rolled corn and vegetable oil. Gunn et al. (2009) observed cattle fed composites had greater plasma urea nitrogen than those fed high-protein diets. These authors reported that cattle fed protein at the same level during a period of growth had decreasing plasma urea nitrogen levels every 30 d regardless of protein source (DDGS or composite). Waller et al. (1980) showed that DDGS protein was used more efficiently than SBM when fed in combination with urea to sheep and cattle. In that same study, the authors demonstrated that protein use was more efficient than in diets including only SBM and urea, but less efficient than in diets including only DDGS and urea as the protein supplement. Because of these unique characteristics, DDGS has been used frequently as a source of RUP (Klopfenstein et al., 1978).

Though the protein component of DGS is partially protected from rumen degradation (Klopfenstein et al., 1978, 2007; McDonald, 1954; Little et al., 1968; Aines et al., 1987), protein from corn gluten feed is highly fermentable and can be almost completely digested in the rumen (Abe and Horii, 1978; Fleck et al., 1985; Wagner et al., 1983). There are benefits to both RUP and MCP in terms of AA delivery to the small intestine, but the most important aspect of a protein supplement is the quality of the protein supplied to the animal. Understanding the extent to which protein is degraded in the rumen is important when determining if the amount of protein that reaches the small intestine is greater than, equal to, or less than the amount of protein consumed (Santos et al., 1984.)

Amino acid, specifically lysine, availability can vary drastically based on source and processing of DDGS. Cromwell et al. (1993) found increased lysine concentrations in lighter colored grains, and increased protein digestibility was reported for lighter colored grains with increased yellowness (b*) values when evaluated with a colorimeter by Fastinger et al. (2006). Cromwell et al. (1993) also showed that physical appearance of DDGS was highly correlated with nutritional properties. Klopfenstein et al. (2007) stated that a large portion of the protein in CDS (which are added back to DDGS) are yeast cells that have been heated and killed during fermentation and concentrated in the solubles. Denatured yeast is incorporated into Maillard Reaction products making the protein fraction of CDS more resistant to lysis, ruminal degradation, and intestinal absorption (Bruning and Yokoyama, 1988). These characteristics may play a role in decreasing the DM and protein digestibility of coproduct feeds (Uwituze et al., 2010; Santos et al., 1984; Klopfenstein et al., 2007).

Rumen Metabolism: Fat

Fat as a dietary component for ruminant diets has interested animal scientists for years mainly because of the energy density and unique fermentative properties. Researchers have examined many sources of supplemental fat. The most common sources of fat in livestock diets are from oilseeds such as soybeans, cottonseed, canola, safflower seed, and sunflower seed (Staples et al., 1998; Williams and Stanko, 1999). Other, sources of supplemental fat in beef cattle diets include fishmeal, tallow, yellow grease, flaked fat, prilled fat, hydrogenated fat, calcium soaps of fat, medium-chain triglycerides, and FFA (Staples et al., 1998; Williams and Sanko, 1999). Fat extracted from oilseeds, as well as corn, contains high levels of PUFAs while rendered fats (tallow and yellow grease) and granulated fats (prilled fats and calcium soaps) contain high levels of MUFAs and saturated fats, respectively (Coppock and Wilks, 1991).

When dietary fat enters the rumen, the microflora begin to hydrolyze and break down various lipids including TAGs, phospholipids, and galactolipids separating fatty acids from glycerol (Funston, 2004). Microorganisms biohydrogenate the unsaturated fatty acids thereby removing the majority of double bonds and changing the orientation of some isomers (Mattos et al., 2000). Polyunsaturated fatty acids are biohydrogenated with 60% to 90% efficiency. Hydrolysis of fatty acids, however, is less efficient. In the case of saturated fatty acids, hydrolysis occurs with 40% to 50% efficiency while PUFA are hydrolyzed with, at most, 35% efficiency therefore; highly unsaturated PUFAs, such as those present in corn oil, are likely to pass through the rumen unhydrolyzed (Thomas et al., 1997).

After hydrolysis of fatty acids, the resulting glycerol is fermented to produce propionate (Byers and Schelling, 1993). It has been suggested that this decrease in the acetate:propionate

ratios may be responsible for improvements in efficiency of energy utilization and partitioning (Funston, 2004) as well as the development of intramuscular fat (Smith and Crouse, 1984).

When diets contain large amounts of fat (>5% of total dry matter intake), fiber digestibility and DM intake are impeded (Byers and Schelling, 1993; Coppock and Wilks, 1991). This occurs because the hydrophobic nature of the lipids forces the fat to surround and encapsulate the carbohydrates, thereby limiting microbial attachment. Also modification of microorganism population, surface-active effects on microbial membranes, and lowered cation availability through the rumen can occur (Jenkins, 1993). Whole cottonseed can be used to supply fat without negative effects on digestibility because the fibrous seedcoat slows ruminal metabolism of the oil (Coppock and Wilks, 1991).

Also, feeding calcium salts with high fat diets has been examined as a mechanism to initiate the formation of calcium soaps in the rumen (Davison and Woods 1963; El Hag and Miller, 1972; Palmquist et al., 1986; Fluharty and Loerch, 1997). These soaps are less soluble in the rumen and presumed non-toxic to bacterial populations that are affected by free LCFA (Palmquist et al., 1986). An advantage of calcium soaps is that there is a complete alleviation of diminished fiber digestion observed with high fat diets (Palmquist et al., 1986; Fluharty and Loerch, 1997). This is better illustrated by Palmquist and Weiss (1994) who found that adding 5% fat (tallow: Megalac, 1:1; wt:wt) increased molar proportion of acetate, and decreased propionate in the rumen of dairy cows. Megalac is a calcium soap of fatty acids extracted from palm plants (Fluharty and Loerch, 1997). Calcium soaps may be beneficial in dairy cattle or as an energy supplement for developing heifers as acetate provides carbons for the synthesis of not only subcutaneous, but also milk fat synthesis (Smith and Crouse, 1984; Grant 1997). However,

in feedlot cattle it is beneficial to shift rumen fermentation toward propionate production; therefore, it may be more prudent to use fats in moderation as opposed to calcium soaps.

Typically, the corn oil fraction remains in the DGS coproduct (Stock et al., 2000) resulting in a high-fat product. It should be noted that fat content, like metabolizable protein, is variable from source to source (Gunn et al., 2009). Klopfestein et al. (2007) outlined an experiment in which DDGS was fed to feedlot cattle in comparison to corn oil. Cattle fed DDGS increased G:F by 8% where cattle fed corn oil decreased G:F by 10% compared to dry rolled corn. Additionally, 81% of the fat fed to DDGS cattle was digested as opposed to 70% by cattle fed corn oil (Klopfenstein et al., 2007). Fatty acids are absorbed via micelles. Unsaturated fatty acids form micelles with greater surface area and allow for more efficient utilization (Zinn, 2000). These data suggests that high fat coproducts such as DGS and CDS could be a valuable energy source; however, most reports with DGS involve its quadratic effect on performance, intake, and feed efficiency with increasing dietary inclusion (Klopfenstein et al., 2007; Loza et al., 2010).

The added value of using corn coproducts, instead of corn, as an energy supplement has been demonstrated (Ham et al., 1994; Lodge et al., 1997a; Vander Pol et al., 2009). Vander Pol et al. (2009) showed increased propionate production in the rumen as well as increased unsaturated fat flow into the intestine in cattle fed WDGS compared to those fed corn oil. Similarly, a decrease in the acetate:propionate ratio was observed by Scott et al. (1998) when corn steep liquor was fed. Steep liquor is a liquid by-product of the wet-milling industry, and with the exception of fat content is very similar in composition to CDS (Vander Pol et al., 2009). Klopfenstein et al. (2007) stated that both DDGS and WDGS have higher feeding values than corn. This is likely attributed to the fat content, the oxidation of excess protein for energy given

the absence of starch, as well as the digestible fiber in DDGS and WDGS. Lodge et al. (1997b) illustrated that the fat and bypass protein of these feeds were equally responsible for their advantage in feeding value over corn by developing composite distillers coproducts using corn gluten meal and tallow and then removing fat or protein. Klopfenstein et al. (2007) hypothesized that this was the result of greater energetic efficiency of bypass protein as well as increased dietary fat passage to small intestine compared to degradable protein or carbohydrates. There are data to suggest that the lipid fraction of DGS and that of CDS behave differently in the rumen. A study by Haack (2011), compared a low-fat (4.72%) WDG diet, with no CDS, to a traditional (6.91% fat) WDGS diet to compare differences in beef quality among strip steaks. The authors found that the low-fat WDG diet decreased redness (a*) and tenderness of beef steaks and it increased the instance of off-flavor (Haack, 2011). Additionally, strip steaks from the low-fat WDG cattle had increased levels of PUFA and decreased shelf-life stability compared to steaks from cattle consuming the traditional WDGS diet (Haack, 2011). These findings led the investigators to conclude that the lipid fraction from CDS is more completely biohydrogenated in the rumen than the lipid fraction from WDG.

Growth and Development of Early-Weaned Calves

Calf Performance and Fat Deposition

Early weaning can be advantageous in terms of calf growth, as well as maintaining the condition of the cow. With decreasing available forage, milk production declines forcing producers to feed calves alternative energy sources. Milk intake has been shown to decline by as much as 45% between and April and August in the Midwestern states (Boggs et al., 1980). Maddox (1965) reported that by 3 months of age, more than half of the total energy intake in young calves comes from sources other than the cow indicating that the calf is consuming forage

or concentrate, if it is provided. This can create a competitive feeding situation between cows and calves, thereby impacting performance of both cow and calf during the summer months (Shike et al., 2007).

Early work comparing early- to normal-weaned calves found that calves fed concentrate during the growing phase had a 0.28 kg/d advantage in gain compared to calves left to nurse their mothers (Harvey et al., 1975). In that same study, when calves were adapted to a feedlot diet, normal-weaned calves had higher ADG (0.09 kg/d) than early-weaned calves. Harvey et al. (1975) also noted that when cattle were harvested, early-weaned calves had a lower percent KPH but tended to have higher marbling scores (MS) and more back fat over the 12^{th} rib (BF). These data are an indication that feeding concentrate diets to early-weaned calves may play a role in developing adipocytes preferentially within certain tissues.

Early weaning research has primarily focused on age or time, at weaning (Harvey et al., 1975; Fluharty et al., 2000; Schoonmaker et al., 2003; Meteer et al., 2011). Richardson et al. (1978) compared differing weaning ages (120 days to 210 days) and placed calves on pasture with ad libitum access to a corn supplement. Adjusted 210-day weights were calculated for all calves and early weaning was found to yield 10.1 kg of additional weight and conformation scores that were 0.18 units greater than normal weaned calves. Normal-weaned heifers had increased post-weaning gains 11.0 kg greater than those of early-weaned calves (Richardson et al. 1978). Greater than or equal post-weaning gains for normal-weaned calves compared to early-weaned calves has been observed in the majority of the literature on calf performance when contrasting early and traditional weaning (Richardson et al., 1978; Myers et al., 1999)

Schoonmaker et al. (2002) compared feedlot entry age (111d vs 202d vs 371d) and performance between steers and bulls. Hormones from implants, as well as endogenous

hormones from bulls, have also led to greater lean protein accretion and subsequently heavier carcasses, larger LMA and proportionally less intramuscular fat percentages (Duckett et al., 1999). Although total dry matter intake (DMI) did not differ among groups, daily DMI was numerically least for early-weaned calves and greatest for yearlings (Schoonmaker et al., 2002). Early-weaned steers had improved ADG by 0.15 kg/d and 0.41 kg/d compared to normal-weaned and yearling calves. Schoonmaker et al. (2002) also observed early-weaned calves were the most efficient, improving G:F by 19 g/kg compared to normal-weaned calves and 47 g/kg compared to yearlings. However, early-weaned steers had the lightest HCW and smallest LMA (Schoonmaker et al., 2002). This is not surprising given that the yearling calves were left on pasture until they entered the feedlot, thereby, increasing lean growth with little fat accumulation.

Calves can increase gain in an early-weaning system when fed a complete diet or high-quality forage compared to calves in a normal weaning system (Neville and McCormick, 1981; Basarab et al., 1986; Lusby and Wettemann, 1986; Schoonmaker et al. 2003; Arthington et al., 2005). Neville and McCormick (1981) demonstrated that calves fed high grain diets in a dry lot gained 0.08 kg/d more than calves offered the same concentrate mix in the pasture indicating that energy density of the diet could affect performance at a young age. Similarly, Lusby et al. (1985) found that early-weaned calves on pasture with creep feeder access were 20 kg lighter upon entry into the feedlot than calves weaned at the same age and fed concentrate in a dry lot. Early weaning can be detrimental to calf performance in systems where low quality forage is the only available feed source. Lusby and Wettemann (1986) supplemented early-weaned calves on native grass pasture and found that calves that were normal-weaned had superior performance.

Arthington et al. (2005) compared feedlot performance and stress level of early- vs. normal-weaned calves in Florida. Early-weaned calves were maintained on annual ryegrass (*Lolium multiflorum*) and stargrass (*Cynodon spp.*) with a commercial grain supplement to achieve a gain of 1% of body weight per day. Upon entering the feedlot, normal-weaned calves were 48 kg heavier than early-weaned calves. Intake, gain, and feed conversion did not differ between groups in the feedlot. These data indicate that in regions where cost-effective concentrate diets are not available and forage is plentiful and of good quality, early-weaning may be less effective at moderating production costs.

Carcass Effects and Intramuscular Fat Deposition in Early-Weaned Calves

The advantages of early weaning for carcass characteristics have been documented for almost 40 years. Harvey et al. (1975) found decreased kidney, pelvic, and heart fat (KPH), increased BF, and a tendency for increased MS in carcasses of early-weaned calves compared to those from calves that had been normal-weaned. Intramuscular fat deposition has been related to number of days that cattle are fed high energy concentrates (Duckett et al., 1993). For example, Loy et al. (1999) compared calves weaned at 67 and 147 days and found increased intramuscular fat percentages (5.7 vs. 5.1) and consequently increased marbling scores (578 vs. 520) and an increased percentage of carcasses grading USDA Choice or higher (38% vs. 14%) for early-weaned calves compared to normal-weaned calves.

Likewise, Shike et al. (2007) noted that marbling scores were increased by two-thirds of a score in cattle that were early-weaned and fed a starch-based diet (71% corn) compared to those that were creep-fed (25% corn), or normal-weaned. This finding is significant because the early-weaned steers in this study were program-fed to gain similarly to the creep-fed steers illustrating

that energy source can impact intramuscular fat deposition independent of performance (Shike et al., 2007).

Myers et al. (1999) found no differences in marbling or percentage of carcasses grading USDA Choice or higher in carcasses from steers weaned at 90, 152, or 215 days. Similarly, studies by Fluharty et al. (2000) and Barker-Neef et al. (2001) also found no difference in carcass characteristics among early-, intermediate-, and normal-weaned calves.

Some studies have reported decreased HCW in early weaned cattle with no difference in other carcass traits (Schoonmaker et al., 2004a; Schoonmaker et al., 2002). This is likely the result of feeding high energy diets ad libitum in the early stages of the calf's physiological development (Schoonmaker et al., 2004a; Schoonmaker et al., 2002). Schoonmaker (2004a) stated that rapid growth rate accelerates physiological maturity and carcass fatness. Restricting intake or limit feeding may be one method for extending the growth curve of early-weaned cattle and allowing for heavier carcasses at the same 12^{th} rib thickness (Shike et al., 2007). The problem with this system is that limit-feeding, while increasing carcass leanness, reduces rate of gain, increases time required for cattle to reach market weight, and can depress marbling scores (Plegge, 1987; Hicks et al., 1990; Murphy and Loerch, 1994). Therefore, producers must learn how to manage energy sources for early-weaned cattle in order to achieve lean gain and adequate carcass weights while preserving carcass quality through intramuscular fat deposition. Schoonmaker et al. (2004a) stated that increased leanness and decreased marbling scores in limit-fed cattle happen as a result of restricting intake from weaning until slaughter. Calves that were limit-fed during the growing phase, and then fed ad-libitum concentrate to finish, had a higher percentage of fat in the *longissimus* muscle than calves fed ad-libitum concentrate or ad libitum forage during the growing phase. This was explained by a 180 day period of

compensatory tissue growth from limit-fed animals that seemed to favor adipose development after cattle were placed on an ad libitum concentrate ration (Schoonmaker et al., 2004a).

Rumen Fermentation

Metabolic Significance of Acetate and Propionate

Volatile fatty acid concentrations have been well researched and are one of the defining characteristics of the ruminant digestive system. These VFA are the primary products of bacterial digestion of feedstuffs in the rumen (Fluharty, 2009), and are predominantly comprised of 3 major constituents: acetate, propionate, and butyrate. Cattle consuming diets with increased fiber such as pasture or hay typically have a VFA profile that is approximately 65-70% acetate, 15-25% propionate and 5-10% butyrate, while cattle consuming high energy concentrate diets would display markedly different patterns of ruminal fermentation: for example, 50-60% acetate, 35-40% propionate, and 5-10% butyrate (Fluharty, 2009). This shift in the acetate: propionate ratio has been shown to have far-reaching effects in the regulation of energy metabolism and subsequently carcass characteristics, which will be discussed later (Vernon, 1980; Johnson et al., 1982; Bines and Hart, 1984; Smith and Crouse, 1984; Smith et al., 1984; Smith, 1995; and Fluharty, 2009).

Ruminal VFA concentration from the fermentation of coproduct feeds is well researched (Firkins et al., 1985; Fleck et al., 1988; Elizalde et al., 1998; Peter et al., 2000; Uwituze et al., 2010). In lambs fed WCGF, Firkins et al. (1985) found initial acetate concentrations were elevated in the rumen post-feeding, probably due to increased digestible fiber content; however, as time post-feeding increased, acetate concentrations decreased while propionate concentration increased (Firkins et al. 1985). Decreased acetate and increased propionate were reported in the

rumen when diets containing WDGS were fed compared to corn bran (Vander Pol et al., 2009). Increased acetate: propionate ratios were reported by Grant (1997) when steers were fed steep liquor, a liquid coproduct similar to distillers solubles. Therefore, it is possible that the level of soluble inclusion in WDGS or DDGS could affect digestion and VFA production (Vander Pol et al., 2009; Leupp et al. 2009). Conversely many other studies have found no differences in ruminal VFA with the addition of DDGS or CGF (Fleck et al., 1988; Elizalde et al., 1998; Peter et al., 2000; Al-Suwaiegh et al., 2002). Additionally, Hussein et al. (1995) found no differences in VFA production when comparing coproduct diets with varying levels of heat damage.

The ability of DGs to shift ruminal fermentation toward a greater propionate production is of immense importance to the improvement of carcass characteristics in fed cattle. Johnson et al. (1982) as well as Bines and Hart (1984) reported that peak glucose concentration associated with increased propionate production led to increased insulin secretion. Insulin inhibits lipolysis and protein breakdown while simultaneously increasing fat and protein synthesis (Fluharty, 2009). Protein and fat synthesis happen in tandem, and are affected by several factors including, but not limited to age, nutrition, and genetic potential. Marbling score is the primary determinant in assigning USDA quality grade, and chiefly affected by intramuscular adipocyte development. Likewise, preliminary yield grade is principally determined by subcutaneous adipocyte development. Development of adipose tissue at both of these sites requires a source of fatty acids and glycerol-3-phosphate (G3P) which is derived from glucose (Fluharty, 2009). Fluharty (2009) stated that acetate is the primary fatty acid precursor in grazing cattle because of increased dietary fiber.

As previously mentioned, ruminal concentrations of propionate increase when cattle are fed concentrate diets, and as a result glucose levels rise. This was better related to adipogenesis

by Smith and Crouse (1984) who conducted an experiment utilizing either corn silage (low starch) or ground corn (high starch) as diets for Angus steers from which adipose tissue samples were collected and subjected to in vitro cell culture in order to determine enzyme activity and primary energy source. Their results indicated that 70 to 80% of the acetyl units for lipogenesis in the subcutaneous adipose tissue were derived from acetate, and that acetate only provided 10-25% of the acetyl units for intramuscular lipogenesis (Smith and Crouse, 1984). On the other hand, glucose (synthesized from propionate) contributed only 1 to10% of the acetyl units for subcutaneous lipogenesis, but provided 50 to 75% of the acetyl units for lipogenesis in the intramuscular adipocytes (Smith and Crouse, 1984). The authors concluded regulatory pathways that control fatty acid synthesis in intramuscular and subcutaneous adipose tissue are different and enzymes responsible for fatty acid synthesis, lipogenesis, and subsequent adipocyte hypertrophy are regulated by VFA produced in the rumen, which vary with dietary energy source (Smith and Crouse, 1984).

Ruminal Fermentation: Early-weaned Calves

Age at weaning is an individual decision made by producers based on a list of priorities. These criteria may include but are not limited to: pasture resources, age of dam, weather, feed costs, and feeder calf prices. Although performance and carcass impacts of early-weaning nutritional strategies have been researched extensively, little work has been done to evaluate rumen fermentation, digestion, and methane production in early-weaned beef calves fed differing energy sources. When calves consume solid feed as opposed to milk at an early age, rumen development occurs sooner (van Ackeren et al., 2009). This is indicated by accelerated rumen motility (McGilliard et al., 1965), smooth muscle development (Harrison et al., 1960), increased short chain fatty acid production (Quigley et al., 1985), and lower ruminal pH (Anderson et al.

1987 a,b). Like older cattle, calves fed high starch diets have increased propionate concentrations and decreased acetate concenrations as well as decreased rumen pH when compared to calves fed a high fiber diet (Schoonmaker et al., 2003). Schoonmaker et al. (2003) also reported elevated insulin levels in calves fed high-concentrate diets compared to those fed high-forage diets in the growing phase. As previously mentioned, increasing propionate production increases gluconeogenesis and subsequently insulin levels which is conducive for intramuscular adipose development (Fluharty, 2009). The VFA proportions and insulin levels observed by Schoonmaker et al. (2003) correlated with increased predicted marbling scores collected via ultrasound while calves were fed experimental diets; however, these differences diminished when cattle were placed on a common diet for finishing.

Wertz et al. (2001) compared calves given ad libitum access to 25% concentrate diet to those that were limit-fed a 90% concentrate diet during a 119-day growing period where both groups were fed to gain the same amount. The authors evaluated rumen fermentation patterns in fistulated steers where, as expected, the 90% concentrate diet resulted in higher rumen propionate concentration and lower rumen acetate concentration compared to the 25% concentrate diet. In this study however, no differences in marbling or quality grade were detected post-harvest (Wertz et al., 2001).

Enteric Methane Production

Methane production from cattle has been a point of interest for ruminant nutritionists for many years (Bratzler and Forbes, 1940; Johnson and Johnson, 1995). However, the focus of these studies was not the prevention or moderation of global warming, but rather the energy inefficiency associated with methanogenesis in the rumen (Johnson and Johnson, 1995).

Methane production in ruminants begins with the first introduction of solid feed into the rumen at or around 4 wk of age (Anderson, et al., 1987b). As the reticulorumen develops, methane production continues to rise (Johnson and Johnson, 1995) and is estimated to plateau at 60 to 71 kg annually for beef cattle or 109 to 126 kg annually for dairy cattle (Johnson and Johnson, 1995). This data might suggest that the dairy industry would be the primary producer of enteric methane from cattle; however, the majority of dairy cattle consume a total mixed ration (TMR) containing some high-quality forage and some grain. On the other hand, the cow-calf sector of the beef industry is comprised of a larger population of cattle consuming much higher levels of forage of variable quality. Due to these differences in population and diet quality, cow-calf operations in the beef industry are responsible for 58% of the methane emissions from beef and dairy cattle in the United States; the dairy industry accounts for 23% of emissions, while the stocker and feedlot operations account for 19% (EPA, 2011). Measurements made by Johnson et al. (1993) using indirect calorimetry, indicate that methane production can account for energy losses of 2-12 % of GE intake. Carbohydrate source is one of the primary factors impacting rumen methane production. The pregastric fermentation of fiber produces acetate. During this process, galacturonic acid is produced from fermentation of pectins and is converted to xylose (Russell and Gahr, 2000). Carbon dioxide (CO_2) is produced as a by-product of this reaction, and can be converted to methane through a series of redox steps facilitated by methanogenic bacteria (Russell and Gahr, 2000). The proportion of methane produced is dependent upon the level of fiber in the diet compared to the level of starch (Russell and Gahr, 2000). The predominant fermentative endpoint of fiber is acetate whereas starch fermentation yields propionate as the primary fermentative product. Propionate can be produced from two distinct pathways. In roughage based diets, the randomizing pathway serves as the

primary (90-95%) synthetic pathway for propionate, wherein pyruvate is converted to acetyl CoA and oxaloacetate consuming a reducing equivalent and producing CO_2. The oxaloacetate is metabolized to produce propionate while acetyl CoA is incorporated into butyrate production (Russell and Gahr, 2000). Conversely, in grain-fed ruminants the acrylate pathway produces 70-90% of the propionate produced (Russell and Gahr, 2000). This is because the acrylate pathway is more robust in the acidic conditions created by rapid fermentation of starch which results in rapid acid production, decreased rumination and less buffering from saliva (Russell and Gahr, 2000). , These conditions are also less conducive to the growth of methanogenic bacterial populations in the rumen (Johnson and Johnson, 1995). In the acrylate pathway, pyruvate is converted to lactate, lactyl-CoA and finally Acrylyl-CoA before entering a series of electron transport steps that produce proponyl-CoA and finally propionate (Russell and Gahr, 2000). Propionate production from the acrylate pathway is a "clean" process in terms of methane production because no CO_2 is formed and therefore no H^+ sink is created.

For these reasons, intensive feedlot systems result in less methane produced per kg of meat produced compared with intensive grazing systems (Clemens and Ahlgrimm, 2001). This is due to high starch diets combined with faster growth rates, and shorter life spans in feedlot cattle (Clemens and Ahlgrimm, 2001). Beauchemin and McGinn (2005) monitored methane production from cattle fed 70% roughage (corn or barley silage) in the backgrounding phase and 80% concentrate (steam-rolled barley, or dry rolled corn) in the feeding phase. Cattle averaged 170.6 g/hd· d^{-1} for corn silage diets which was greater ($P < 0.001$) than cattle fed barley silage (129.7 g/hd· d^{-1}; Beauchemin and McGinn, 2005). While cattle receiving high starch diets during the feedlot phase were not different from each other, they did exhibit reduced ($P < 0.001$)

methane losses (62.1 and 80.4 g/hd· d^{-1} for corn and barley, respectively) compared to the backgrounding phase (Beauchemin and McGinn, 2005).

Type of fiber may also play a role in methane emissions. Ruminal fermentation of cell wall components results in increased energy losses in the form of methane (Moe and Tyrrell, 1979; Beever et al., 1989). Research monitoring methane production from grazing cattle is extremely limited and can only be obtained by use of a tracer gas such as sulfur hexafluoride (SF_6; Johnson et al., 1994). McCaughey et al. (1999) compared lactating cows grazing grass-only [100% meadow brome (*Bromus biebersteinii*)] to lactating cows grazing grass-legume [78% alfalfa (*Medicago sativa L.*) – 22% meadow brome]. Cows grazing grass-legume pasture had increased voluntary forage intake (11.4 vs. 9.7 kg/d) compared to those grazing grass-only pasture; however, methane production was lower on grass-legume pastures (373.8 vs. 411.0 L/d; McCaughey et al., 1999). Digestibility and passage rate of legume-based pasture is greater than that of grass-based pasture (Minson and Wilson 1994). This may partially explain the decrease in observed methane production, but no other studies exist for comparison (McCaughey et al., 1999).

Very little research exists to study the effects of supplementation on grazing cattle methane production. Boadi et al. (2001) compared cattle supplemented with steam-rolled barley to unsupplemented cattle grazing legume-grass pasture. No differences were observed between supplementation groups for methane production (Boadi et al., 2001).

Research regarding supplementation strategies to reduce methane production is lacking, but some research has been conducted to examine the addition of certain lipids and essential oils in cattle diets. Lipids have a negative impact on methane production through several processes, including enhancing propionate production, increasing hydrogen ions used for biohydrogenation,

and protozoal inhibition (Johnson and Johnson, 1995). Czerkawski et al. (1966) infused the rumen of sheep with oleic, linoleic, or linolenic acid. All animals displayed decreased ($P < 0.01$) methane production by at least 13.8% with infusion of polyunsaturated fatty acids (PUFA; Czerkawski et al., 1966). The authors hypothesized that the reduction in methane was due to biohydrogenation of the double bonds by rumen microorganisms, and that the PUFA provided an alternative hydrogen sink to CO_2 (Czerkawski et al., 1966). However, the amount of metabolic hydrogen ions used in the biohydrogenation of ethylene bonds is small (1%) compared to that used in the reduction of CO_2 to methane (48%), VFA synthesis (33%), and bacterial cell synthesis (12%; Czerkawski, 1986; Johnson and Johnson et al., 1995). Czerkawski et al. (1966) also noted a similar decrease in methane production from sheep infused with palmitate. Also, methane levels took as long as 8 d to return to level observed prior to infusion (Czerkawski et al., 1966). The authors hypothesized that this was due to the inhibition of methanogenic microorganisms in the rumen (Czerkawski et al., 1966). It was also noted that methanogenic populations were solely affected by the addition of PUFA because general carbohydrate fermentation proceeded as expected even when methane levels were half their pre-infusion levels (Czerkawski et al., 1966). Other studies have revealed similar results with diets containing soybean oil and tallow compared with isocaloric controls (Swift et al., 1948; Haaland, 1978; Van der Honing et al., 1981). These studies attributed decreased methane production to encapsulation of feed particles by lipid thereby limiting the opportunity for microbial attachment and decreasing the amount of fermentable substrate (Johnson and Johnson, 1995).

Ionophores are antimicrobial compounds used in the beef industry to improve feed efficiency and shift rumen fermentation toward propionate. These compounds have also been found to reduce methane production by as much as 25% (Benz and Johnson, 1982; Garrett, 1982;

Wedegaertner and Johnson, 1983). However, these effects have been shown to dissipate if cattle are kept on ionophores for an extended period of time (Saa et al., 1993; Johnson and Johnson, 1995). McGinn et al. (2004) compared 75% barley silage diets with monensin or sunflower oil. Monensin, the primary ionophore used for cattle, had no effect on methane production while addition of sunflower oil reduced emissions from 166.2 g to 129.0 g, a 22% decrease (McGinn et al., 2004). Many of the studies showing ionophores reducing methane production were conducted in animals fed concentrate diets whereas McGinn et al. (2004) fed silage-based rations. It should also be noted that ionophores are already a widely accepted and utilized practice in the U.S. beef industry and for strategies to warrant future research they should have some element of novelty, for without changes in management, greenhouse gas mitigation is not possible.

Cattle are presumed to account for 73% of the 80 Tg of methane produces by livestock each year (Gibbs and Johnson, 1994), and since the majority of beef cattle spend at least 6 months of the year on pasture it is vital for scientists to explore strategies that decrease methane production from cattle consuming roughage. Also, as the milling industry continues to create new, fiber-based, coproduct feeds, it is important to understand the behavior of these feeds in the rumen and how they impact greenhouse gas production in various beef production scenarios.

Source of Energy

As previously discussed, glucose provides 50 to 75% of the acetyl units for in vitro lipogenesis of intramuscular fat, but only 1 to 10% of the acetyl units for subcutaneous adipose tissue (Smith and Crouse, 1984). The majority of the lipogenic substrate units in subcutaneous adipose tissue are acetate which only accounts for 10 to 25% of the substrate units utilized in

intramuscular lipogenesis (Smith and Crouse, 1984). Fermentation of starch by the rumen increases blood glucose levels suggesting the possibility that high starch diets could target intramuscular lipogenesis instead of subcutaneous fat deposition. This is possible because feeding high starch diets will shift the rumen fermentation patterns lowering the acetate: propionate ratio, increasing glucose production (May et al., 2009).

Adipose tissue develops by cell proliferation (hyperplasia) or cell enlargement (hypertrophy); therefore, an increase in adiposity may be *apparent*, because of the filling of preadipocytes with lipid, or *genuine*, because of differentiation or proliferation of new preadipocytes (Hood, 1982). Schoonmaker et al. (2004b) found that in cattle fed an ad libitum concentrate growing diet, increased BF thickness was the result of increased adipocyte diameter, or hypertrophy, when compared to cattle that were limit-fed concentrate or given ad libitum access to forage during the growing phase. In that same study, ad libitum concentrate fed cattle had fewer adipocyte cells than cattle fed alternative diets (Schoonmaker et al., 2004b). From these findings, the authors concluded that adipocyte hypertrophy was affected by the energy density of the diet; whereas, adipocyte hyperplasia was affected by the source of energy (Schoonmaker et al., 2004b). This is in agreement with Cianzio et al. (1985) who reported that as BF thickness increased from 11 to 17 months of age the number of adipocytes per gram of tissue decreased and the average diameter of adipocytes in the subcutaneous and intramuscular tissue increased indicating that hypertrophy is the primary mechanism of adipocyte development in feedlot cattle.

Marbling has historically been considered a late-stage fat depot that was not fully developed when cattle are typically marketed (Hood and Allen, 1973; Cianzio et al., 1985; May et al., 1994; Schoonmaker et al., 2004b). Therefore, carcasses have been produced with large

amounts of internal and subcutaneous fat and relatively small amounts of intramuscular fat. Hood and Allen (1973) reported that subcutaneous fat from cattle harvested at 1.2 cm of backfat exhibited a monophasic cell distribution, whereas intramuscular fat from cattle killed at the same compositional endpoint exhibited a biphasic cell distribution suggesting that different regulatory mechanisms are in place for differing depot sites. Cell distributions of subcutaneous adipose tissue in obese cattle (greater than 5.1 cm of backfat) have been reported to exhibit a similar biphasic distribution to that of intramuscular fat in typical feedlot cattle (Allen, 1976). Schoonmaker et al. (2004b) found biphasic cell clusters in subcutaneous and intramuscular adipose tissue from steers fed concentrate-based, growing diets whereas only monophasic distributions were found in cattle fed a forage-based growing diet. This data indicates that the energy source early in life may play a role in the development of new preadipocyte populations (Schoonmaker et al, 2004b). While energy source certainly impacts the type and rate of fat deposition there are also genetic factors that must be considered. Grauganard et al. (2009) found that high starch diets up-regulated genes that code for several key lipogenic enzymes in the *longissimus lumborum* tissue of early-weaned calves when compared to those fed high forage diets.

In a similar study, Meteer et al. (2011) compared starch to fiber as energy sources for 200 hd of early- or normal-weaned calves in the first 100 d of the growing phase before adapting to a common feedlot ration. The authors observed increased ADG and G:F for early-weaned calves during the growing phase; however, in the feedlot, creep-fed calves out performed early-weaned calves. After slaughter, early-weaned calves had improved marbling scores compared to cattle that were creep-fed or traditionally weaned with no supplementation (Meteer et al., 2011). Interestingly, there was no difference in marbling score among cattle fed starch vs. fiber (Meteer,

2011). This is a significant finding because, previously, marbling development was thought to be directly related to time on concentrate diet. The fiber source utilized by Meteer (2011) was corn bran from a supplier that didn't extract oil from the product resulting in a feedstuff that was 9.14% fat. Thus, it is reasonable to hypothesize that dietary fat concentration may have been responsible for the similarity in marbling score either by depositing excess fat in the tissue or by shifting rumen fermentation in a manner similar to starch.

Adipogenesis in Beef Cattle

Adipose Tissue

Adipose tissue contains primarily two major cell types (Pickworth, 2009). Preadipocytes are stromo-vascular, undifferentiated, interstitial cells that include endothelial vascular cells, mast cells, and macrophages, and most importantly do not contain lipids (Cornelius et al., 1994). The second major cell type are the mature adipocytes. Intramuscular adipocytes are smaller (40-90 μm diameter) and more uniform in terms of size and shape than those in seam fat, mesenteric fat, or subcutaneous fat (Cianzio et al., 1985).

The principal function of adipose tissue is energy storage. Adipose tissue is the primary lipogenic organ in beef cattle, and is responsible for TAGs when energy is in excess of maintenance requirements. Lipolysis, defined as the hydrolysis of TAGs and release of fatty acids and glycerol into the bloodstream when energy is required, is also carried out extensively in adipose tissue (Pickworth, 2009). Additionally, adipose functions in fat soluble vitamin storage and regulation of the reproductive and immune systems (Cornelius et al., 1994). Adipose also functions as an endocrine organ, secreting leptin, resisten, complement-related proteins, and IGF-1 (Doglio et al., 1987; Pickworth, 2009).

Proliferation of Adipose Tissue

Hyperplasia and hypertrophy have been mentioned previously and are defined as follows: 1) hyperplasia, the increase in the number of cells, and 2) hypertrophy, the increase in cell size through the formation and storage of TAGs inside the cell (Hood and Allen, 1973; Cianzio et al., 1985). These are the two mechanisms by which adipose tissue may grow. The true origin of the cells which develop into preadipocytes and ultimately adipose tissue is not yet known (Ailhaud et al., 1992). Proliferation of preadipocytes begins in utero and continues throughout calfhood (Pickworth, 2009). Hood and Allen (1973) studied the cellulosity of bovine adipose tissue and reported that hyperplasic growth is over by one year of age, and that any increase in fatness was due solely to hypertrophy (Hood and Allen, 1973). Conversely, May et al. (1994) illustrated via adipose cell cultures that bovine preadipocytes are capable of hyperplasic growth throughout the life of the animal. This is in agreement with data presented by Cianzio et al. (1985) and Schoonmaker et al. (2004b) suggesting that this process may continue up to 17 m of age if the energy source is one that will provide adequate glucose units to the tissue. The mechanisms regulating preadipocyte differentiation have not yet been identified. However, differentiated adipocytes are not capable of undergoing further hyperplasia and are limited to hypertrophy as a mechanism for further growth (Pickworth, 2009). The accretion of adipose tissue is impacted by numerous factors including: gender, depot, nutritional status, age, genetics, and environment (Pickworth, 2009).

Differentiation of Adipose Tissue

The advancement of adipocyte differentiation involves the modification of over 100 proteins, changes in phenotype, and TAG accumulation (Smas and Sul, 1995). The majority of

these changes are at the transcriptional level of the gene with post-translational regulation being a gene specific occurrence. Preadipocytes resemble fibroblasts in terms of structure and gene expression during growth and proliferation (Smas and Sul, 1995). Preadipocytes are unique in the over-expression of metabolism-associated, cytoskeletal, and extracellular matrix genes, yet the regulatory factors that control preadipocyte differentiation are not well understood (Pickworth, 2009).

Smas and Sul (1995) outlined the process of adipocyte differentiation. Differentiation begins with growth arrest which forces the preadipocyte out of the cell cycle. Arresting the growth of preadipocytes involves CCAAT/enhancer binding protein (C/EBP) α and peroxisome proliferator-activated receptor (PPAR)γ (Smas and Sul, 1995). Smas and Sul (1995) also reported that C/EBPα and PPARγ are expressed in low concentrations in the preadipocyte, but upon initiation of differentiation, concentrations increase greatly. At least one final round of clonal division is completed immediately following growth arrest (Gregiore et al., 1998). Peroxisome proliferator-activated receptor γ is the master regulator for adipocyte differentiation and is necessary for the activation of adipogenesis (Rosen et al., 2002; Moisa, 2011). Studies have also shown that C/EBPα transactivates several genes that are coordinately expressed during adipocyte differentiation including stearoyl-CoA desaturase (SCD; Christy et al., 1989), GLUT-4 transporter (Kaestner et al., 1991) and phosphoenolpyruvate carboxykinase (PEPCK) genes (Smas and Sul, 1995).

The second step of adipose differentiation is characterized by changes in gene expression for structural proteins and the extracellular matrix (Smas and Sul, 1995; Pickworth, 2009). Specifically, fibronectin, collagen type IIIA1, collagen type VA1, collagen type VIA3, thrombospondin 1, 2, and 4, matrix metalloprotein, osteonectin, and decorin are all up-regulated

(Urs et al., 2004). The increased expression of these structural proteins is more responsible for the difference in cell shape between preadipocytes and mature adipocytes than the filling of adipocytes with lipid (Pickworth, 2009).

The terminal phase of differentiation is characterized by increased de novo lipogenesis as well as the activity level of proteins and/or messenger RNAs (mRNA), for ATP citrate lyase (ACL), malic enzyme (ME), acetyl-CoA carboxylase (ACC), SCD, glycerol-phosphate acyltrasferase (GPAT), glycerol-3-phosphate dehydrogenase, fatty acid synthase (FAS), and glyceraldehyde-3-phosphate dehydrogenase increase 10-100 fold (Smas and Sul, 1995). Adipocytes also become sensitive to insulin in the final phase of differentiation (Pickworth, 2009).

Terminal differentiation of adipocyte is regulated by hormones and transcription factors. It has been demonstrated that insulin, GH, IGF-1, glucocorticoid, triiodothyronin, and cyclic adenosine monophosphate (cAMP) induce differentiation of adipose tissue (Student et al., 1980; Gregiore et al., 1998). This induction is accomplished through proteins that mediate adipocyte function (Moisa, 2011). The C/EBPs α, β, and δ, are expressed in a cascade that begins with induction of C/EBPβ which induces C/EBPδ thereby inducing C/EBPα (Moisa, 2011). Peroxisome proliferator activated receptor is transactivated by C/EBPα. Both transcription regulators work together to promote adipogenesis (Moisa, 2011).

Lipid Metabolism in Ruminants

The ruminant digestive system is unique from monogastrics in many ways. The metabolism of lipid is extremely distinctive in the ruminant because the nature of lipid ingested is vastly different than that which is absorbed in the small intestine. Lipid degradation in the

rumen is extensive allowing very few monoglycerides or diglycerides to leave the rumen intact and proceed to the lower gastrointestinal tract (Drackley, 2004). The first step in rumen degradation of fat is hydrolysis. Hydrolysis is accomplished by rumen bacteria with greater than or equal to 85% efficiency (Bauman et al., 2003). Examples include *Anaerovibrio lipolytica* which hydrolyzes triglycerides, and *Butyrivibrio fibrisolvens* which is responsible for hydrolysis of phospholipids and glycolipids (Harfoot and Hazlewood, 1997).

The second form of ruminal lipid degradation is biohydrogenation. Unsaturated fatty acids are very toxic to rumen microflora (Maia et al., 2010); therefore, anaerobic bacteria biohydrogenate unsaturated fatty acids to remove double bonds in the fatty acid chains (Moisa, 2011). Biohydrogenation is attributed to extracellular enzymes of bacteria in the rumen (Harfoot and Hazlewood, 1997). The primary substrates of these enzymes are linoleic and linolenic acids (Bauman et al., 2003). Biohydrogenation occurs at a faster rate as level of unsaturation within the lipid fraction of the rumen increases usually resulting in 70 to 95% efficiency for linoleic acid and 85 to 100% efficiency for linolenic acid (Doreau and Ferlay, 1994; Beam et al., 2000; Mattos et al., 2000; Bauman et al., 2003). Biohydrogenation is reduced under two primary circumstances. High levels of concentrate in the diet decreases pH, adversely affecting lypolytic enzymes associated with rumen microbes (Van Nevel and Demeyer, 1995; Van Nevel and Demeyer, 1996). Also, diets high in fat interfere with microbial populations in the rumen and can have a negative impact on rumen biohydrogenation (Jenkins, 1993).

Fatty acids in the ruminants, like monogastrics, are absorbed in the small intestine. Fatty acids form micelles in the lumen of the small intestine. Micelles are vesicles composed of a phospholipid bilayer that contains bile salts and insoluble lipids (Moisa, 2011). Once in the enterocyte, fatty acids are assimilated into triacylglycerol (TAG) predominantly through the

monoacylglycerol pathway. Newly formed TAGs are transported to the endoplasmic reticulum and formed into lipoproteins called chylomicrons. These particles are composed of TAGs, cholesterols, phospholipids, and apolipoproteins A and B48. Chylomicrons are exported to the lymphatic ducts and finally into circulation. Once in the bloodstream chylomicrons pick up apolipoprotein E and CII from circulating HDL, and the apolipoprotein CII activates LPL in adipose tissue (Davidson and Shelness, 2000). Lipoprotein lipase oxidizes TAG to free fatty acids. Fatty acids enter the adipose cells and are re-esterified to form TAG and stored in the lipid droplet (Bauman, 2003). Chylomicron remnants are transported to the liver and are either broken down via β-oxidation or re-packaged into VLDL and released into circulation.

Fatty Acid Synthesis

Palmitic, stearic, and oleic acids are the primary products of fatty acid synthesis in cattle (Moisa, 2011). Rate of fatty acid synthesis can be affected by age of the animal, energy density of the diet, and subsequent concentrations of acetate, glucose, lactate, pyruvate, NADPH, NADH, and ATP (Hood et al., 1972). Lipid metabolism is affected in the short-term by insulin and catecholemines, and in the long-term by GH, thyroid hormone, and glucocorticoids (Moisa, 2011). It was observed that acetate concentration increased the effect of insulin on glucose oxidation in bovine adipose tissue by increasing the tissues binding affinity or glucose (Mears and Mendel 1974; Yang and Baldwin 1973). Insulin not only initiates fatty acid synthesis via dephosphorylation of ACC by phosphatase, but inhibits lipolysis and fatty acid mobilization by inducing re-esterification as well as stimulating synthesis of LPL, VLDL, and chylomicron to adipose capillaries (Moisa, 2011).

The primary site of fatty acid synthesis in beef cattle is the adipose tissue, and as previously mentioned, acetate and glucose are the primary energy substrates for fatty acid synthesis (Smith and Crouse, 1984). Baldwin et al. (1973) reported that carbon from acetate is a more efficient substrate for fatty acid synthesis in ruminants than glucose. Historically, intramuscular adipose tissue was considered a late-developing depot. This line of thought led to management strategies that included weaning calves at 200 or more days of age and, in many cases, backgrounding calves on pasture for an additional 80-120 d. Calves managed in this way were not exposed to high concentrate diets until a much later stage of physiological development than calves that are managed using accelerated finishing systems, such as early weaning or calf feeding. Therefore, traditionally managed calves were not likely exposed to the elevated glucose and insulin levels that are beneficial for the development of intramuscular fat until later in life.

Acetyl CoA Carboxylase is the rate-limiting enzyme in the fatty acid synthetic pathway, and carries out the conversion of acetyl CoA to malonyl CoA. This enzyme is activated allosterically by the aforementioned phosphatase which is activated by insulin. Phosphorylation and subsequent deactivation of ACC is mediated by cAMP-activated protein kinase (AMPK; Moss et al., 1972). Citrate may also feed-forward activated ACC, additionally malonyl-CoA and long-chain fatty acids inhibit the enzyme. The bulk of fatty acid synthesis is carried out by fatty acid synthase (FAS) which is a 7 enzyme complex encoded by a single gene. Fatty acid synthase converts acetyl units from acetate or glucose to palmitate, stearate, or other long-chain fatty acids. The primary regulation of FAS takes place at the level of the gene and is mediated by sterol responsive element binding protein 1 (SREBP1) transcription factor. Insulin and glucagon mediate the activity of SREBP1 via the SREBP-1c gene. Insulin binding triggers the activation of phosohotidyl inositol-3-kinase which in turn phosphorylates and activates Akt which activates

SREBP-1c gene expression. In the fasted state, when glucagon is high, cAMP activates protein kinase A which inhibits the SREBP-1c gene, thereby down-regulating fatty acid synthesis, when dietary energy is low and adipose energy stores need to be utilized.

Gene Expression

Real Time Quantitative Polymerase Chain Reaction

Real time quantitative polymerase chain reaction (qPCR) is a commonly used biotechnology for quantifying expression levels of specific genes and was described in detail by Clark (2008). This process requires that mRNA be extracted from tissue and used to synthesize complementary DNA (cDNA; Clark, 2008). This cDNA is plated with forward and reverse primers, as well as a probe, which is a complementary sequence to the gene of interest contained in the strand of cDNA. A fluorescent dye is bound to the 5' end of the probe sequence, and a quencher is bound to the 3' end (Clark, 2008). This quencher inhibits fluorescence of the dye so long as both are bound in close proximity to the primer. The qPCR reaction takes place in a thermal cycler and involves a series of heating and cooling steps which cause the primers and probe to anneal to the cDNA. As the process of heating and cooling continues, the primer recruits nucleic acids and elongates the primer sequence. When the polymerase enzyme reaches the probe, it removes the dye and quencher causing the dye to fluoresce. The fluorescence increases each time a new copy of DNA is produced and is read at the end of each cycle. The number of cycles required to reach a predetermined threshold is known as the cycle threshold (Ct) value (Clark, 2008). The Ct-value has an inverse relationship with the amount of mRNA expressed from the target gene; therefore, a lower Ct-value implies that it required fewer cycles

to reach the threshold, and consequently there is a higher level of gene expression present (Clark, 2008).

Techniques, such as qPCR, are used to analyze the transcription of mRNA, because the presence of a specific DNA sequence in the genome of an animal does not necessarily mean that the sequence will be transcribed; therefore, it is assumed that mRNA is the instrument that mediates the function of the genome (Schoonik, 2002). The transcriptome responds to differing physiological conditions, and, thus, can be exploited to study the qualitative and quantitative aspects of gene expression under the aforementioned conditions (Berthier et al., 2006).

Wang et al. (2009) utilized qPCR to evaluate adipogenic and lipogenic-related enzymes in cattle populations with different genetic potentials for marbling. The authors observed that adipose differentiation-associated gene coding for C/EBPs, fatty acid metabolism-associated genes coding for adiponectin (FABP and FAS), lipogensis-associated genes coding for thyroid hormone responsive SPOT14 (THRSP), and secreted frizzled-related protein 5 (SFRP5), FAS, and LPL all exhibited increased expression in crossbred Hereford × Wagyu cattle compared to Hereford × Piedmontese as early as 7 months of age (Wang et al., 2009). These differences in expression were also observed in cattle that were 25 and 30 months of age, respectively, indicating that marbling is initiated in the early post-weaning phase of life and continues until harvest. It is interesting that PPARγ, a known precursor for marbling development, was not found to be differentially expressed among the 2 breeds until 25 months of age; however, the authors noted that C/EBP activation is necessary for subsequent induction of PPARγ (Wang et al., 2009).

Graugnard et al. (2010) examined the effects of dietary starch vs. fiber as an energy source for early-weaned calves and how these dietary treatments affect marbling-associated gene expression. Increased expression of PPARγ was observed as early as 56 d in cattle consuming starch as the primary energy source (Graugnard et al., 2010). This disagrees with the data presented by Wang et al. (2009). In addition to PPARγ, ATP citrate lyase, G6P dehydrogenase, FAS, FABP, SCD, glycerol-3-phosphate acyltransferase, mitochondrial (GPAM), diacylglycerol *O*-acyltransferase homologue 2 (DGAT2), adiponectin, and insulin-induced gene 1 exhibited increased expression as early as d 56 in cattle fed starch as the primary energy source (Graugnard et al., 2010). These results indicate that feeding starch as the primary energy source to early-weaned calves induces precocious preadipocyte differentiation and lipid filling earlier in life via the up-regulation of PPARγ, SREBF1, and MLX interacting protein-like (MLXIPL) and their target genes in the first half of the growing phase (Graugnard et al., 2010).

Summary

Marbling has historically been considered a late-stage fat depot that was not fully developed when cattle were marketed (Hood and Allen, 1973; Cianzio et al., 1985; May et al., 1994; Schoonmaker et al., 2004b). However, with the advent of early weaning, researchers began to note increased carcass quality as a result of marbling in calves that were early weaned and fed concentrates (Loy et al., 1999, Schoonmaker et al., 2003; Schoonmaker et al., 2004ab Shike et al., 2007). More recently, intramuscular fat deposition has been redefined as a depot whose development begins *in utero* with hyperplasic growth, can be impacted nutritionally up until at least 1 year of age (Hood and Allen, 1973; Pickworth, 2009), and continues with hypertrophic growth until slaughter if the diet contains sufficient energy.

The primary energy substrate used in the development of intramuscular fat is glucose (Smith and Crouse, 1984), and in ruminants glucose is largely derived from propionate production. This explains the positive effects of high starch concentrates on marbling development (Schoonmaker et al., 2003; Schoonmaker et al., 2004 ab; Shike et al., 2007; Graugnard et al., 2009); however, Meteer (2011) observed similar marbling scores in cattle fed starch and those fed high-fat coproducts. This is significant because with an expanding ethanol industry, coproducts are common place in the feed market and are often competitively priced.

Finally, with the growing concern that methane production from cattle is harmful to the environment, and the fact that methane production is energetically inefficient for growing and finishing cattle, it is important to understand the impacts of nutritional and management strategies on the production of greenhouse gases from ruminants. Feeding lipids can inhibit methane production via biohydrogenation, growth inhibition of methanogenic bacteria and decreased fiber digestion; therefore, it is important to understand the mechanism by which lipids from coproducts react in the rumen.

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CHAPTER 3

EFFECTS OF PROTEIN AND FAT CONCENTRATION IN COPRODUCT-BASED GROWING CALF DIETS ON PERFORMANCE AND CARCASS COMPOSITION

ABSTRACT

Crossbred heifers (n=150) and steers (n=100) were used to evaluate 1 of 5 growing diets: 1) corn-based control; 2) low fat, low protein coproduct blend; 3) high fat, low protein coproduct blend; 4) low fat, high protein coproduct blend; 5) high fat, high protein coproduct blend in a 2×2+1 factorial arrangement. Low protein and low fat diets were formulated to be isonitrogenous and isofat to control (16.0% CP, 3.0% fat), and high protein and high fat diets were formulated to be 20.0% CP and 5.0% fat respectively. Calves were weaned at 85 $\pm$ 18d, blocked by sex then by weight and allotted to 25 pens (10 hd/pen). The objective of this experiment was to determine if differing concentrations of protein and fat in coproduct-based growing diets of early-weaned calves affect feedlot performance and carcass composition. Calves were fed experimental diets for 112 d and then acclimated to a common feedlot diet for an additional 112 d. Body weight, hip height (HH), and ultrasound data were collected at the end of each 112d feeding phase. Carcass data included HCW, LM area (LMA), 12th rib back fat (BF), marbling score (MS), KPH, and USDA QG. No interactions ($P \geq 0.27$) of fat and protein concentration were detected; therefore, main effects are discussed. No effects ($P \geq 0.12$) of control, protein, or fat were detected for BW, or HH. Calves consuming increased dietary protein from coproducts had increased ($P = 0.04$) ADG in the growing phase. Feeding cattle

control decreased (P = 0.04) DMI, and increased (P <0.01) G:F during the growing phase and feeding phase. Ultrasound revealed increased (P = 0.05) BF in calves fed high fat at d 112. High protein diets decreased (P = 0.02) ultrasound MS at d 112. Carcasses from cattle fed high fat diets had greater (P = 0.03) MS compared to those from cattle fed low levels of dietary fat. Carcasses from cattle fed high protein diets had reduced (P < 0.01) percentage of carcasses that graded Prime compared to carcasses from cattle fed increased concentrations of fat. No differences ($P \geq 0.15$) were observed for HCW, LMA, BF, KPH, or YG. Cattle fed high protein diets produced fewer (P < 0.01) carcasses that graded Prime than cattle fed low protein diets. These data indicate that growth was unaffected by protein and fat concentration in growing calf diets, but MS and QG were positively influenced by fat and protein concentration in early calf diets.

INTRODUCTION

Early weaning is a management system used by beef producers to increase reproductive efficiency (Vaz and Lobato, 2010), and shorten the feeding phase needed for market animals to reach the choice grade (Loy et al., 1999). Early-weaned calf management has been extensively researched in comparison to traditional weaning practices (Harvey et al., 1975; Richardson et al., 1978; Myers et al., 1999; Schoonmaker et al., 2003, 2004a; Shike et al., 2007; Du et al., 2009; Du et al., 2010). Du et al. (2009) noted that nutritional manipulation of marbling is more effective in utrero, in neonates, and in early-weaned calves because the abundance of multipotent stem cells (potential adipocytes) is greater in younger animals. In early-weaned calves this leaves a window from 150 to 250 d of age in which marbling can be affected by nutritional management (Du et al., 2010)

Historically, it was believed that dietary starch was a necessity for early-weaned calves to improve marbling (Schoonmaker et al., 2003, 2004a) and subsequent carcass quality (Myers et al., 1999; Shike et al., 2007). More recently, research has indicated that early-weaned calves fed growing diets that include distillers grains, corn bran, and other coproducts with varying levels of fat and protein produce carcasses with similar marbling scores to those fed starch-based diets (Bedwell et al., 2008; Retallick et al., 2010; Meteer et al., 2011). With the large amounts of coproduct feeds available and the relatively high concentrations of fat and protein in many of these ingredients, it may be possible to replace the dietary energy previously provided as starch without adverse effects on meat quality. Therefore, the objective of this experiment was to determine if starch, protein, fat, and their interaction in coproduct-based, growing diets fed to early-weaned calves affect feedlot performance or carcass composition.

MATERIALS AND METHODS

Animal and Diet Management

Two hundred fifty crossbred calves (heifers = 150; steers = 100; BW = 156 $\pm$ 22kg) were weaned (Age = 85 $\pm$ 18d) at the Dixon Springs Agricultural Research Station in Simpson, IL and shipped to the University of Illinois Beef Cattle Field Research Laboratory in Urbana, IL. Calves were managed according to the guidelines recommended in the Guide for the Care and Use of Agricultural Animals in Agricultural Research and Teaching (FASS, 2010). All experimental procedures were approved by the University of Illinois Institute for Animal Care and Use Committee.

Calves were vaccinated and dewormed 14 d prior to weaning and again at weaning. Calves were vaccinated against infection by Clostridial diseases (i.e. *Cl. chauvoie, Cl. septicum, Cl novyi, Cl. sordellii, Cl. perfreingens type B, C,* and *D*) and bovine pneumonia (*Mannheimia*

(pasturella) haemolytica type A1) using One Shot Ultra®7 (Pfizer Inc., Kalamazoo, MI). Calves were also vaccinated for infectious bovine rhinotracheitis, bovine viral diarrhea Types 1 and 2, parainfluenza-3, and bovine respiratory syncytial virus using Bovi-Shield Gold® finishing phase® 5 L5 HB (Pfizer Inc., New York, NY). Finally, calves were vaccinated against Mycoplasma bovis using Pulmo-Guard MpB (American Animal Health, Inc., Grand Praire, TX). Deworming was accomplished via transdermal eprinomectin (IVOMEC® EPRINEX®, Merial Ltd., Duluth, GA).

Calves were fed a common receiving diet containing 29.7% corn husklage, 29.0% soybean hull pellets, 30.9% wet corn gluten feed, and 10.4% vitamin and mineral supplement from weaning until initiation of the trial at 141 ± 18d of age. At the initiation of the growing phase, BW measurements were collected on 2 consecutive days and averaged to calculate initial BW. Calves (Age = 141 ± 18d) were blocked by sex and BW then randomly assigned within block to 25 pens (pen = 10 animals; 5 pens/block). Calves were housed in 2 barns constructed of wood frames with ribbed metal roofs, and siding on the north, west, and east sides. The South side of each barn was covered with PVC coated 1.27 cm × 1.27 cm wire mesh bird screen and equipped with retractable curtains for wind protection. Within each barn, calves were housed in 4.88 m × 4.88 m pens (10 calves) constructed of 5.08 cm galvanized steel tubing. Pens had slatted concrete floors covered by interlocking rubber matting. Diets were fed in concrete fenceline bunks (0.49 m bunk space per calf) which were monitored daily and consumption recorded on a pen basis.

Pen was randomly assigned to experimental growing diets including a starch-based control, or 1 of 4 coproduct diets in a 2 × 2 factorial arrangement of fat and protein. Nutrient compositions for these diets are presented in Table 3.1. Coproduct diets included: 1) high

fat/high protein, 2) high fat/low protein, 3) low fat/high protein, and 4) low fat/low protein. Protein requirements were calculated using NRC (1996) guidelines. The control diet was formulated to contain 16.0% CP and 3.0% fat. Diets designated low fat or low protein were formulated to be isonitrogenous to control with similar fat content. Diets designated HF or HP were formulated to contain 20.0% CP and 5.0% fat, respectively. Diets were delivered to pens once daily, and were fed for *ad libitum* access to diets. Experimental diets were fed for a 112 d growing period after which cattle were adapted to a common coproduct-based finishing ration (Table 3.1). Samples (50g) of dietary ingredients were collected upon delivery and composited prior to laboratory analysis. Chemical composition of all dietary ingredients was analyzed by Rock River Laboratory, Inc. (Watertown, WI).

On d 112, calves began adaptation to common feedlot diet (Table 3.1) which was fed for *ad libitum* intake until d 224. Body weight and hip height were collected at 112 d intervals throughout the growing phase and finishing phase.

Ultrasound Data

Ultrasound measurements for BF, and marbling score (MS) were collected on d 112 and 224 by a trained technician from the University of Illinois Beef Cattle Research Laboratory. The ultrasound system included an Aloka SSD-500V equipped with a 12.5 cm-3.5 MHz transducer (Aloka Co. Ltd., Wallingford, CT). Soybean oil was used as a sound wave copulant. Ultrasound images were captured and measured using CPEC Ultrasound Image Software (Cattle Performance Enhancement Co., LLC, Oakley, KS). Ultrasound images were collected on the animal's right side parallel to the spinal column and perpendicular to the 11^{th}, 12^{th}, and 13^{th} ribs, halfway between the axial and transverse processes of the lumbar vertebrae. The ultrasound location was clipped free of hair and curried clean prior to image collection.

Carcass Data Collection

On d 225, cattle were sold and shipped 296.1 km to a commercial harvest facility (Joslin, IL). Cattle were humanely slaughtered under USDA inspection. Immediately post-harvest, HCW was collected and carcasses were chilled for 24 h at -4˚C. At approximately 24 h post-mortem, the right side of the carcass was ribbed between the 12th and 13th ribs and carcass data including LM area, BF, MS, and percent kidney, pelvic, and heart fat (KPH) were collected by plant personnel. University of Illinois trained personnel recorded measurements and determined quality grade (QG) and yield grade (YG). The equation: [2.5 + (2.5 × in. of BF) + (0.20 × %KPH) + (0.0038 × lbs of HCW) – (0.32 × REA in^2)] was used to calculate YG (Taylor, 1994).

Statistical Analysis

The experiment employed a randomized complete block design. Treatments were arranged as a $2 \times 2 + 1$ factorial, to test the effects of protein concentration (P), fat concentration (F), and protein × fat concentration interaction. Pen was defined as the experimental unit. A contrast was used to compare control to all coproduct diets. Least squares means for treatment within feeding phase were generated and separated using the PDIFF option of LSMEANS. Performance, ultrasonic, and carcass data were analyzed using the MIXED (noncategorical data) and GENMOD (categorical data: QG) procedures of SAS (SAS Institute Inc., Cary, NC). No interactions were detected so only main effects of treatment will be discussed. Differences were considered significant at $\alpha = 0.05$ and trends were considered present at $0.05 < \alpha < 0.10$.

RESULTS

Performance Data

Performance data are presented in Table 3.2. Final BW was not different ($P \geq 0.45$) at the end of the growing or finishing phases; however, within coproduct diets ADG increased ($P = 0.04$) by 0.08 kg at d 112 in calves consuming diets containing increased dietary protein compared to those fed decreased dietary protein. After cattle were acclimated to a common finishing diet, cattle that consumed coproducts during the growing phase tended ($P = 0.09$) to experience increased ADG compared to cattle that had been fed control during the growing phase.Additionally, cattle fed coproduct diets with increased concentrations of dietary fat during the growing phase tended ($P = 0.08$) to experience increased ADG during the finishing phase compared to those fed diets with decreased concentrations of dietary fat in the growing phase. The improved ADG observed at d 112 in calves fed increased protein was not ($P \geq 0.20$) sufficient to affect cumulative ADG measured from weaning until slaughter.

Growing phase DMI was 0.66 kg less ($P = 0.04$) in calves fed control compared to those fed coproducts. During the finishing phase, DMI was not different ($P \geq 0.17$) among treatments. The decreased ($P = 0.04$) DMI of control calves in the growing phase was sufficient to produce a tendency ($P = 0.08$) for reduced cumulative DMI in cattle consuming control instead of coproducts. Neither protein nor fat concentration had any effect on DMI during either phase of production.

Cattle consuming control were more ($P < 0.01$) efficient during the growing phase and finishing phases, but were not different ($P = 0.19$) when G:F was calculated from weaning till

slaughter. Also, hip height was not affected by diet during the growing phase ($P \geq 0.47$) or finishing phase ($P \geq 0.12$), respectively.

Ultrasound Data

No differences ($P \geq 0.11$) in BF were observed between calves fed control and coproduct diets (Table 3.3). However, dietary fat concentration increased ($P = 0.05$) BF by 0.52 mm at the end of the growing phase. No treatment differences ($P \geq 0.65$) in BF were detected via ultrasound at d 224 between cattle fed control vs. cattle fed coproducts, or as a result of protein ($P = 0.65$), or fat ($P = 0.65$) concentration in the diet.

No treatment difference ($P = 0.11$) in marbling score was observed via ultrasound between cattle consuming control and those consuming coproducts during the growing phase. Elevated protein concentration in the diet decreased ($P = 0.02$) MS in growing calves fed coproducts by 18 units at d 112. Marbling score as predicted by ultrasound 1 d prior to slaughter was not different ($P \geq 0.40$) among all treatments.

Carcass Data

Carcass traits including HCW, REA, BF, KPH, and YG were not affected by any treatment (Table 3.4.). High fat growing diets improved ($P = 0.03$) marbling by 1/3 of a score compared with low fat coproduct diets. Also, high protein growing diets decreased ($P < 0.01$) the percentage of carcasses grading USDA Prime by 9.9%. Also, a higher percentage of carcasses from cattle fed diets with increased fat graded USDA Choice^{+}Percentage of carcasses that graded USDA Select, Choice^{-}, or Choice^{o} were not different ($P \geq 0.23$) among treatments.

DISCUSSION

Calves fed the corn-based control had increased efficiency combined with decreased DMI during the growing phase of this trial; however, intake and efficiency were similar in the feeding phase. Also, growing phase ADG was increased by increased protein concentration in coproduct diets (Table 3.2). Historically, starch-based diets have improved ADG when compared to forage-based diets (Neville and McCormick, 1981; Schoonmaker et al. 2003; Arthington et al., 2005). Coproduct diets used in this study contained 0.5 Mcal $\cdot$ kg^{-1} less NEg than control; however, consuming coproduct diets increased DMI by 0.66 $kg \cdot d^{-1}$ and 0.63 $kg \cdot d^{-1}$ during the growing and finishing phases respectively. Therefore, it is likely that increased energy of the control diet failed to improve overall ADG because of increased DMI of coproduct-based diets. These findings are similar to those of Meteer (2011) who observed no differences in ADG in early-weaned calves fed either starch or coproduct-based growing diets. However, Schoonmaker et al. (2003) reported an ADG increase of 0.38 $kg \cdot d^{-1}$ from steers fed corn-based diets compared steers fed fiber-based diets containing hay and soybean hulls during the growing phase. Schoonmaker et al. (2003), Bedwell et al. (2008), and Retallick et al. (2010) also illustrated that the difference in growing phase ADG was sufficient to improve overall ADG. Results from this experiment suggest that when coproducts are used as the primary source of dietary energy, growing phase ADG was not different from calves fed corn-based diets and, therefore, did not affect overall ADG. However, within coproduct diets, increased ADG was observed during the growing phase for cattle consuming diets with increased protein.

This data indicates that control diets decreased DMI, increased G:F, and, in the finishing phase, tended to decrease ADG which disagrees with that of Schoonmaker et al. (2003 and 2004b) who reported no differences in DMI between early-weaned calves fed either starch or

fiber-based diets during the growing phase (Schoonmaker et al., 2003; Schoonmaker et al., 2004b). Meteer et al. (2011) found that early-weaned calves fed fiber-based diets consumed 0.88 kg/d more than calves fed starch-based diets. This incongruity may be explained by the source of fiber used in the previous work. Fiber-based diets used by Schoonmaker et al. (2003; 2004b) included either Smooth Bromegrass (*Bromus* inermis Leyss.) hay or haylage, while Meteer et al. (2011) used corn bran. Therefore it is likely that the increased particle size of the hay and haylage decreased passage rate from the rumen and subsequently decreased DMI; whereas, the decreased particle size of corn bran and other coproducts improved passage rate through the reticulo-rumen and decreased the physical competition for feed particles to escape. Increased passage rate due to decreased particle-size has been demonstrated in coproduct feeds, such as corn gluten feed (Firkins et al., 1985). Therefore, it is possible that increased escape from the rumen improved DMI by decreasing gut fill both in the current experiment as well as that by Meteer et al. (2011).

In the carcass, high fat coproduct diets increased final MS by 1/3 of a score and subsequently increased the percentage of carcasses grading Choice^{+} or better. Mean MS of carcasses from cattle fed high fat coproduct blends during the growing phase was 511 (Modest^{11}) while mean MS of carcasses from cattle fed low fat coproduct blends was 478 (Small^{78}). Mean MS of carcasses from cattle fed control during the growing phase was 508 (Modest^{08}), and though not different from cattle fed coproducts, these results suggest that high fat coproducts fed during the growing phase may increase marbling development similar to starch. Historically high-starch diets have been reported to increase intramuscular fat percentage (Schoonmaker et al., 2004a; Schoonmaker et al., 2004b) and subsequent marbling score (Myers et al., 1999) when fed during the growing phase and compared to fiber-based diets. Therefore, it was believed that

starch was a necessary dietary component for early-weaned calves to improve marbling and subsequent carcass quality. Increased MS in early-weaned calves fed starch-based diets were attributed to the increased intramuscular adipogenesis resulting from increased blood glucose concentrations. Blood glucose concentration in ruminants is primarily maintained by gluconeogenesis because less than 10% of the glucose requirement is supplied by direct absorption from the digestive tract. Of the VFAs produced from ruminal fermentation of carbohydrates, propionate is the only major carbon substrate for gluconeogenesis (Young, 1977; Russell and Gahr, 2000). The ruminal propionate concentration increases with the fermentation of starch (Ciccioli et al., 2005; Huntington et al., 2006; May et al., 2009), thereby increasing the amount of carbon substrate available for gluconeogenesis. Smith and Crouse (1984) illustrated that glucose was the primary energy substrate used for intramuscular adipogenesis and hypothesized that increased ruminal propionate production may be the mechanism by which starch-fed cattle improve marbling scores compared to those fed fiber.

Similar to results presented in the current experiment, Meteer et al. (2011) found no difference in MS between cattle fed corn and those fed fiber in the form of corn bran (9.85% Fat). Increasing the concentration of lipids in the rumen has been shown to increase ruminal propionate concentration (Ikwuegbu and Sutton, 1982; Chalupa et al. 1984; Czerkawski and Clapperton, 1984; Boggs et al., 1987; Jenkins, 1993). Fat from coproduct diets used both in the current experiment and by Meteer et al. (2011) may increase the relative concentration of propionate and, subsequently, glucose available for intramuscular lipogenesis.

Although only 5.6% of cattle reached the Prime grade, high protein diets decreased the percentage of carcasses grading Prime by 9.1 percentage units. Although the mechanism for this finding is unclear, it is possible increased dietary protein intake decreased intramuscular fat

development. Two studies have reported a trend for decreased intramuscular fat deposition in feedlot cattle fed barley-based diets when dietary protein content was increased (Oddy et al., 2000; Pethick et al., 2000). These results agree with our findings; however, Oddy et al. (2000) and Pethick et al. (2000) attributed the aforementioned trend for decreased IMF to increased DMI by cattle fed low protein diets. In the current experiment, there was no difference in DMI among cattle fed differing levels of dietary protein.

CONCLUSIONS AND IMPLICATIONS

Feeding control decreased DMI and increased G:F in the growing phase. During the finishing phase, DMI and G:F were unaffected by feeding control during the growing phase; however, ADG tended to be decreased in control-fed calves after cattle were acclimated to a common finishing diet. Feeding increased dietary protein concentrations from coproducts during the growing phase increased ADG in the initial 112 d, but had no effect during the finishing phase. Also, feeding diets high in dietary fat during the growing phase resulted in cattle that gained less and were less efficient in the feedlot.

Carcasses from cattle fed coproducts during the growing phase resulted in similar marbling scores when compared to carcasses from cattle fed corn-based growing diets suggesting that increased dietary starch concentration may not be necessary to produce high quality carcasses from early-weaned calves. Increased marbling scores of carcasses from cattle fed high fat coproducts during the growing phase may have resulted from increased blood glucose resulting from increase ruminal propionate production. More research is needed to determine the exact mechanism for this process. However, this research indicates that feeding corn coproduct blends to early-weaned calves produces carcasses similar in quality to those from cattle fed corn during the growing phase. Additionally, feeding coproduct blends with increased concentrations

of dietary fat improves marbling score in the carcass compared to those fed coproduct blends with decreased concentrations of dietary fat. The information provided in this research is of value to producers who are exploring early-weaning as alternative management strategy.

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Tables and Figures

Table 3.1. Dry matter composition and nutrient analysis of experimental and common feedlot diets offered to early-weaned calves fed coproduct blends containing differing levels of fat and protein during the growing phase

		High Fat		Low Fat		
	Control	High CP	Low CP	High CP	Low CP	Common Diet
Ingredient, % DM						
Corn Husklage	20.0	20.0	20.0	20.0	20.0	20.0
Soybean Hulls	-	30.0	30.0	30.0	30.0	-
Cracked Corn	58.0	-	-	-	-	35.0
Soybean Meal	17.0	6.0	-	11.0	2.0	2.5
DDGS[1]	-	34.0	26.0	13.0	11.0	-
WDGS[2]	-	-	-	-	-	40.0
Corn Gluten Feed	-	5.0	10.0	21.0	32.0	-
Corn Bran	-	-	9.0	-	-	-
Ground Corn	3.04	3.04	3.04	3.04	3.04	3.04
Limestone	1.71	1.71	1.71	1.71	1.71	1.71
Rumensin 80[3]	0.02	0.02	0.02	0.02	0.02	0.02
Tylan 40[4]	0.01	0.01	0.01	0.01	0.01	0.01
Trace Mineral Salt[5]	0.11	0.11	0.11	0.11	0.11	0.11
Copper Sulfate	0.01	0.01	0.01	0.01	0.01	0.01
Vitamin Premix[6]	0.01	0.01	0.01	0.01	0.01	0.01
Liquid Fat	0.08	0.08	0.08	0.08	0.08	0.08
Chemical Composition, % DM						
CP	16.95	19.15	16.37	20.46	18.12	15.99
NDF	21.07	45.75	46.91	45.35	47.84	33.49
ADF	7.77	25.89	25.62	24.95	25.20	12.73
Ether Extract	3.28	4.55	4.79	3.43	3.53	5.17
Ash	4.67	6.64	6.47	6.64	6.50	5.19
Ca	0.97	1.09	1.05	0.70	1.06	0.91
P	0.36	0.54	0.55	0.56	0.59	0.52
NEm, Mcal · kg^{-1} [7]	2.22	1.67	1.67	1.69	1.69	2.04
NEg, Mcal · kg^{-1} [8]	1.52	1.06	1.06	1.07	1.07	1.38

[1]Dried distillers grains with solubles
[2]Wet distillers grains with solubles
[3]Rumensin 176 g/kg (Elanco Animal Health, Greenfield, IN)
[4]Tylosin 88 g/kg (Elanco Animal Health, Greenfield, IN)
[5]Trace Mineral Salt = 80-85% Salt, 2.57% Iron, 2.86% Zinc, 5,710 ppm Manganese, 2,290 ppm Copper, 100 ppm Iodine, 85.7 ppm Selenium
[6]Vitamin A = 3,306,900 IU/kg, vitamin D = 330,690 IU/kg, vitamin E = 2,204.6 mg/kg, vitamin B_{12} = 17.6 mg/kg, Riboflavin
[7]Calculated by Rock River Laboratory (Watertown, WI) based on analyzed ADF value
[8] Calculated by Rock River Laboratory (Watertown, WI) based on analyzed ADF value

Table 3.2. Performance data for early-weaned calves fed coproduct blends containing differing levels of fat and protein during the growing phase.

Item	Control	High Fat		Low Fat		SEM[1]	Contrast[2]	P value[3]	
		High CP	Low CP	High CP	Low CP		Control vs All	Protein	Fat
Initial BW, kg	156	157	158	159	156	13.22	0.92	0.93	0.99
d 112[4]									
BW, kg	354	358	351	354	343	15.59	0.83	0.42	0.56
ADG, kg·d^{-1}	1.76	1.79	1.72	1.74	1.66	0.04	0.31	0.04	0.11
DMI, kg·d^{-1}	6.26	6.99	6.73	6.93	7.01	0.37	0.04	0.72	0.68
G:F	0.28	0.26	0.26	0.25	0.24	0.01	< 0.01	0.41	0.20
HH[5], cm	119.1	119.0	119.0	119.2	119.7	2.1	0.47	0.83	0.87
d 224[6]									
BW, kg	489	492	494	499	491	15.57	0.68	0.81	0.83
ADG, kg·d^{-1}	1.20	1.23	1.25	1.30	1.33	0.05	0.09	0.62	0.08
DMI, kg·d^{-1}	7.45	7.59	7.63	7.98	7.36	0.22	0.44	0.79	0.17
G:F	0.17	0.16	0.16	0.17	0.18	0.01	0.76	0.40	0.08
HH, cm	124.8	126.7	127.3	126.8	126.7	1.2	0.12	0.81	0.81
Cumulative									
ADG, kg·d^{-1}	1.48	1.51	1.48	1.52	1.49	0.03	0.46	0.20	0.62
DMI, kg·d^{-1}	6.84	7.28	7.17	7.44	7.18	0.21	0.08	0.37	0.68
G:F	0.22	0.21	0.21	0.21	0.21	0.01	0.19	1.00	1.00

[1]SEM presented are from the contrast comparing CONTROL to all coproduct diets
[2]Contrast = the comparison of calves fed control diets to those fed coproducts
[3]Protein = the main effect of protein on performance; Fat = the main effect of fat on performance; Protein × Fat interaction was not detected ($P \geq 0.17$; SEM ≤ 15.16) for performance data
[4]Last day of growing phase during which experimental diets were fed
[5]HH = Hip Height
[6]Last day of feedlot phase during which a common diet was fed

Table 3.3. Carcass ultrasound data for early-weaned calves fed coproduct blends containing differing levels of fat and protein during the growing phase.

		High Fat		Low Fat			Contrast[2]	P value[3]	
Item	Control	High CP	Low CP	High CP	Low CP	SEM[1]	Control vs All	Protein	Fat
d 112[4]									
Back Fat, mm	4.95	5.61	4.79	4.67	4.69	0.26	0.98	0.20	0.05
Marbling	314	296	304	284	312	8.0	0.11	0.02	0.74
d 224[5]									
Back Fat, mm	9.78	9.44	9.58	9.69	9.70	0.59	0.97	0.65	0.65
Marbling	547	528	534	521	521	22.0	0.40	0.88	0.64

[1]SEM presented are from the contrast comparing CONTROL to all coproduct diets
[2]Contrast = the comparison of calves fed control diets to those fed coproducts
[3]Protein = the main effect of protein on performance; Fat = the main effect of fat on performance; Protein × Fat interaction was not detected ($P \geq 0.17$; SEM ≤ 15.16) for performance data
[4]Last day of growing phase during which experimental diets were fed
[4] 200 = Traces^{00}; 300 = Slight^{00}; 400 = Small^{00}; 500 = Modest^{00}
[5]Last day of feedlot phase during which a common diet was fed

Table 3.4. Carcass data for early-weaned calves fed coproduct blends containing differing levels of fat and protein during the growing phase.

		High Fat		Low Fat			Contrast[2]	P value[3]	
Item	Control	High CP	Low CP	High CP	Low CP	SEM[1]	Control vs All	Protein	Fat
HCW, kg	297.1	302.5	302.4	306.7	301.1	9.71	0.24	0.60	0.84
REA, cm^2	73.8	73.9	73.7	75.6	74.8	0.14	0.52	0.63	0.15
Marbling[4]	508	508	513	471	485	15.88	0.36	0.52	0.03
Fat Thickness, cm	1.2	1.2	1.3	1.3	1.3	0.02	0.14	0.42	0.59
KPH, %	2.3	2.3	2.4	2.3	2.3	0.04	0.60	0.15	0.66
Yield Grade[5]	3.0	3.1	3.1	3.1	3.1	0.08	0.26	0.50	0.61
Quality Grade[6]									
Select, %	18.0	18.0	14.3	17.0	26.0	0.56	0.95	0.70	0.38
$Choice^-$ or better, %	82.0	82.0	85.7	83.0	74.0	0.56	0.94	0.72	0.36
$Choice^0$ or better, %	48.0	48.0	44.9	34.0	42.0	0.42	0.46	0.71	0.23
$Choice^+$ or better,%	20.0	24.0	30.6	12.8	16.0	0.58	1.00	0.42	0.03
Prime, %	6.0	2.0	12.2	0.0	8.0	1.01	0.25	0.002	0.19

[1]SEM presented are from the contrast comparing CONTROL to all coproduct diets
[2]Contrast = the comparison of calves fed control diets to those fed coproducts
[3] Protein = the main effect of protein on performance; Fat = the main effect of fat on performance; Protein × Fat interaction was not detected ($P \geq 0.17$; SEM ≤ 15.16) for performance data
Protein × Fat interaction was not detected ($P \geq 0.24$; SEM ≤ 1.00) for carcass data
[4] 100=practically devoid, 200=traces, 300=slight, 400=small, 500=modest, 600=moderate, 700=slightly abundant, 800=moderately abundant
[5]Yield Grade = $[2.5 + (2.5 \times \text{in. of BF}) + (0.20 \times \%\text{KPH}) + (0.0038 \times \text{lbs of HCW}) - (0.32 \times \text{REA in in.}^2)]$

CHAPTER 4

EFFECTS OF PROTEIN AND FAT CONCENTRATION IN COPRODUCT-BASED GROWING CALF DIETS ON ADIPOGENIC GENE EXPRESSION, BLOOD METABOLITES AND CARCASS COMPOSITION

ABSTRACT

Longissimus lumborum of 30 crossbred calves (Age = 95 ± 2 d; BW = 179 ± 18 kg) fed 1 of 5 growing diets: 1) corn-based control; 2) low fat, low protein coproduct blend ; 3) high fat, low protein coproduct blend; 4) low fat, high protein coproduct blend; 5) high fat, high protein coproduct blend for 112 d (growing phase) followed by a common corn-based finishing diet (d 113 - 224; finishing phase) were biopsied at 0, 112, and 224 d for gene expression analysis via RT-qPCR of 14 genes associated with adipogenesis and lipogenesis within the muscle. Also, serum was collected at d 0, 112, and 224 and analyzed for leptin, IGF1, and growth hormone concentration. Data were analyzed to ascertain the effects of protein concentration, fat concentration, time, and their interactions. A combination of increased protein and decreased fat in the growing diet resulted in a carryover effect between d 112 and 224 which increased ($P < 0.01$) gene expression of PPAR gamma, insulin induced gene 1, thyroid hormone responsive SPOT14 protein, ATP citrate lyase, adiponectin, diacylglycerol O-acyltransferase homologue 2, fatty acid binding protein 4, fatty acid synthase, phosphoenolpyruvate carboxykinase 1, and stearoyl-CoA desaturase as well as serum leptin concentrations. Expression of sterol regulatory element binding transcription factor 1 was increased ($P < 0.01$) at d 112 in steers fed high protein, high fat diets compared to those fed high protein, low fat diets. A fat × day interaction ($P < 0.01$) occurred for the expression of adiponectin receptor 2 and CCAAT/enhancer binding

protein alpha resulting in a carryover effect wherein low fat diets fed before d 112 increased expression of both genes at the end of the finishing phase (d 224). After slaughter, cattle fed control during the growing phase tended ($P = 0.09$) to have higher marbling scores while other carcass parameters were not different ($P \geq 0.13$). These data indicate that feeding differing levels of dietary fat and protein during the growing phase affects intramuscular adipogenesis at the transcriptional level; however, differences in gene expression were not sufficient to affect carcass quality among cattle fed coproducts.

INTRODUCTION

Recently, research has indicated that early-weaned calves fed growing diets that include distillers grains and other coproducts with high concentrations of fat and protein produce carcasses with similar marbling scores to those fed starch-based diets (Retallick et al., 2010; Meteer et al., 2011; Segers et al., 2012). We hypothesize that increased protein and fat in coproducts will result in improved intramuscular fat deposition similar to corn.

Several studies have reported performance and carcass characteristics of early-weaned calves (Harvey et al., 1975; Richardson et al., 1978; Loy et al., 1999; Myers et al., 1999; Schoonmaker et al., 2003, 2004ab; Retallick et al., 2010; Meteer et al., 2011). Little work has been done to compare coproduct diets with differing nutrient compositions and their impact on carcass quality in early life and at the transcriptional level. Therefore, the objective of this experiment was to assess the effect of dietary fat and protein concentration on serum concentrations of leptin, insulin-like growth factor 1 (IGF1) and growth hormone (GH), carcass traits, and gene expression of 14 genes that regulate lipid metabolism and adipogenesis.

Marbling is extremely complex and falls under the control of not only environmental factors, but of interconnected gene networks, each exerting small effects that combine to produce physiological changes (Wu et al., 2006). Biochemical studies of adipose tissue (Smith and Crouse, 1984; Rhoades et al., 2007) and muscle protein (Gingras et al., 2007) metabolism have provided insights into basic tissue development as it pertains to nutrition and growth. Enzyme activity in the energy metabolism and lipogenic pathways are largely a result of the rate at which the enzymes are synthesized (Salati et al., 2004; Freyssenet, 2007). Metabolic regulation relies heavily on transcriptional regulation as a long-term mechanism for determining the expression level of key enzymes (Desvergne et al., 2006).

MATERIALS AND METHODS

Cattle and Diet Management

Two hundred fifty crossbred calves (heifers = 150 and steers = 100; BW = 156 $\pm$ 22kg) were weaned (Age = 85 $\pm$ 18d) at the Dixon Springs Agricultural Research Station in Simpson, IL and shipped to the University of Illinois Beef Cattle Field Research Laboratory in Urbana, IL (Segers et al., 2012). Thirty calves (Age = 95 ± 2 d; BW = 179 $\pm$ 18 kg) were selected as a subset of the larger experiment for blood metabolite and gene expression analysis and managed identically to the larger group. Calves were managed according to the guidelines recommended in the Guide for the Care and Use of Agricultural Animals in Agricultural Research and Teaching (Consortium, 1988). All experimental procedures were approved by the University of Illinois Laboratory Animal Care and Use Committee.

Calves were vaccinated and dewormed 14 d prior to weaning and again at weaning. Calves were vaccinated against infection by Clostridial diseases (i.e. *Cl. chauvoie, Cl. septicum, Cl novyi, Cl. sordellii, Cl. perfreingens type B, C,* and *D*) and bovine pneumonia (*Mannheimia*

(pasturella) haemolytica type A1) using One Shot Ultra®7 (Pfizer Inc., Kalamazoo, MI). Calves were also vaccinated for infectious bovine rhinotracheitis, bovine viral diarrhea Types 1 and 2, parainfluenza-3, and bovine respiratory syncytial virus using Bovi-Shield Gold® finishing phase® 5 L5 HB (Pfizer Inc., New York, NY). Finally, calves were vaccinated against Mycoplasma bovis using Pulmo-Guard MpB (American Animal Health, Inc., Grand Prairie, TX). Deworming was accomplished via transdermal eprinomectin (IVOMEC® EPRINEX®, Merial Ltd., Duluth, GA).

Calves were housed in two barns constructed of wood frames with ribbed metal roofs, and siding on the North, West, and East sides. The South side of each barn was covered with PVC coated 1.27 cm × 1.27 cm wire mesh bird screen and equipped with retractable curtains for wind protection. Within each barn, calves were housed in 4.88 m × 4.88 m pens constructed of 5.08 cm galvanized steel tubing. Pens had slatted concrete floors covered by interlocking rubber matting. Diets were fed in concrete fenceline bunks (0.49 m bunk space per calf) which were monitored daily and consumption recorded.

Calves from the larger study were blocked by sex and by weight, then within block, were randomly assigned to pen. The heavy weight block of steers were chosen as the subset for the current experiment. Pens were randomly assigned to experimental growing diets including a starch-based control, or 4 coproduct diets with two levels of fat and protein. Comproduct diets included: 1) high fat/high protein; 2) high fat/low protein; 3) low fat/ high protein; and 4) low fat/ low protein.Nutrient composition for these diets is presented in Table 4.1. Protein requirements were calculated using NRC (1996) guidelines. The control diet was formulated to contain 16.0% CP and 3.0% fat. Diets that were designated low fat or low protein were formulated to be isonitrogenous to control with similar fat content. Diets designated high fat or

high protein were formulated to contain 20.0% CP and 5.0% fat, respectively. Control and common diets contained 1.52 and 1.38 Mcal·kg^{-1} respectively of NE_g. All coproduct diets contained 1.1 Mcal·kg^{-1} of NE_g. Diets were delivered to pens once daily, and cattle were fed for *ad libitum* access to diets. Experimental diets were fed for a 112 d growing period after which cattle were adapted to a common coproduct-based finishing ration (Table 4.1). Samples (50g) of dietary ingredients were collected upon delivery and composited prior to laboratory analysis. Chemical composition of all dietary ingredients was ascertained by Rock River Laboratory, Inc. (Watertown, WI; Table 4.1.). On d 112, calves began adaptation to common feedlot diet (Table 4.1) which was fed for *ad libitum* intake until d 224.

Blood Collection

At d 0, 112, and 224 blood was collected via jugular venipuncture prior to biopsy procedure. Serum was isolated (Sorval Legend XFR Centrifuge, Newtown, CT), and shipped to a commercial lab for analysis of serum leptin, insulin-like growth factor 1 (IGF1), and growth hormone (GH) concentrations.

Muscle Biopsies

Muscle biopsies were collected according to the procedures outlined by Graugnard et al., 2010. Muscle biopsies were collected at d 0 (prior to feeding experimental diets), d 112 (transition from experimental to common diet) and d 224 (1 d preharvest). Tissue was obtained from the Longissimus muscle via needle biopsy (12 gauge core biopsy needle; Bard Magnum, C. R. Bard, Covington, GA). To allow repeated sampling across a different area of the muscle, the initial biopsy was collected 5 cm anterior to the tuber coxae of the ilium, and each subsequent biopsy was collected 5 cm anterior to the previous biopsy site. Lidocaine-HCl (3 mL) was injected intramuscularly to anesthetize the biopsy area. Over 0.5 g of tissue was collected from

each steer at each time point and was stored in liquid-N_2 until RNA extraction. Surgical staples (APPOSE™ UCL; Auto Suture) were used to close the incision and iodine ointment (Povidone ointment, 10%; Henry Schein®, Melville, NY, USA) was applied to the wound. The animals were monitored daily for evidence of behavioral signs of discomfort or local infection in the incision site. Staples that remained 7 d post-biopsy, were removed.

Carcass Data Collection

On d 225, cattle were sold and shipped 296.1 km to a commercial harvest facility (Joslin, IL). Cattle were humanely slaughtered under USDA Inspection. Immediately post-harvest, HCW was collected, and carcasses were chilled for 24 h at -4˚C. At approximately 24 h post-mortem, the right side of the carcass was ribbed between the 12th and 13th ribs and carcass data including LM area, BF, MS, and percent kidney, pelvic, and heart fat (KPH) were collected by plant personnel. University of Illinois trained personnel recorded measurements and determined quality grade (QG) and yield grade (YG). The equation: $[2.5 + (2.5 \times \text{in. of BF}) + (0.20 \times \%\text{KPH}) + (0.0038 \times \text{lbs of HCW}) - (0.32 \times \text{REA in}^2)]$ was used to calculate YG (Taylor, 1994).

RNA Extraction, Evaluation and RT-qPCR

Muscle tissue was weighed (0.5 g) and RNA was extracted using 3 mL ice-cold Trizol® (Invitrogen Corp., Carlsbad, CA) and 1 µL of Linear Acrylamide (Ambion® Cat. No. 9520, Invitrogen Corp., Carlsbad, CA) as a coprecipitant. Genomic DNA was removed from RNA via DNase from RNeasy Mini Kit columns (Qiagen, Düsseldorf Germany). Concentration of RNA was measured using a NanoDrop ND-1000 spectrophotometer (NanoDrop Technologies, Wilmington, DE). The purity of RNA (A_{260}/A_{280}) for all samples was above 1.99. Quality of RNA was assessed by randomly selecting 10 samples and using a 2100 Bioanalyzer (RNA

Integrity Number = 7.2; Agilent Technologies Inc., Santa Clara, CA). A portion of RNA was diluted to 100 mg/L using DNase/RNase free water prior to reverse transcription.

Complementary DNA (cDNA) was synthesized using 100 ng RNA, 1 µg dT18 (Operon Biotechnologies, Huntsville, AL), 1 µL 10 mmol/L dNTP mix (Invitrogen Corp., Carlsbad, CA), 1 µL random primers (Invitrogen Corp., Carlsbad, CA), and 10 µL DNase/RNase free water. The mixture was incubated at 65 °C for 5 min and placed on ice for 3 min. Six µL of master mix containing 4.5 µL 5X First-Strand Buffer, 1 µL 0.1 M DTT, 0.25 µL (50 U) of SuperScriptTM III RT (Invitrogen Corp., Carlsbad, CA), and 0.25 µL of RNase Inhibitor (10 U, Promega, WI) was then added. The reaction was carried out in an Eppendorf Mastercycler® Gradient (Eppendorf Corp., Hamburg, Germany) using the following temperature program: 25 °C for 5 min, 50 °C for 60 min and 70 °C for 15 min. Complementary DNA was then diluted 1:4 with DNase/RNase free water.

Quantitative PCR (qPCR) was performed using 4 µL diluted cDNA combined with 6 µL of a mixture composed of 5 µL 1 × SYBR Green master mix (Applied Biosystems, Foster City, CA), 0.4 µL each of 10 µM forward and reverse primers, and 0.2 µL DNase/RNase free water in a MicroAmp™ Optical 384-Well Reaction Plate (Applied Biosystems, Foster City, CA). Samples were reacted in triplicate and a 6 point relative standard curve plus the non-template control (NTC) were used (User Bulletin #2, Applied Biosystems, Foster City, CA). A composite sample of cDNA was made by adding 10 µL cDNA to a common tube. The 6 point standard curve was made by first making a 1:2 dilution with the composited cDNA and DNase/RNase free water and then making 5 serial 1:4 dilutions to achieve final concentrations of 50%, 12.5%, 3.125%, 0.7813%, 0.1953%, and 0.0488%. The reactions were carried out in an ABI Prism 7900 HT SDS instrument (Applied Biosystems, Foster City CA) using the following conditions: 2 min

at 50 °C, 10 min at 95 °C, 40 cycles of 15 s at 95 °C (denaturation) and 1 min at 60 °C (annealing + extension). The presence of a single PCR product were verified by the dissociation protocol using incremental temperatures to 95 °C for 15 s plus 65 °C for 15 s. Data were calculated with the 7900 HT Sequence Detection Systems Software (version 2.2.1, Applied Biosystems, Foster City, CA). The final data were normalized using the geometric mean of the genes UXT, MTG1 and RPS15A (Graugnard et al., 2009), which are considered as internal control genes due to their stability, and lack of variation in the muscle tissue, or in response to experimental treatment (Vandesompele et al., 2002).

Primers are listed in Table 4.2. Primers have been designed by members of the NutriPhysioGenmoics Laboratory at the University of Illinois, using Primer Express 2.0 with minimum amplicon size of 100 bp and limited 3' G+C (Applied Biosystems, Foster City, CA). When possible, primer sets were designed to fall across exon–exon junctions. Primers were aligned against publicly available databases using BLASTN at NCBI (3) and UCSC's Cow (Bos taurus) Genome Browser Gateway.

Statistical Analysis

Data were analyzed using the MIXED procedure in SAS (SAS Institute, Cary, NC). The proportional change in expression was calculated at all time points to obtain fold-change relative to d 0. Two models were used to characterize expression of each gene. The first model was used measure the effect of protein and fat level in coproduct diets and their interaction with each other and days on feed. The first model contained fixed effects of protein level, fat level, days on feed, and their interactions. A repeated measures statement using a compound symmetry covariate structure was used for blood metabolites and qPCR data.

The second model was used to measure the effect of the starch based control against the average of the coproduct diets. The second model contained fixed effects of treatment, time, and treatment × time. Within this procedure, a single degree of freedom contrast was used to compare control to coproduct diets. The random effect of steer within diet was used for analyzing response variables that were not treated as repeated measures. Binomial data (i.e. USDA Quality Grade) were analyzed using the GENMOD procedure of SAS (SAS Institute, Cary, NC). Statistical differences were declared significant at $P \leq 0.05$ and trends were considered present at $0.05 < \alpha < 0.10$..

RESULTS

Gene Markers for Adipogenesis

A protein × fat × time interaction ($P < 0.01$) occurred for the expression of peroxisome proliferator-activated receptor gamma (PPARG; Figure 4.1A). At d 112, expression of PPARG in LM from steers was not different ($P \geq 0.96$); however, at d 224, expression increased ($P < 0.01$) by 5.36 fold compared to d 112. Within high protein diets, expression in the LM of steers fed low fat diets was 4.63 fold greater ($P < 0.01$) than in that of steers fed high fat diets. Expression of PPARG was not different ($P \geq 0.99$) in steers fed low protein diets with either high or low fat inclusion. Expression of PPARG in coproduct diets was not different ($P = 0.73$) from control. A fat × day interaction ($P < 0.01$) occurred for the expression of CCAAT/enhancer binding protein alpha (CEBPA; Figure 4.1B). Expression of CEBPA was similar ($P = 0.99$) at d 112; however, at d 224 steers fed low fat diets during the growing phase exhibited increased ($P < 0.01$) expression of CEBPA by 2.82 fold over steers fed high fat diets. Expression of CEBPA in coproduct diets was not different ($P = 0.90$) from control.

There was a protein × fat × time interaction ($P < 0.01$) for the expression of insulin induced gene 1 (INSIG1; Figure 4.1C). At d 112, INSIG1 expression in the LM from steers were not different ($P = 0.41$) at d 112; however, at d 224, within high protein diets, expression increased ($P = 0.02$) by 5.36 fold in response to feeding low concentrations of dietary fat. The combination of high protein and low fat produced INSIG1 expression that was 5.11 fold greater than expression in steers fed diets that were fed combinations of high protein and fat. Expression of INSIG1 in steers fed coproduct diets was not different ($P = 0.98$) from steers fed control.

A protein × fat × time interaction ($P < 0.01$) was observed for the expression of sterol regulatory element binding transcription factor 1 (SREBF1; Figure 4.1D). Within steers fed high protein diets, expression of SREBF1increased ($P < 0.01$) by 1.80 fold at d 112 in high fat diets compared to low fat diets; however, by d 224 expression of SREBF1 in cattle fed high protein diets was not different ($P = 0.16$) among fat levels. Within steers fed low protein diets, expression of SREBF1 was not different ($P = 0.67$) at d 112 regardless of fat level, but by d 224, steers that consumed diets low in fat during the growing phase increased ($P = 0.02$) expression of SREBF1 by 0.86 fold over steers fed high fat deits before d 112. Feeding coproduct diets during the growing phase increased ($P < 0.01$) expression of SREBF1 (Figure 4.1D) compared to feeding control. Expression of SREBF1 in the muscle of coproduct-fed steers was increased by 1.11 and 1.47 fold compared to control-fed steers at d 112 and 224, respectively (Figure 4.2).

There was a protein × fat × day interaction ($P < 0.01$) for the expression of thyroid hormone responsive SPOT14 protein (THRSP; Figure 4.1E). Within cattle fed high protein diets, expression was not different at d 112 ($P = 0.17$), but by d 224, feeding coporoduct diets low in fat during the growing phase had increased ($P < 0.01$) expression of THRSP by 19.80 fold compared to diets with high levels of fat. Expression of THRSP was not different ($P \geq 0.99$) in

steers fed low protein diets with either high or low fat inclusion. Expression of THRSP in coproduct diets was not different ($P = 0.87$) from control.

There was a protein × fat × day interaction ($P < 0.01$) for the expression of ATP citrate lyase (ACLY; Figure 4.3A). There were no differences ($P \geq 0.12$) in expression of ACLY at d 112, but at d 224, within low protein diets, steers fed high fat had increased ($P = 0.01$) expression of ACLY by 2.27 fold compared to steers fed diets low in fat. Conversely, within high protein diets, steers fed diets low in fat during the growing phase, increased ($P < 0.01$) expression of ACLY by 4.71 fold compared to steers fed diets high in protein and fat. Expression of ACLY in coproduct diets was not different ($P = 0.59$) from control.

There was a protein × fat × day interaction ($P < 0.01$) for the expression of diacylglycerol O-acyltransferase homologue 2 (DGAT2; Figure 4.3B). Expression of DGAT2 was not different ($P \geq 0.97$) at d 112; however, within high protein diets, steers fed low fat during the growing phase increased ($P < 0.01$) expression of DGAT2 10.98 fold at d 224 compared to expression in muscle from steers fed growing phase diets containing high fat. Expression of DGAT2 was not different ($P \geq 0.83$) in steers fed low protein diets with either high or low fat inclusion. Expression of DGAT2 in coproduct diets was not different ($P = 0.14$) from control.

A protein × fat × day interaction ($P < 0.01$) was observed for expression of fatty acid binding protein 4 (FABP4; Figure 4.3C). Expression of FABP4 was not different ($P \geq 0.43$) at d 112; however, within steers fed high protein diets, low fat fed during the growing phase increased ($P < 0.01$) expression of FABP4 by 2.10 fold at d 224 compared to steers fed high fat. Expression of FABP4 was not different ($P \geq 0.99$) in steers fed low protein diets with either high or low fat inclusion. Expression of FABP4 in coproduct diets was not different ($P = 0.76$) from control.

There was a protein × fat × day interaction ($P < 0.01$) for the expression of fatty acid synthase (FASN; Figure 4.3D). Expression of FASN was not different ($P = 0.40$) at d 112, but at d 224, witin steers fed high protein, FASN expression increased ($P < 0.01$) by 5.11 fold in steers fed low fat compared to steers fed high fat during the growing phase. Expression of FASN was not different ($P \geq 0.99$) in steers fed low protein diets with either high or low fat inclusion. Expression of FASN in coproduct diets was not different ($P = 0.43$) from control.

There was a protein × fat × day interaction ($P < 0.01$) for the expression of phosphoenolpyruvate carboxykinase 1 (PCK1; Figure 4.3E). Expression of PCK1 was not different ($P \geq 0.98$) at d 112, but at d 224, within steers fed high protein, PCK1 expression increased ($P < 0.01$) in steers fed low fat by 56.14 fold over steers fed high fat during the growing phase. Expression of PCK1 was not different ($P \geq 0.99$) in steers fed low protein diets with either high or low fat inclusion. Expression of PCK1 in coproduct diets was not different ($P = 0.28$) from control.

There was a protein × fat × day interaction ($P < 0.01$) for the expression of stearoyl-CoA desaturase (SCD; Figure 4.3F). Expression of SCD was not different ($P \geq 0.99$) at d 112, but at d 224, within steers fed high protein, SCD expression increased ($P < 0.01$) by 9.48 fold in steers fed low fat compared to steers fed diets containing high fat during the growing phase. Expression of SCD was not different ($P \geq 0.99$) in steers fed low protein diets with either high or low fat inclusion. Expression of SCD in coproduct diets was not different ($P = 0.16$) from control.

There was a protein × fat × day interaction ($P < 0.01$) for the expression of adiponectin (ADIPOQ; Figure 4.4A). Expression of ADIPOQ was not different ($P \geq 0.21$) at d 112, but at d 224, ADIPOQ expression increased within high protein ($P < 0.01$) by 7.45 fold in steers fed

diets low in fat compared to steers fed diets high in both protein and fat during the growing phase. Expression of ADIPOQ was not different ($P \geq 0.96$) in steers fed low protein diets with either high or low fat inclusion. Expression of ADIPOQ in coproduct diets was not different ($P = 0.13$) from control.

A fat × day interaction ($P < 0.01$) was detected for the expression of adiponectin receptor 2 (ADIPOR2; Figure 4B). At d 112, expression of ADIPOR2 in steers fed high or low fat diets was not different ($P = 0.25$); however, by d 224 ADIPOR2 expression in the muscle of steers fed low fat diets during the growing phase was 0.74 fold ($P = 0.02$) greater than that of steers fed high fat diets during the growing phase. Expression of ADIPOR2 was not different ($P \geq 0.33$) in steers fed differing levels of protein. Expression of ADIPOR2 in coproduct diets was not different ($P = 0.66$) from control.

There was a protein × fat × day interaction ($P < 0.01$) for the expression of leptin (LEP; Figure 4.4C). Expression of LEP was not different ($P \geq 0.99$) at d 112, but at d 224, within steers fed high protein diets LEP expression increased ($P < 0.01$) by 42.36 fold in steers fed diets low in fat over steers fed diets high in fat during the growing phase. Expression of LEP was not different ($P \geq 0.99$) in steers fed low protein diets with either high or low fat inclusion. Expression of LEP in coproduct diets was not different ($P = 0.19$) from control.

Blood Metabolites and Hormones

There was a protein × fat × day interaction (P = 0.007) where serum leptin concentration was increased ($P < 0.01$) at d 224 by 4.45 ng/mL in steers fed high protein diets that were low in fat compared to calves fed high protein diets that were high in fat during the growing phase (Figure 4.5). Serum leptin concentrations were not different ($P \geq 0.48$) in low protein diets

containing high or low levels of fat. Leptin concentration in steers fed control were not different ($P = 0.86$) compared to steers fed coproducts. Serum concentrations of IgF1 were lowest ($P < 0.01$) at d 0, highest ($P < 0.01$) at d 112 and intermediate ($P < 0.01$) at d 224 (Table 4.3). A protein × fat interaction was observed for IgF1which illustrated that steers fed high protein diets that were high in fat had decreased ($P = 0.03$) serum concentrations of IgF1 compared to steers fed diets high in protein and low in fat, or steers fed diets low in protein with either high or low levels of fat inclusion. Dietary treatment did not affect ($P \geq 0.45$) serum growth hormone concentrations (Table 4.3).

Carcass Characteristics

Carcass measurements indicated no difference ($P \geq 0.16$) in HCW, LM area, back fat thickness, KPH, or yield grade (Table 4.4). However, marbling score tended ($P = 0.09$) to be higher in carcasses from steers fed control during the growing phase compared to steers fed coproduct diets. Carcasses from control-fed steers achieved marbling scores of 550 (Modest[50]) while steers fed coproduct diets produced carcasses with an average marbling score of 480 (Small[80]). This tendency was not sufficient to affect ($P \geq 0.13$) USDA quality grade distributions.

DISCUSSION

Segers et al. (2012) reported that cattle fed high fat coproduct diets during a 112 d growing phase after early-weaning, increased final MS by one third of a score and subsequently increased the percentage of carcasses grading Choice^{+} or better compared to cattle fed low fat diets. Results also indicated that high fat coproducts fed during the growing phase may increase marbling development similar to starch (Segers et al., 2012). Increasing the concentration of

lipids in the rumen has been shown to decrease the acetate: propionate ratio in the rumen similar to starch (Ikwuegbu and Sutton, 1982; Chalupa et al. 1984; Czerkawski and Clapperton, 1984; Boggs et al., 1987; Jenkins, 1993).

Our hypothesis was that increased intake of protein and fatty acids from corn coproducts would up-regulate adipogenesis in the muscle similar to starch because it is well established that fiber alone as an energy source is insufficient to increase intramuscular fat deposition (Schoonmaker et al., 2004b; Arthington et al., 2005). This increase in intramuscular fat deposition was expected to occur by two mechanisms, first, by increasing ruminal propionate and subsequent blood glucose concentration, and second, by increasing PPARγ activation via fatty acids. Increased blood glucose concentration provides the appropriate carbon substrate for intramuscular lipogenesis (Smith and Crouse, 1984). Also increased blood glucose signals the release of insulin which is a known activator of PPARγ, SREBF1, INSIG1, FASN, and SCD (Fernyhough et al., 2007). Additionally, long-chain fatty acids act as natural ligands and have the ability to activate PPARγ (Chinetti et al., 2000; Rosen and Spiegelman, 2001; Farmer, 2005; Lehrke and Lazar, 2005). Polyunsaturated fatty acids, such as those found in corn coproducts, have lower binding affinity to PPARγ than saturated fatty acids in monogastrics(Rosen and Spiegelman, 2001) while saturated fatty acids are more potent inducers of PPARγ in ruminants (Bionaz et al., 2013); therefore, these compounds are more effective activators of preadipocyte differentiation (Fernyhough et al., 2007) which was our goal. Results indicated that within low protein diets, fat level during the growing phase had no effect on PPARG, INSIG1, THRSP, ADIPOQ, DGAT2, FABP4, FASN, PCK1, or SCD expression; however in muscle from steers fed high protein diets with low levels of dietary fat prior to d 112, expression of the aforementioned genes increased dramatically after steers were transitioned to a common diet.

The mechanism for ths observation is unclear, but it is possible that cattle consuming high protein and low fat in combination where hypersensitized to insulin, so that when cattle were adapted to a common diet, insulin induced genes were heavily expressed. However, there may have been a regulatory process that impeded expression of these genes post-transcriptionally.

It is possible that starch restriction prior to 112 d induced a compensatory response in adipocyte differentiation after cattle were transitioned to a common starch-based diet; however, it is unclear why these effects were restricted only to steers fed high protein, low fat diets during the growing phase. Studies conducted in rat models (Webster, 1993) have revealed that animals consume feed to maintain lean body gain. When animals consume diets which contain relatively more energy than amino acids, they will increase intake until their amino acid requirements are met. Dry matter intake data for the calves in this study were reported by Segers et al. (2012), and revealed increased DMI in cattle fed coproducts compared to those fed control. Protein from coproducts behaves differently in the rumen dependent on the coproduct being used. Corn gluten feed (DIP = 75%; UIP = 25%; NRC, 1996) is highly fermentable and can be readily digested in the rumen (Abe and Horii, 1978; Fleck et al., 1985; Wagner et al., 1983), whereas the protein component of distillers grains plus solubles (DIP = 27%; UIP = 73%; NRC, 1996) is partially protected from rumen degradation (Klopfenstein et al., 1978, 2007; Little et al., 1968; Aines et al., 1987). It is possible that steer calves, in the current experiment, fed coproducts met or exceeded amino acid requirements before they met energy requirements resulting in increased intake similar to the aforementioned rat models reported by Webster (1993). This is of interest because data from Oddy et al. (2000) revealed a statistical trend that suggested increased protein: energy ratio fed to cattle and sheep in the feedlot may decrease intramuscular fat deposition. In our experiment, we created a similar scenario wherein cattle received high protein and low fat

(energy); however, we also provided an opportunity for compensatory adipogenesis by transitioning to a high starch diet for the final 112 d before slaughter.

It is also possible that the similar carryover effects observed in the aforementioned genes may indicate a form of metabolic imprinting by the combination of high protein and low fat during the growing phase. Metabolic imprinting has been demonstrated in rat models where pups were fed isocaloric diets that were either high fat (rat milk) or high carbohydrate (milk replacer;Srinivasan and Patel, 2008). Results from these studies indicated that sustained hyperinsulinemia due to high carbohydrate diets caused lasting negative effects on the neuroendocrine system that regulate metabolism resulting in chronic hyperinsulinemia and early adult-onset obesity (Srinivasan and Patel, 2008). Sudden up-regulation of PPARG, INSIG1, THRSP, ACLY, ADIPOQ, DGAT2, FABP4, FASN, PCK1, and SCD after d 112 suggests that that steers fed a combination of high protein and low fat were metabolically programmed possibly through insulin sensitization to increase adipogenic and lipogenic activity when exposed to a high starch diet.

Another carryover effect was observed for the expression of CEBPA. Although expression was not different during the growing phase, steers fed low fat diets before d 112 experienced an increase in expression of CEBPA after d 112 compared to steers fed low fat diets. Expression of CEBPA occurs late in the adipogenesis in culture (Wu et al., 1999). Therefore, expression of CEBPA occurs after PPARG, but before most other proteins that typify fully differentiated adipocytes (Wu et al., 1999). Expression of CEBPA allows adipocytes to store larger lipid droplets and as a result increase in size (Wu et al., 1999). However, the most notable function of CEBPα is to serve as part of a positive feedback loop with PPARγ (Wu et al., 1999). This means that although CEBPA expression is induced by PPARγ, its expression is necessary to

maintain active levels of PPARγ in differentiated adipocytes. These data indicate that expression patterns for CEBPA and PPARG should be similar; however, in the current study this was only partially true. Expression of CEBPA increased between d 0 and d 112 similar to PPARG; however, between d 112 and d 224 expression of CEBPA increased in response to low levels of dietary fat independent of protein level.

Although expression was not different during the growing phase, steers fed low fat diets before d 112 experienced an increase in expression of ADIPOR2 after d 112 compared to steers fed low fat diets. Adiponectin is an insulin-regulated hormone secreted by adipocytes that mediates energy homeostasis and increases insulin sensitivity (Sun et al., 2009). The effect on lipid metabolism is mediated by the Adiponectin Receptor 2 in the liver. Sun et al. (2009) reported a decrease in ADIPOR2 expression in cultured bovine adipocytes by way of the phosphoinositol-3-kinase pathway. Reduced expression of ADIPOR2 impairs fatty acid oxidation. Our results clearly illustrate (Figure 4B) that the fat × day interaction observed at d 224 for the expression of ADIPOR2 is being driven by the low expression of ADIPOR2 at d 224 in muscle of steers fed high fat, low protein diets during the growing phase. The opposite nutrient combination (high protein, low fat) was responsible for the spike in expression of PPARG, INSIG1, THRSP, ADIPOQ, DGAT2, FABP4, FASN, PCK1, and SCD. Increased starch consumption during the feeding phase likely caused an increase in insulin which inhibited expression of ADIPOR2.

Expression of SREBF1 was affected by diet during the growing phase. Within high protein diets, low fat levels decreased expression of SREBF1 at d 112 compared to diets high in protein and in fat; however, by d 224 expression of SREBF1 was similar among treatments. In cell cultures, SREBF1 is expressed very early (d 1) in the adipogenic process (Kim and

Spiegelman, 1996). . It is unclear why SREBF1 expression decreased in the muscle of steer calves fed high protein, low fat diets while other adipogenic gene expression either increased or was not different during the growing phase; however, SREBF1 expression did increase between d 112 and 224 similar to expression patterns observed in other genes.

As expected, serum leptin concentrations increased over time, with a similar protein × fat × day interaction to LEP expression in the muscle. Steers that were fed growing diets high in protein but low in fat exhibited increased serum leptin concentrations at d 224. Leptin is produced in the adipose tissue and plays a regulatory role in body homeostasis; energy intake, storage, and expenditure; fertility; and immune function (Chilliard et al., 2005). Leptin decreases insulin and glucocorticoid, and stimulates growth hormone, catecholamine, and thyroid hormone production (Chilliard et al, 2005). These mechanisms allow leptin to stimulate lipolysis, inhibit lipogenesis, increase insulin sensitivity and glucose utilization, and increase fatty acid oxidation in the liver and muscle (Chilliard et al., 2005). Results for serum leptin concentration in the current study mirror those of LEP expression which is likely a function of increased adipogenesis in cattle fed starch following a growing phase diet with high levels of dietary protein and low levels of fat.

There were no differences in HCW, LM area, back fat thickness, KPH, yield grade, and USDA quality grade. However, marbling score tended to be higher in carcasses from steers fed control during the growing phase. Carcasses from control-fed steers achieved marbling scores of 550 (Modest^{50}) while steers fed coproduct diets produced carcasses with an average marbling score of 480 (Small^{80}). However, this was a small subset of 30 animals. In the larger study from which these steers were selected, high fat coproduct diets increased final MS by one third of a

score and consequently increased the percentage of carcasses grading Choice^{+} or better (Segers et al., 2012).

Segers et al (2012) reported mean marbling score of carcasses from cattle fed high fat coproduct blends during the growing phase was 511 (Modest^{11}) while mean marbling score of carcasses from cattle fed low fat coproduct blends was 478 (Small^{78}). Mean MS of carcasses from cattle fed control during the growing phase was 508 (Modest^{08}), and though not different from cattle fed coproducts, these results suggest that high fat coproducts fed during the growing phase increase marbling development similar to starch.

In the current study, a combination of high protein and low fat fed during the growing phase increased the expression of several genes associated with adipogenesis and lipid metabolism in the *longissimus lumborum* muscle of steers during the feedlot phase. This up-regulation of these genes, however, was not sufficient to cause a phenotypic change in the carcass. In fact, data from the larger study (Segers et al., 2012) suggests that feeding high fat rather than low fat during the growing phase may be a more effective mechanism to increase intramuscular adipogenesis.

CONCLUSIONS AND IMPLICATIONS

The combination of increased dietary protein and decreased dietary fat induces an increase in the expression of PPARG, INSIG1, THRSP, ACLY, ADIPOQ, DGAT2, FABP4, FASN, PCK1, and SCD as well as serum leptin concentrations. The mechanism responsible for this interaction warrants further investigation. This research provides insight into the effects of elevated protein and fat from corn coproducts on the molecular regulation of intramuscular fat development. These data indicate that feeding differing levels of dietary fat and protein during

the growing phase does affect intramuscular adipogenesis at the transcriptional level, but differences in gene expression were not sufficient to affect carcass quality among cattle fed coproducts.

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Tables and Figures

Table 4.1. Dry matter composition and nutrient analysis of experimental and feedlot diets offered to early-weaned calves fed coproduct blends containing differing levels of fat and protein during the growing phase.

		High Fat		Low Fat		
	Control	High CP	Low CP	High CP	Low CP	Common Diet
Ingredient, % DM						
Corn Husklage	20.0	20.0	20.0	20.0	20.0	20.0
Soybean Hulls	-	30.0	30.0	30.0	30.0	-
Cracked Corn	58.0	-	-	-	-	35.0
Soybean Meal	17.0	6.0	-	11.0	2.0	2.5
DDGS[1]	-	34.0	26.0	13.0	11.0	-
WDGS[2]	-	-	-	-	-	40.0
Corn Gluten Feed	-	5.0	10.0	21.0	32.0	-
Corn Bran	-	-	9.0	-	-	-
Ground Corn	3.04	3.04	3.04	3.04	3.04	3.04
Limestone	1.71	1.71	1.71	1.71	1.71	1.71
Rumensin 80[3]	0.02	0.02	0.02	0.02	0.02	0.02
Tylan 40[4]	0.01	0.01	0.01	0.01	0.01	0.01
Trace Mineral Salt[5]	0.11	0.11	0.11	0.11	0.11	0.11
Copper Sulfate	0.01	0.01	0.01	0.01	0.01	0.01
Vitamin Premix[6]	0.01	0.01	0.01	0.01	0.01	0.01
Liquid Fat	0.08	0.08	0.08	0.08	0.08	0.08
Chemical Composition, % DM						
CP	16.95	19.15	16.37	20.46	18.12	15.99
NDF	21.07	45.75	46.91	45.35	47.84	33.49
ADF	7.77	25.89	25.62	24.95	25.20	12.73
Ether Extract	3.28	4.55	4.79	3.43	3.53	5.17
Ash	4.67	6.64	6.47	6.64	6.50	5.19
Ca	0.97	1.09	1.05	0.70	1.06	0.91
P	0.36	0.54	0.55	0.56	0.59	0.52
NEm, Mcal · kg^{-1}[7]	2.22	1.67	1.67	1.69	1.69	2.04
NEg, Mcal · kg^{-1}[8]	1.52	1.06	1.06	1.07	1.07	1.38

[1]Dried distillers grains with solubles
[2]Wet distillers grains with solubles
[3]Rumensin 176 g/kg (Elanco Animal Health, Greenfield, IN)
[4]Tylosin 88 g/kg (Elanco Animal Health, Greenfield, IN)
[5] Trace Mineral Salt = 80-85% Salt, 2.57% Iron, 2.86% Zinc, 5,710 ppm Manganese, 2,290 ppm Copper, 100 ppm Iodine, 85.7 ppm Selenium
[6]Vitamin A = 3,306,900 IU/kg, vitamin D = 330,690 IU/kg, vitamin E = 2,204.6 mg/kg, vitamin B_{12} = 17.6 mg/kg, Riboflavin
[7]Calculated by Rock River Laboratory (Watertown, WI) based on analyzed ADF value
[8] Calculated by Rock River Laboratory (Watertown, WI) based on analyzed ADF value

Table 4.2. Gene ID, GenBank accession number, hybridization position, sequence and amplicon size of primers for Bos Taurus used to analyze gene expression by qPCR.

Gene ID	Accession #	Gene	Primers[1]	Primers (5'-3')[2]	bp
511135	NM_001037457.1	*ACLY*	F.1724	CCAGAGGTAGACGTG CTAATCAAC	90
		ACLY	R.1813	GGTCCGGATCTGAGCG TAATT	
282865	NM_174742.2	*ADIPOQ*	F.261	GATCCAGGTCTTGTTG GTCCTAA	65
		ADIPOQ	R.325	GAGCGGTATACATAG GCACTTTCT	
407234	NM_001040499.1	*ADIPOR2*	F.25	CATCCACCCTCCCAAG AAGAA	120
		ADIPOR2	R.144	AGCTGGCTCTGGAGTC TTGCT	
281677	NM_176784.2	*CEBPA*[3]		GCAAAGCCAAGAAGT CCG	
		CEBPA		GGCTCAGTTGTTCCAC CCGCTT	
404129	NM_205793.2	*DGAT2*	F.389	CATGTACACATTCTGC ACCGATT	104
		DGAT2	R.492	ACTGTGACCTCCTGCC ACCTT	
281759	DV778074	*FABP4*	F.402	TGGTGCTGGAATGTGT CATGA	102
		FABP4	R.559	TGGAGTTCGATGCAAA CGTC	
281152	CR552737	*FASN*	F.6383	ACCTCGTGAAGGCTGT GACTCA	92
		FASN	R.6474	TGAGTCGAGGCCAAG GTCTGAA	
511899	CX736793	*INSIG1*	F.82	CATCGACAGTCACCTT GGAGA	108
		INSIG1	R.189	TCCAGTTTAGCACTAG CGTGGT	
280836	NM_173928.2	*LEP*	F.2243	CAGGGCACGTCAGCAT CTATT	100
		LEP	R.2342	GTCTGCTGTTATGGTC TTAGGTATTTT	
509768	NM_001025327.2	*MTG1*	F.277	GATCTGAAGGAGCAG CAGAAAATT	110
		MTG1	R.386	GTTGGGATGACCTGCT TGACA	

Table 4.2. continued. Gene ID, GeneBank accession number, bybridization position, sequence and amplicon size of primers for Bos Taurus used to analyze gene expression by qPCR

282855	NM_174737	*PCK1*	F.601	AAGATTGGCATCGAGCTGACA	120
		PCK1	R.720	GTGGAGGCATTGACGAACTC	
281993	Y12420	*PPARG*	F.1356	GAGCCCAAGTTCGAGTTTGC	100
		PPARG	R.1455	GGCGGTCTCCACTGAGAATAAT	
619131	BC108231	*RPS15A*	F.31	GAATGGTGCGCATGAATGTC	101
		RPS15A	R.131	GACTTTGGAGCACGGCCTAA	
280924	BC112700.1	*SCD*	F.974	AAAGAAAAGGGTTCCACGCTAA	80
		SCD	R.1053	GGTTTGTAGTACCTCCTCTGGAACA	
539371	XM_001790600.1	*SREBF1*	F.1638	GTGCTGAGGGCAGAGATGGT	106
		SREBF1	R.1743	ACAAAGAGAAGTGCCAAGGAGAA	
515940	AY656814	*THRSP*	F.266	CCGAGGGAGCTGAGACTGAA	101
		THRSP	R.366	AGCGAAGTGCAGGTGCAACT	
525680	NM_001037471.2	*UXT*	F.300	GGTTGTCGCTGAGCTCTGTG	101
		UXT	R.400	TGTGGCCCTTGGATATGGTT	

[1] Primer direction (F = forward; R = reverse) and hybridization position on the sequence.

[2] Amplicon size in base pair (bp).

[3]Ohsaki, H., T. Sawa, S. Sasazaki, K. Kano, M. Taniguchi, F. Mukai, and H. Mannen. 2007. Stearoyl-CoA desaturase mRNA expression during bovine adipocyte differentiation in primary culture derived from Japanese Black and Holstein cattle. Comp. Biochem. Physiol. A Mol. Integr. Physiol. 148:629–634.

Table 4.3. Blood serum concentrations of insulin-like growth factor 1 (IgF1) and growth hormone (GH) over time (T) at 0, 112 and 224 days post-weaning for early-weaned calves fed coproduct blends containing either high (H) or low (L) levels of fat (F) and protein (P) during the growing phase.

		HF		LF			Contrast	P Value			
	Control	HP	LP	HP	LP	SEM	Control vs. All	P	F	T	P × F
IgF1, ng/mL						15.56	0.75	0.29	0.60	< 0.01	0.03
0	78.91	60.20	93.82	78.49	66.05						
112	170.66	156.73	156.99	160.47	152.96						
224	94.08	88.54	141.08	131.42	115.14						
GH, ng/mL											
0	5.31	14.24	18.59	17.47	18.26	7.18	0.88	0.45	0.88	< 0.01	0.40
112	30.30	16.57	19.31	20.83	24.40						
224	10.50	5.65	14.83	5.23	2.39						

[1]No interactions ($P \geq 0.08$) were observed for serum IgF1 and GH concentrations

Table 4.4. Carcass characteristics for early-weaned calves fed coproduct blends containing differing levels of fat and protein during the growing phase.

		High Fat		Low Fat			Contrast	P value[1]	
Item	Control	High Protein	Low Protein	High Protein	Low Protein	SEM	Control vs. All	Protein	Fat
Carcasses	6	6	6	6	6				
HCW, kg	331	317	344	322	329	15.13	0.88	0.32	0.78
LM area, cm^2	76.48	73.16	76.68	74.18	78.22	2.48	0.74	0.16	0.63
Marbling Score[2]	550	477	502	482	460	35.03	0.09	0.96	0.59
Back Fat, cm	1.33	1.27	1.22	1.29	1.29	0.13	0.37	0.85	0.72
KPH, %	2.27	2.17	2.26	2.26	2.16	0.08	0.37	0.55	0.61
Yield Grade[3]	3.24	3.21	3.21	3.24	3.08	0.19	0.81	0.68	0.82
Quality Grade[4]									
Select, %	0.00	33.33	0.00	33.33	33.33	0.15	0.14	0.13	0.13
$Choice^-$ or better, %	100.00	66.67	100.00	66.67	66.67	0.15	0.14	0.13	0.13
$Choice^0$ or better, %	66.67	50.00	66.67	50.00	33.33	0.20	0.45	1.00	0.41

[1]Protein × Fat interaction was not detected ($P \geq 0.24$; SEM ≤ 1.00) for carcass data

[2] 100=practically devoid, 200=traces, 300=slight, 400=small, 500=modest, 600=moderate, 700=slightly abundant, 800=moderately abundant

[3]Yield Grade = $[2.5 + (2.5 \times \text{in. of BF}) + (0.20 \times \%\text{KPH}) + (0.0038 \times \text{lbs of HCW}) - (0.32 \times \text{REA in in.}^2)]$

[4]Values reflect the percentage of carcass achieving the indicated grade or higher

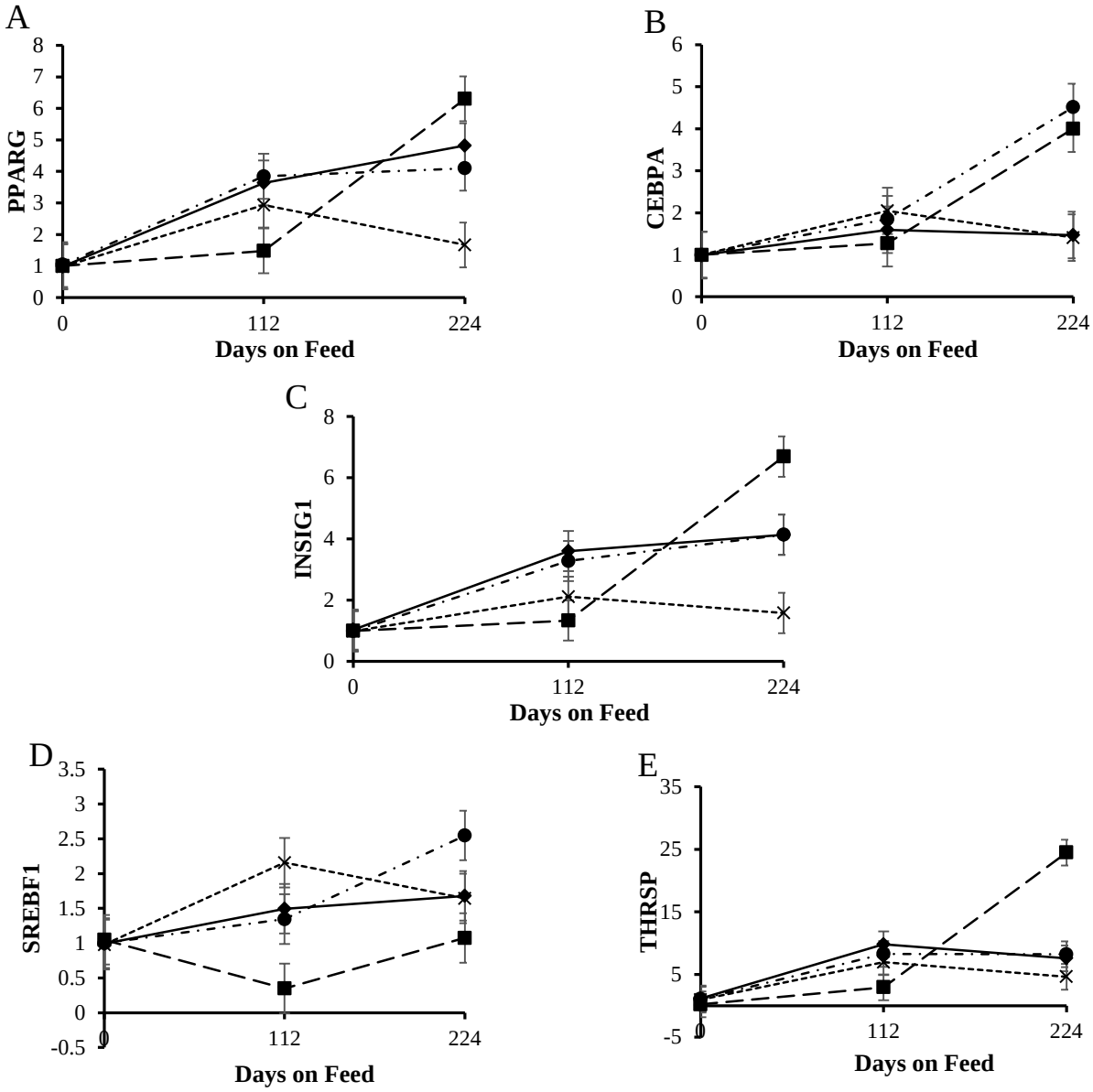

Figure 4.1. Patterns of mRNA expression of transcription regulators in longissimus lumborum tissue from crossbred steers (6 animals/treatment) fed a starch-based control (not shown) or one of four coproduct diets with two levels of dietary fat and protein: high fat-low protein (HFLP; ♦); high fat-high protein (HFHP; ×); low fat-low protein (LFLP;●); low fat-high protein (LFHP; ■) for 112d then fed a common feedlot diet until d 224. A) peroxisome proliferator activated receptor λ (PPARG) Protein × Fat × Day ($P < 0.01$); B) CCAAT/enhancer binding protein, alpha (CEBPA) Fat × Day ($P < 0.01$); C) insulin-induced gene 1 (INSIG1) Protein × Fat × Day ($P < 0.01$); D) sterol regulatory element-binding transcription factor 1 (SREBF1) Protein × Fat × Day ($P < 0.01$); E) thyroid hormone responsive SPOT14 protein(THRSP) Protein × Fat × Day ($P < 0.01$). Values are means, with standard errors represented by vertical bars.

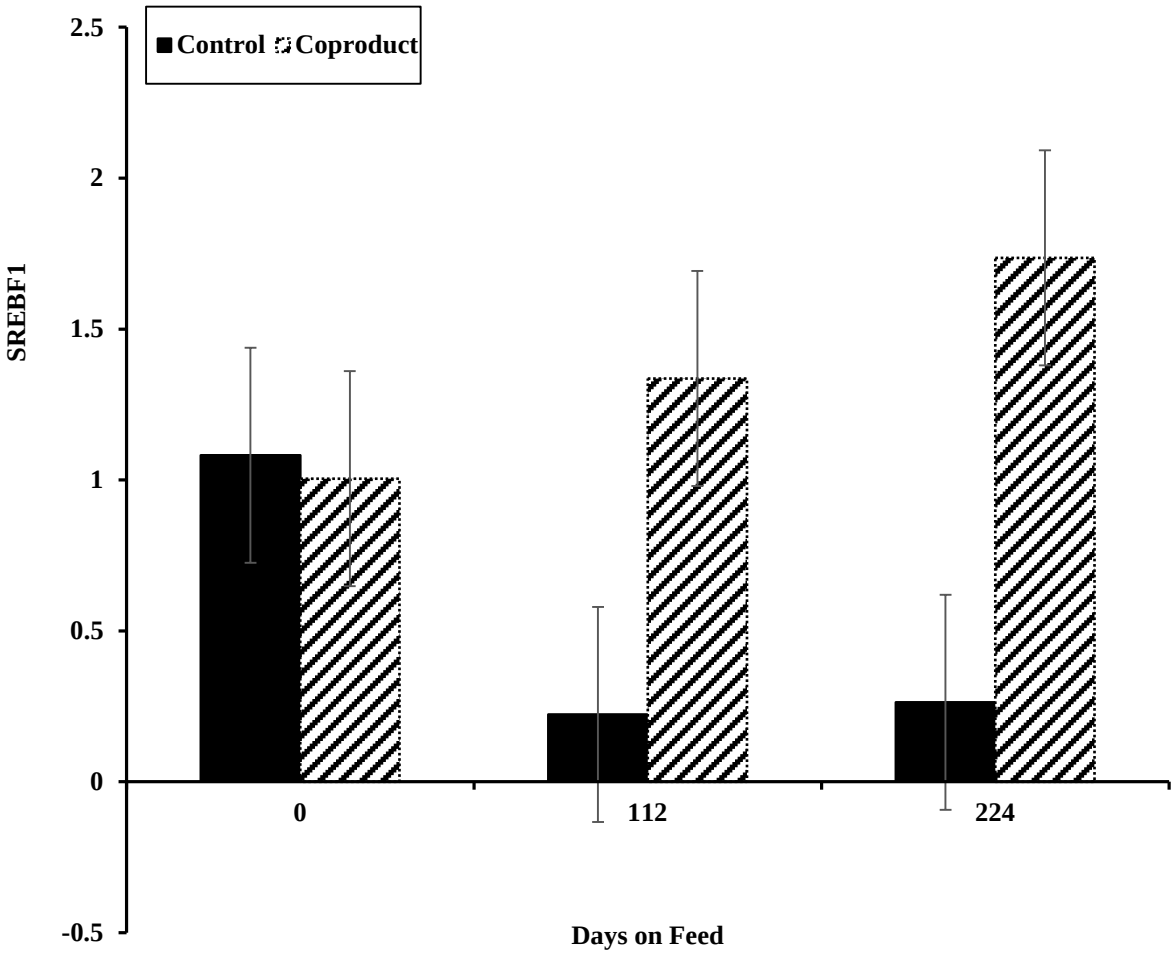

Figure 4.2. Patterns of mRNA expression of sterol regulatory element-binding transcription factor 1 (SREBF1) in longissimus lumborum tissue from crossbred steers (6 animals/treatment) fed a high-starch control or one of four coproduct diets. Single degree of freedom contrasts revealed differences over time: Control vs Coproduct at d 0 ($P = 0.83$); Control vs Coproduct at d 112 ($P < 0.01$); Control vs Coproduct at d 224 ($P < 0.01$). Values are means, with standard errors represented by vertical bars.

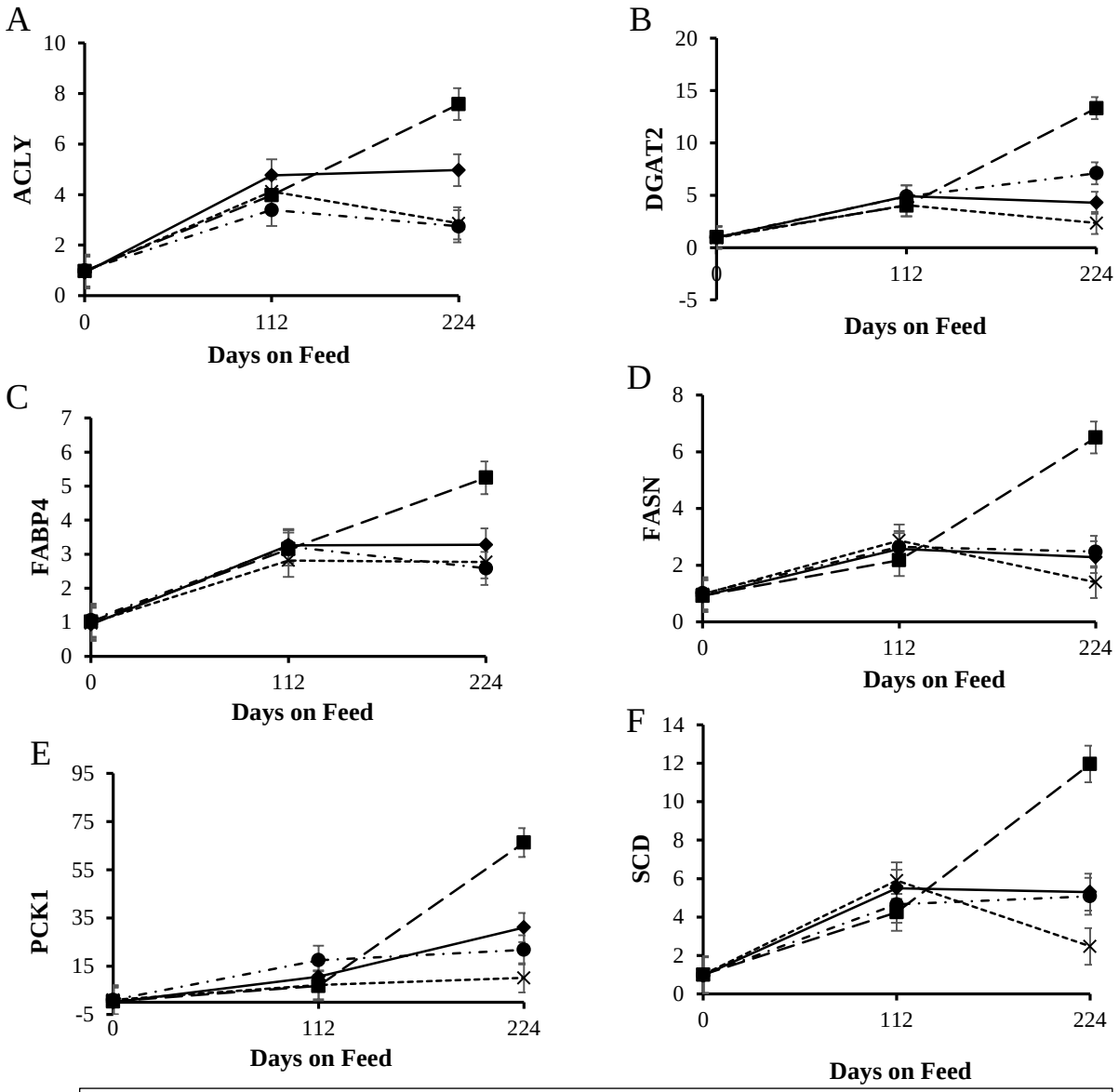

Figure 4.3. Patterns of mRNA expression of lipogenic enzymes in longissimus lumborum tissue from crossbred steers (6 animals/treatment) fed a starch-based control (not shown) or one of four coproduct diets with two levels of dietary fat and protein: high fat-low protein (HFLP; ♦); high fat-high protein (HFHP; ×); low fat-low protein (LFLP;●); low fat-high protein (LFHP; ■) for 112 d then fed a common feedlot diet until d 224. A) ATP Citrate Lyase (ACLY) Protein × Fat × Day ($P < 0.01$); B) Diacylglycerol O-acyltransferase homologue 2 (mouse) (DGAT2) Protein × Fat × Day ($P < 0.01$); C) Fatty Acid-Binding Protein 4 (FABP4) Protein × Fat × Day ($P < 0.01$); D) Fatty Acid Synthase (FASN) Protein × Fat × Day ($P < 0.01$); E) Phosphoenolpyruvate carboxykinase 1 (PCK1) Protein × Fat × Day ($P < 0.01$); F) Stearoyl-CoA-desaturase (SCD) Protein × Fat × Day ($P < 0.01$). Values are means, with standard errors represented by vertical bars.

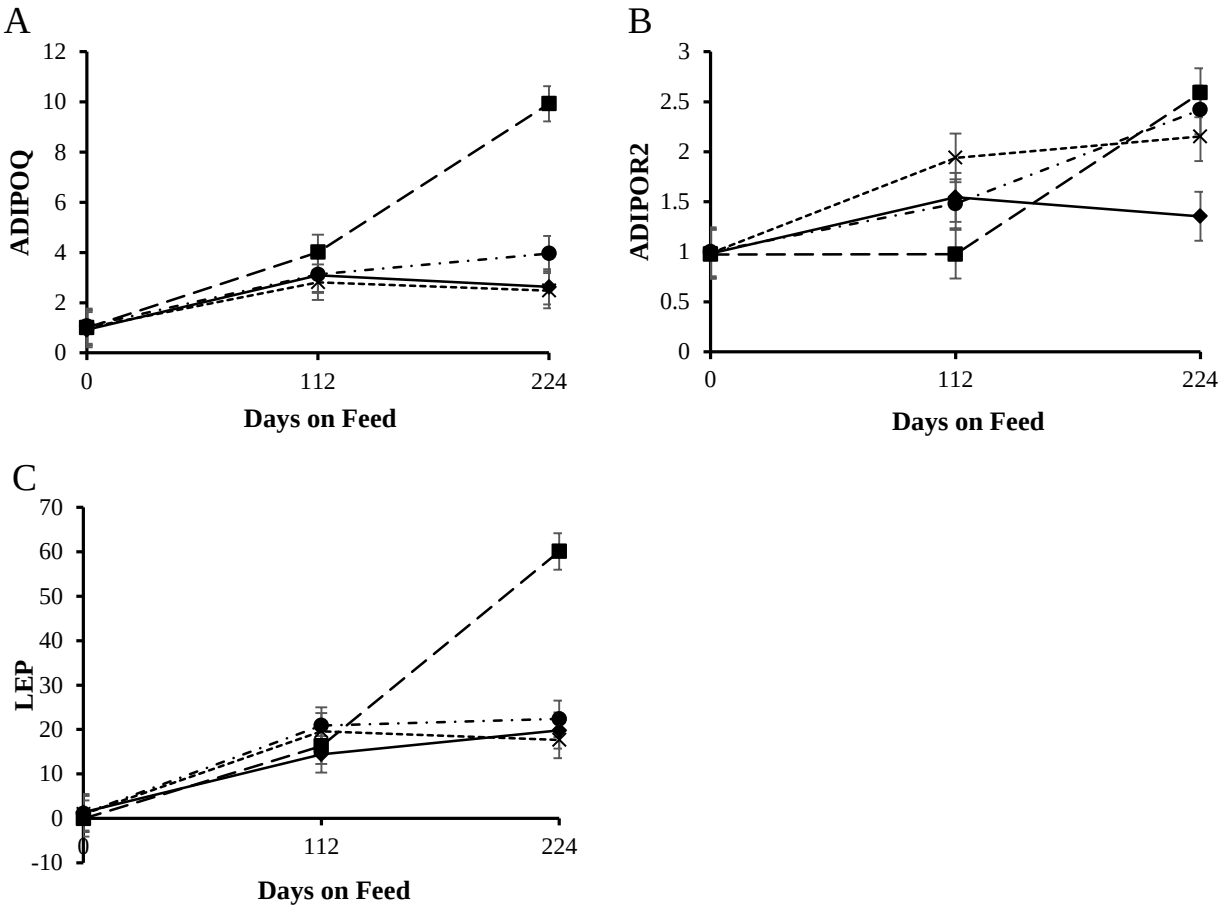

Figure 4.4. Patterns of mRNA expression of adipokines in longissimus lumborum tissue from crossbred steers (6 animals/treatment) fed a starch-based control (not shown) or one of four coproduct diets with two levels of dietary fat and protein: high fat-low protein (HFLP; ♦); high fat-high protein (HFHP; ×); low fat-low protein (LFLP;●); low fat-high protein (LFHP; ■) for 112d then fed a common feedlot diet until d 224. A) Adiponectin (ADIPOQ) Protein × Fat × Day ($P < 0.01$); B) Adiponectin Receptor 2 (ADIPOR2) Fat × Day ($P < 0.01$); C) Leptin (LEP) Protein × Fat × Day ($P < 0.01$). Values are means, with standard errors represented by vertical bars.

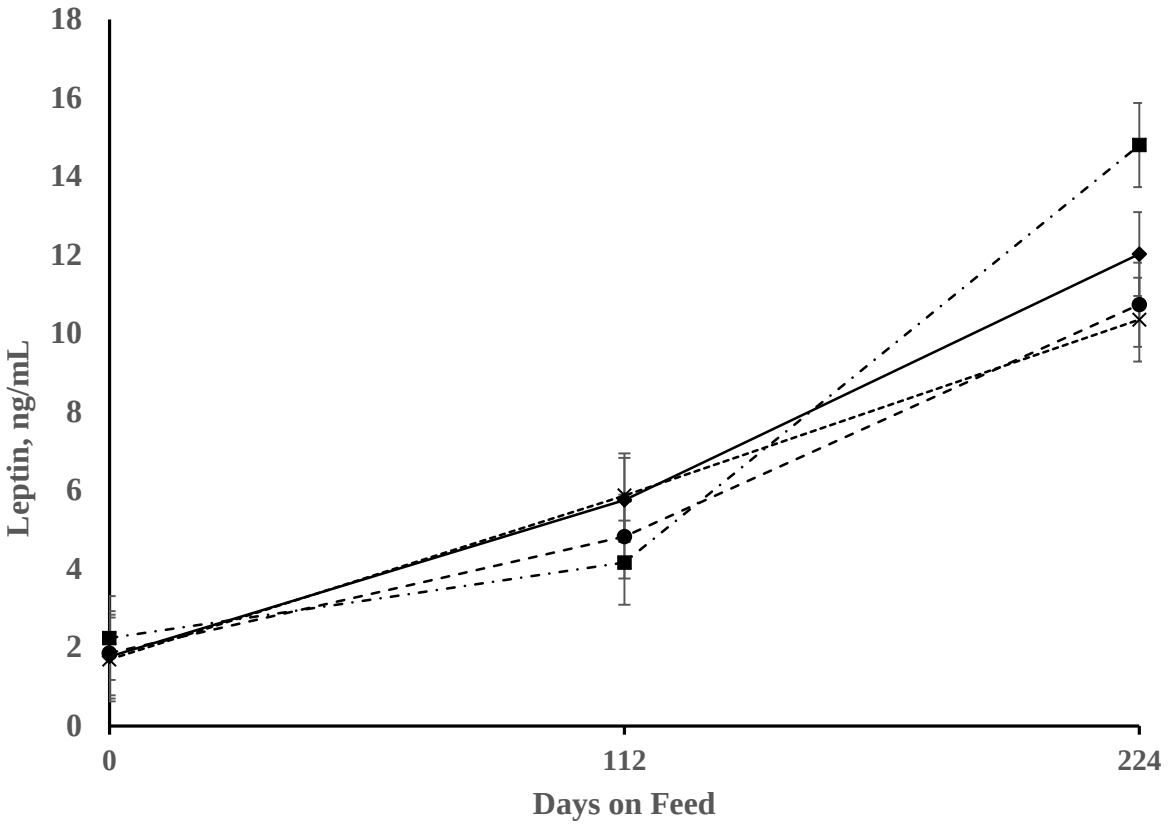

Figure 4.5. Blood serum concentrations of Leptin in crossbred steers (6 animals/treatment) fed a high-starch control (not shown) or four coproduct diets with two levels of dietary fat and protein: high fat-low protein (HFLP; ♦); high fat-high protein (HFHP; ×); low fat-low protein (LFLP; ●); low fat-high protein (LFHP; ■) for 112d then fed a common feedlot diet until d 224. Values are means with standard errors represented by vertical bars. Serum leptin concentration in steers fed control was not different (P = 0.86) from steers fed coproducts. Serum leptin concentration increased (P < 0.01) over time. There was a Protein × Fat × Day interaction (P = 0.007) where serum leptin concentration was increased at d 224 in calves fed LFHP vs calves fed HFHP.

CHAPTER 5

EFFECT OF DIETARY FAT CONCENTRATION FROM CONDENSED CORN DISTILLERS SOLUBLES, DURING THE GROWING PHASE, ON BEEF CATTLE PERFORMANCE, CARCASS TRAITS, DIGESTIBILITY, RUMINAL METABOLISM AND METHANE PRODUCTION

ABSTRACT

The objective of this research was to study the effect of fat concentration from corn coproducts, fed during the growing phase, on DMI, gain, carcass traits, digestibility, ruminal metabolism, and methane emissions of steers. *Exp. 1*: 40 steers (age = 136 ± 20 d; BW = 185 ± 11 kg) were randomly allotted to 1 of 5 dietary treatments: 1) corn-based control (CNT), 2) 0% corn distillers solubles (CDS), 3) 10% CDS, 4) 19% CDS, or 5) 27% CDS. Diets 2 through 5 included coproducts (corn gluten feed and soybean hulls) and were formulated to achieve fat concentrations of 3, 5, 7, and 9%, respectively. Diets were fed once daily for 106 d (growing phase, GP). All steers were fed a corn-based diet from d107 to 196 (finishing phase, FP). Contrasts were used to examine a) the difference between CNT and 10% CDS; b) linear and quadratic effects of CDS inclusion. During the GP, steers fed CNT had increased ($P = 0.01$) ADG and G:F compared to those fed 10% CDS. Increasing CDS inclusion increased (linear; $P = 0.01$) ADG and G:F. At the conclusion of the GP, back fat thickness (BF) determined via ultrasound was greater ($P = 0.05$) in CNT-fed calves compared to 10% CDS. There were no treatment differences ($P \geq 0.13$) in FP ADG, DMI, or G:F. Steers fed CNT had increased ($P =$

0.01) overall ADG compared to steers fed 10% CDS, and increasing CDS inclusion increased (linear; $P = 0.05$) overall ADG. Ooverall DMI and G:F were not different ($P \geq 0.11$). Carcass ultrasound revealed an increase ($P = 0.05$) in predicted marbling score as CDS inclusion increased in the growing diet. There were no effects ($P \geq 0.10$) of treatment on carcass traits. *Exp. 2*: steers (n = 5; BW = 335 ± 46 kg) were fed Exp.1 diets for ad libitum intakes in a 5x5 Latin square design. Apparent dry matter digestibility (DMD) increased (linear; $P = 0.02$) with increasing dietary CDS inclusion. Steers fed CNT increased ($P = 0.01$) DMD compared to those fed 10% CDS. Fat digestibility increased (linear; $P < 0.01$) in steers with increasing CDS, but NDF and ADF digestibility was not affected ($P \geq 0.17$) by treatment. Similarly, ruminal pH and VFA concentrations were not affected ($P \geq 0.13$). Also, there was no difference ($P \geq 0.37$) in ruminal methane emissions. Feeding a coproduct diet with 10% CDS during the GP decreased overall ADG compared to feeding corn, but increase predicted marbling score as predicted by ultrasound. Also, increasing CDS inclusion improved DM and fat digestibility as well as overall ADG.

Key Words: beef calves, dietary fat, rumen metabolism, methane production.

INTRODUCTION

Recently, it has been found that early-weaned calves fed growing diets that include distillers grains and other coproducts produce carcasses with similar marbling scores to those fed starch-based diets (Retallick et al., 2010; Meteer et al., 2011; Segers et al., 2012). It is possible that increased dietary fat in some coproducts may be sufficient to improve marbling score and subsequent USDA quality grade (Segers et al., 2012). The ability of dietary fat to shift ruminal fermentation toward propionate production is a possible mechanism that may help explain the similar marbling scores observed in carcasses from calves fed coproducts and those fed starch-based diets during the growing phase (Chalupa et al., 1986; Retallick et al., 2010; Meteer et al., 2011; Segers et al., 2012). Increased molar proportions of propionate are also a possible mechanism for the reduction of methane emissions from cattle. Russell and Gahr (2000) explained that increased methane production is a result of increased ruminal propionate production. Cattle that consume low to medium quality forages have been shown to produce more acetate and subsequently methane than cattle consuming grain or high quality forages (Johnson and Johnson 1995). Additionally, stocker and feedlot operations in the beef industry are responsible for 19% of the methane emissions from beef and dairy cattle in the United States (EPA, 2011). With the growing interest in environmental sustainability, it is important to understand the effect of these diets on ruminal methane production.

Condensed distillers solubles (CDS) are a liquid coproduct from the ethanol industry. Lardy (2007) reported fat concentrations in CDS ranging from 9 to 15%, but fat concentrations can exceed 18%, dependent upon source (Pesta et al., 2012). The increased availability of CDS in the Midwest makes this ingredient a useful option for inclusion in a variety of cattle feeding strategies such as the development of early-weaned calves. It is, therefore, important to

understand the effect of this ingredient in the rumen as well as how it impacts compositional development and subsequent carcass characteristicsTherefore, the objectives of these experiments are to evaluate performance, carcass traits, ruminal characteristics, nutrient digestibility, and ruminal methane production associated with feeding either corn-based diets or increasing levels of CDS.

MATERIALS AND METHODS

Experiment 1

Animal and Diet Management

Forty crossbred steers (BW = 185 ± 11 kg) were weaned (age = 136 ± 20) at the University of Illinois Beef Cattle Field Research Laboratory in Urbana, IL. Calves were managed according to the guidelines recommended in the Guide for the Care and Use of Agricultural Animals in Agricultural Research and Teaching (FASS, 2010). All experimental procedures were approved by the University of Illinois Institutional Animal Care and Use Committee.

Calves were castrated 21 d prior to weaning. At castration, calves were given penicillin (Pen Ject; Bimeda, Inc., Irwindale, CA) and vaccinated for Clostridial diseases (i.e. *Cl. chauvoie, Cl. septicum, Cl. haemolyticum, C.l novyi Type B, Cl. tetani, Cl. perfreingens types C,* and *D*) using Covexin 8 (Schering-Plough Animal Health Corp., Omaha, NE) and bovine pneumonia (*Mannheimia (pasturella) haemolytica type A1*) using One Shot Ultra®7 (Pfizer Inc., Kalamazoo, MI). Calves were also vaccinated for infectious bovine rhinotracheitis, bovine viral diarrhea Types 1 and 2, parainfluenza-3, and bovine respiratory syncytial virus using Bovi-Shield Gold® Finishing Phase® 5 L5 HB (Pfizer Inc., New York, NY). Finally, calves were vaccinated against

Mycoplasma bovis using Pulmo-Guard MpB (American Animal Health, Inc., Grand Prairie, TX). Calves were vaccinated again at weaning using the previously describe regimen with an additional vaccine for the prevention of bovine respiratory disease (INFORCE 3, Zoetis, Kalamazoo, MI) Deworming was accomplished via transdermal eprinomectin (IVOMEC® EPRINEX®, Merial Ltd., Duluth, GA). Calves were implanted at the initiation of the experiment with 100 mg progesterone USP, 10 mg estradiol benzoate and 29 mg tylosin tartrate (Component E-C, Ivy Animal Health, Overland Park, KS) and again at d 106 with 24 mg estradiol (Compudose, Ivy Animal Health, Overland Park, KS).

At the initiation of the growing phase, BW measurements were collected prior to feeding on 2 consecutive days and averaged to calculate initial BW. Calves were then randomly assigned to 5 pens (pen = 8 animals). Calves were housed in a barn constructed of a wood frame with a ribbed metal roof, and siding on the North, West, and East sides. The South side of the barn is covered with PVC coated 1.27 cm × 1.27 cm wire mesh bird screen and equipped with retractable curtains for wind protection. Within the barn, calves were housed in 4.88 m × 4.88 m pens (10 calves per pen) constructed of 5.08 cm galvanized steel tubing. Pens have slatted concrete floors covered by interlocking rubber matting. Diets were fed using the GrowSafe® (GrowSafe Systems Ltd. Airdrie, AB Canada) which continuously monitored and recorded feed consumption on an individual basis.

Pens were randomly assigned to 1 of 5 experimental growing diets: 1) corn-based control, 2) 0% corn distillers solubles (CDS), 3) 10% CDS, 4) 19% CDS, or 5) 27% CDS (Table 5.1). In addition to CDS, diets 2 to 5 included corn gluten feed and soybean hulls and were formulated to achieve fat concentrations of 3, 5, 7, and 9%, respectively. Both the control and common diets were formulated to contain 5.0% fat. Diets were delivered to pens once daily for 106 d (growing

phase), and were fed for *ad libitum* access to diets. All steers were then fed a corn-based diet from d 107 to 196 (finishing phase) when final BW, hip height, and ultrasound measurements were collected.

Sampling and Analysis

Feed ingredients were collected every 35 d, between the initiation and conclusion of the experiment. Composited feed samples were freeze-dried (Labconco, FreeZone[12] Kansas City, MO) then ground using a Wiley mill (1-mm screen, Arthur H. Thomas, Philadelphia, PA). All samples were analyzed for DM (24 h at 100°C). All freeze-dried samples were subjected to perchloric acid digestion and inductively coupled plasma atomic emission spectroscopy analysis of complete minerals (method 975.03: AOAC, 1988). Freeze-dried samples were analyzed for ADF and NDF (using Ankom Technology method 5 and 6, respectively; Ankom[200] Fiber Analyzer, Ankom Technology, Macedon, NY), CP (Leco TruMac, LECO Corporation, St. Joseph, MI), fat (ether extract method; Ankom Technology), and total ash (500° C for 12 h, HotPack Muffle Oven Model: 770750, HotPack Corp., Philadephia, PA). Ingredients were individually analyzed for nutrient composition, and the resulting values were used to calculate nutrient composition of the diets.

Ultrasound Data

Ultrasound measurements for 12th rib back fat thickness (BF) and marbling score (MS) were collected on d 0, 106 and 196 by a trained technician from the University of Illinois. The ultrasound system included an Aloka SSD-500V equipped with a 12.5 cm-3.5 MHz transducer (Aloka Co. Ltd., Wallingford, CT). Soybean oil was used as a sound wave copulant. Ultrasound images were captured and measured using CPEC Ultrasound Image Software (Cattle Performance Enhancement Co., LLC, Oakley, KS). Ultrasound images were collected on the

animal's right side parallel to the spinal column and perpendicular to the 11th, 12th, and 13th ribs, halfway between the axial and transverse processes of the lumbar vertebrae. The ultrasound location was clipped free of hair and curried clean prior to image collection.

Carcass Data Collection

On d 225, cattle were sold and shipped 296.1 km to a commercial harvest facility (Joslin, IL). Cattle were humanely slaughtered under USDA Inspection. Immediately post-harvest, HCW was collected. Carcasses were then chilled for 24 h at -4˚C. At approximately 24 h post-mortem, the right side of the carcass was ribbed between the 12th and 13th ribs and carcass data including LM area, BF, marbling score, and percent kidney, pelvic, and heart fat (KPH) were collected by plant personnel using video image analysis (VBS2000 E+V Technology GmbH, Oranienburg, Germany). University of Illinois trained personnel recorded measurements and determined quality grade (QG) and yield grade (YG). The equation: [2.5 + (2.5 + (2.5 × in. of BF) + (0.20 × %KPH) + (0.0038 × lbs of HCW) – (0.32 × REA in^2)] was used to calculate YG (Taylor, 1994).

Statistical Analysis

The experiment employed a completely randomized design. Performance, ultrasonic, and carcass data were analyzed using the MIXED procedures of SAS (SAS Institute Inc., Cary, NC). Additionally the IML procedures of SAS (SAS Institute Inc., Cary, NC) were used to generate coefficients for unevenly spaced levels of CDS inclusion (e.g. 0, 10, 19, and 27%). These coefficients were used to generate linear and quadratic contrasts to determine effects of increasing CDS inclusion. Additionally, a single degree of freedom contrast was used to compare control to the 10% CDS diet because these diets contained similar dietary fat

concentrations from different sources. Animal was defined as the experimental unit. Least squares means for treatment within feeding phase were generated and separated using the P-DIFF option of LSMEANS. Differences were considered significant at $P \leq 0.05$ and trends were considered present at $0.05 < P < 0.10$.

Experiment 2

Animal and Diet Management

Five Angus-Simmental steers (BW = 335 $\pm$ 56 kg) fitted with rumen cannulae were housed in metabolism stalls at the Beef Cattle Field Research Laboratory at the University of Illinois, Urbana. Stalls (2.3 x 1.3 m) contain non-siphoning water bowls and plastic feed bunks. Barn is also equipped with an HVAC controlled environment and fitted with removable collection hoods for the measure of methane emissions via indirect calorimetry. Cattle were allotted to 1 of 5 dietary treatments according to Patterson and Lucas (1962). Dietary treatments (Table 5.1) included: 1) corn-based control (CNT), 2) 0% corn distillers solubles (CDS), 3) 10% CDS, 4) 19% CDS, or 5) 27% CDS. Diets 2–5 included coproducts (corn gluten feed and soybean hulls) and were formulated to achieve fat concentrations of 3, 5, 7, and 9%, respectively. Feed was delivered once daily to allow ad libitum access to assigned diets. Refusals were collected and individual DMI was calculated.

Sampling and Analysis

Sampling periods were 21 days with 14 day acclimation periods for each treatment and 5 days for sampling. After initial acclimation to TMR, steers underwent partial rumen evacuations (8L). The rumen contents from evacuation were mixed and then redistributed to each animal to minimize initial differences in rumen microbial population. At the initiation of each subsequent

acclimation period rumens were totally evacuated and the contents from steers on each diet were transfused into the rumen of the steer assigned to that same diet for the following collection period.

On d 14-19, intake and fecal output were measured. Feed ingredient and refusal samples (50 g) were taken during this phase. Feed and refusal samples were collected 5 times during the collection phase, composited and freeze-dried (Labconco, FreeZone[12] Kansas City, MO) then processed as described in Exp 1. Refusals were collected and weighed and 10 % of the refusals were retained for nutrient analysis. Feces were collected in canvas bags secured by a leather harness attached to the girth and under the neck. Feces were collected twice a day and weighed, and, 5% of the feces were retained for nutrient analysis. Retained samples were composited by animal within period.

Rumen Fluid and Methane Collection

On d 19, 150 ml of ruminal fluid was collected via rumen cannula at 0, 3, 6, 9, 12 and 18 h post-feeding, filtered through 4 layers of cheesecloth, and pH was measured. Measurement of pH was accomplished within 2 min of collection using a FE20/FG2 pH meter (Mettler Toledo, Columbus, OH). To measure pH, the electrode (3 in 1 pH Electrode LE438 polyoxymethylene body gel-filled electrode with Ag/AgCl reference system and 1.2m; BNC/Cinch connection) was submersed in unmodified rumen fluid. Samples for rumen VFA concentration were collected at 0, 3 and 6 h post-feeding and stored for subsequent analysis.

On d 20, steers were placed in the Ruminant Emission Measurement System (REMS), and gas exchange data were collected for the following 24 h. Methane emissions were calculated using the following equation adapted from (Moody et al., 2008):

$$Emission\ Rate = Q \times \left(\frac{M}{V_m}\right) \times 10^{-6} \times \left(\left(\frac{v_{out}}{v_{in}}\right) C_{CH4}^{out} - C_{CH4}^{in}\right) \times \frac{T_{STD}}{T_{in}} \times \frac{P_{barometric}}{P_{STD}}$$

Where:

$$C_{CH4}^{out} = concentration\ of\ methane\ leaving\ the\ chamber, ppm_v$$

$$C_{CH4}^{in} = concentration\ of\ methane\ from\ external\ environment, ppm_v$$

$$Q = ventilation\ rate\ of\ recycled\ barn\ air\ entering\ the\ chamber, \frac{m^3}{s}$$

$$M = molar\ mass\ of\ methane = \ 16.01\ g/mol$$

$$V_m = molecular\ volume\ of\ gas\ at\ standard\ conmditons = .2241\ L/mol$$

$$v_{out,in} = specific\ volume\ of\ air, \frac{m^3}{kg}$$

$$T_{STD} = temperature\ at\ standard\ conditons = 293.15\ K$$

$$T_{in} = Temperature\ of\ recycled\ barn\ air\ entering\ chamber, K$$

$$P_{STD} = barometric\ pressure\ at\ standard\ conditons = 101325\ Pa$$

$$P_{barometric} = barometric\ pressure\ according\ to\ ASHRAE\ model = \ Pa$$

The ruminant emission measurement system efficiently collects gas samples, measures environmental conditions, and calculates gas emissions. It is comprised of: 1) six individual positively pressurized polycarbonate chambers designed to restrain the animal's head and neck, 2) thermal environmental control and fresh air supply to maintain animal comfort, and 3) gas sampling systems that use infrared photoacoustic multi-gas technology (IR-PAS, INNOVA 1412, California Analytical, Inc., Orange, CA) to measure CH_4. System utilized a solenoid valve multiplexer that sampled (10 consecutive samples) gas from each chamber every 83.33 min. Feed and water was provided inside the chamber for ad libitum intake.

At 0, 3 and 6 h, rumen fluid was sampled for quantification of VFAs. Samples (50 – 75 mL) of rumen fluid were mixed with 10 mL of H_3PO_4 and deionized water was added to achieve

a 2:1 dilution. The mixture was then be placed in a refrigerator and remixed by shaking several times per day for 2 d. On d 3, samples were removed from the refrigerator and 40 mL of rumen fluid was centrifuged at 20,000 × g at 25°C for 20 min. Supernatant was filtered through a 0.45-µm filter. Filtered sample was then transferred in 1-mL aliquots to gas chromatography vials with 0.1 mL of 2-ethyl butyrate as an internal standard. Vials were then stored at -20°C until analyzed using a gas chromatograph (Model 5890A, Hewlett-Packard, Palo Alto, CA) for VFA.

Statistical Analysis

Experiment 2 was a 5 × 5 Latin square design with treatments assigned to animals according to Patterson and Lucas (1962). The data was analyzed using the MIXED procedures of SAS (SAS Institute, Cary, NC). The IML procedures of SAS (SAS Institute Inc., Cary, NC) were used to generate coefficients for unevenly spaced levels of CDS inclusion. These coefficients were used to generate linear and quadratic contrasts to determine effects of increasing CDS inclusion. The model included treatment, time post-feeding, and period. Additionally, a single degree of freedom contrast was used to compare control to the 10% CDS diet because these diets contained similar fat concentrations from differing sources. The REPEATED statement was used to analyze the effect of animal within treatment on rumen pH and VFA concentration. Least squares means were generated and separated using the PDIFF option of LSMEANS. Differences were considered significant at $P \leq 0.05$ and trends were considered present at $0.05 < \alpha < 0.10$.

RESULTS

Experiment 1

At the end of the growing phase (d 106), calves fed control had increased ($P < 0.01$) ADG by 0.49 kg for calves fed the starch-based control compared to those fed 10% CDS.

Increasing inclusion of CDS resulted in increased (linear; $P = 0.01$) ADG. As a result, calves fed control had increased ($P = 0.03$) BW by 59 kg compared to calves fed 10% CDS diets (Table 5.2). Also, BW tended (linear; $P = 0.07$) to increase as CDS inclusion increased in coproduct diets. Calves consuming 0% CDS were lightest (350 kg) while cattle consuming 19% CDS were heaviest (392 kg) at d 106 among cattle fed coproducts. Similar to BW, Dry matter intake was within a 1.13 kg range for all treatments during the growing phase; therefore, no differences ($P \geq 0.23$) were observed in DMI during the growing phase.

At the end of the finishing phase (d 196), steers fed control tended ($P = 0.06$) to be heavier than steers fed 10% CDS; however, level of CDS inclusion fed during the growing phase did not affect ($P \geq 0.11$) final BW. Finishing phase ADG, DMI and G:F were not affected ($P \geq 0.13$) by control or increasing CDS inclusion. However, growing phase differences in ADG were sufficient to affect overall ADG from weaning to slaughter. Steers fed control had an increased ($P = 0.01$) ADG by 0.22 kg between weaning and slaughter. Also, increasing dietary inclusion of CDS increased ($P = 0.05$) overall ADG from 1.63 kg in steers fed 0% CDS to 1.76 kg in steers fed 27% CDS. Overall DMI and G:F were not different ($P \geq 0.20$).

Ultrasound indicated that back fat was increased ($P = 0.05$) by 2.14 mm in steers fed control compared to 10% CDS (Table 5.3) at the end of growing phase; however, back fat thickness was unaffected ($P = 0.34$) by CDS inclusion at the end of growing phase. There was no difference ($P \geq 0.18$) in marbling score at the end of the growing phase. Ultrasound measurements collected the day before harvest revealed no difference ($P \geq 0.20$) in back fat thickness; however, marbling score increased ($P = 0.05$) with the inclusion of CDS in coproduct-based growing diets. Additionally steers fed control tended ($P = 0.06$) to have higher ultrasound marbling scores than cattle fed 10% CDS.

Hot carcass weight tended ($P = 0.07$) to be increased in steers fed control during the growing phase compared to those fed CDS at 10% of the diet (Table 5.4). Also, HCW tended (linear; $P = 0.08$) to increase as dietary CDS inclusion increased. Marbling differences predicted by ultrasound were not detected ($P \geq 0.33$) in the carcass. Other carcass traits, including LM area, BF, KPH, yield grade and USDA quality grade, were unaffected ($P \geq 0.14$) by control or CDS inclusion.

Experiment 2

There was no effect ($P \geq 0.24$) of treatment on DMI; however, DM digestibility in calves fed control was increased ($P = 0.01$) by 5.84 percentage units compared to calves fed diets with 10% CDS inclusion (Table 5.5). Also, DM digestibility in calves fed coproduct diets increased (linear; $P = 0.02$) by 4.54 percentage units as dietary CDS inclusion increased. Similarly, fat digestibility increased (linear; $P < 0.01$) as dietary inclusion of CDS increased. Steers fed control tended to have decreased ($P = 0.07$) fat digestibility compared to steers fed 10% CDS. Digestibility of NDF was not affected ($P \geq 0.17$) by CDS inclusion.

There was no effect of treatment ($P = 0.87$) and no treatment × time interaction ($P = 0.84$) on rumnial pH; however, time post-feeding decreased ($P < 0.01$) pH until h 12 (Fig. 5.1). Concentrations of acetate, propionate, and total VFAs were not affected by treatment ($P \geq 0.55$) and no treatment × time interactions ($P \geq 0.47$) were observed (Table 5.6.). There was an effect of time ($P < 0.01$) on concentrations of acetate and propionate; they increased between 0 and 3 h post-feeding, but remained similar ($P \geq 0.73$) between 3 and 6 h. Acetate: propionate ratio decreased ($P < 0.01$) between 0 and 3 h after feeding but did not differ ($P = 0.71$) from 3 to 6 h post-feeding. Finally, methane emissions from steers fed corn were not different ($P = 0.37$). Also, CDS inclusion level had no effect ($P \geq 0.57$) on ruminal methane emissions (Figure 5.2).

DISCUSSION

Experiment 1

At the end of the growing phase, steers fed control were more efficient, faster growing, and heavier than those fed 10% CDS. This response was likely the result of increased energy in the control diet. Both control and 10% CDS contain similar fat concentrations, but control also contained corn whereas 10% CDS contained predominantly corn gluten feed and soy bean hulls. The contrast of control to the 10% CDS coproduct diet was made to illustrate the effect of corn in a standard early-weaned calf diet compared to a coproduct diet with similar concentrations of dietary fat (5.5 and 5.6%, respectively). Increased ADG in cattle fed starch compared to those fed fiber-based energy sources has been observed (Neville and McCormick, 1981; Schoonmaker et al. 2003; Arthington et al., 2005). These studies differ from the current study in that they used forage-based diets in comparison to corn. Meteer (2011) observed no differences in ADG in early-weaned calves fed either starch or coproduct-based growing diets, but in that study calves consuming coproduct diets consumed 0.88 kg/d more than calves fed starch-based diets. Segers et al. (2012) noted increased ADG in cattle fed corn during the growing phase, but increased DMI in cattle fed coproducts. Segers et al. (2012) observed no difference in final BW (Segers et al., 2012). These data indicate that while starch-based diets are more energy dense and tend to produce higher gains, they may also limit DMI compared to coproducts such as distillers grains or corn gluten feed.

Replacing starch with some coproducts, such as corn gluten feed and soybean hulls, has been shown to alleviate intake-limiting factors associated with corn-based diets such as negative associative effects as well as subacute and clinical acidosis (Green et al., 1987; Krehbiel et al., 1995). In the current study, decreased performance observed in calves fed coproducts (10%

CDS inclucsion) compared to control during the growing phase is likely a function of decreased energy intake due to similar DMI observed in calves from all treatments. It is unclear why calves fed coproducts in the current study exhibited reduced DMI compared to previous research. Experimental diets were fed between June and October, it is possible that high temperatures decreased intake of coproduct diets and produced the observed differences in performance.

Carcasses from steers fed control tended to be heavier than those from steers fed coproducts with 10% CDS inclusion. Also, HCW tended to increase linearly as CDS inclusion increased in coproduct-based growing diets. This was expected. As noted earlier, the performance advantage of control over coproducts with 10% CDS inclusion is likely a function of increased dietary energy of corn

Although final carcass ultrasound indicated a linear increase in marbling score as CDS inclusion increased, carcass data revealed no difference in marbling score among treatments; however, animal numbers were low making it difficult to detect differences in marbling. High starch diets have been shown to improve IMF (Schoonmaker et al., 2003, 2004b) and subsequent marbling score (Myers et al., 1999) compared to fiber when used in accelerated finishing systems that employ early-weaning. Therefore, it was believed that starch was a necessary dietary component to improve marbling and subsequent carcass quality in early-weaned calves. However, more recent research indicates there may be an alternative mechanism for using early calf nutrition to maintain high quality beef using coproducts instead of starch during the growing phase. Meteer et al. (2011) found no difference in marbling score when comparing corn to corn bran (9% fat) as energy sources fed to early-weaned calves. Also, Segers et al. (2012) illustrated that coproduct diets containing 5% fat fed to early-weaned calves produce carcasses with similar marbling scores to those from calves fed corn in the first 112 d post-weaning.

Experiment 2

In the current study, we hypothesized that increasing dietary fat from CDS would increase ruminal propionate concentration, thereby increasing the potential for increased intramuscular fat deposition and greater marbling scores in feedlot cattle. Dry matter intake was not different among treatments for fistulated steers. Fistulated steers were confined to a HVAC climate controlled barn which may have helped to stabilize intake compared to *Exp. 1*. However, Gilbery et al. (2006) observed a linear increase in DMI and digestibility when CDS was fed at 0, 5, 10, or 15% DM inclusion with switchgrass hay (*Panicum vergatum L.*). This was attributed to increased DIP in CDS, providing sufficient nitrogen for fibrolytic microbial populations to flourish in the rumen (Gilbery et al., 2006). In the current experiment, digestibility of DM was increased in control-fed steers compared to steers fed coproducts with 10% CDS inclusion, but DM digestibility increased as CDS inclusion increased in coproduct diets. Similarly, fat digestibility increased as CDS inclusion increased. These data were not unexpected as corn is a readily fermentable substrate, and CDS has already been shown to increase the digestibility of low quality hay (Gilbery et al., 2006). However, there was no effect of CDS inclusion on NDF or ADF digestibility. The reason for this finding remains unclear. Historically, when diets contained high concentrations of fat (>5% of total dry matter intake), fiber digestibility and dry matter intake were impeded (Byers and Schelling, 1993; Coppock and Wilks, 1991). This occurs because the hydrophobic nature of the lipids forces the fat to surround and encapsulate the carbohydrates thereby limiting microbial attachment. Also, modification of microorganism population, surface-active effects on microbial membranes, and lowered cation availability through the rumen can occur with little to no effect on microflora populations (Jenkins, 1993). Currently, it is thought that perhaps fat from corn coproducts such as distillers grains with

solubles or CDS behaves differently in the rumen than other unsaturated fat supplements such as corn oil. Klopfenstein et al. (2008) outlined an experiment in which DDGS was fed to feedlot cattle in comparison to corn oil. Cattle fed DDGS increased G:F by 8% where cattle fed corn oil decreased G:F by 10% compared to dry rolled corn. Additionally, 81% of the fat fed to DDGS cattle was digested as opposed to 70% by cattle fed corn oil (Klopfenstein et al., 2008)

There was no effect of treatment on ruminal pH or VFA concentration. The reason for this finding is unclear. In the rumen, polyunsaturated fatty acids are biohydrogenated with 60% to 90% efficiency. Hydrolysis of fatty acids, however, is less efficient. In the case of saturated fatty acids, hydrolysis occurs with 40% to 50% efficiency while PUFA are hydrolyzed with, at most, 35% efficiency therefore; highly unsaturated PUFAs are likely to pass through the rumen without modification (Thomas et al., 1997). After hydrolysis, the resulting glycerol is fermented to produce propionate (Byers and Schelling, 1993). It has been suggested that this decrease in the acetate: propionate ratios may be responsible for improvements in efficiency of energy utilization and partitioning (Funston, 2004). Smith and Crouse (1984) hypothesized that increased ruminal propionate production, in cattle fed high starch diets, caused increased blood glucose concentration providing more carbon substrate for intramuscular lipogenesis. Felix et al. (2012) reported decreased concentrations of propionate at 0 h post-feeding in cattle fed 60% DDGS diets compared to those fed 25% DDGS diets; however, at 3 and 6 h post-feeding ruminal propionate concentrations were higher in cattle fed 60% DDGS diets. Vander Pol et al. (2009) reported decreased acetate and increased propionate were found in diets containing WDGS compared to corn bran. They hypothesized that it is possible that the level of soluble inclusion in WDGS or DDGS could affect digestion and VFA concentration (Vander Pol et al., 2009).

Ruminal methane production was not affected by treatment in the current study. This finding is surprising becuase we hypothesized that increasing dietary fat from CDS would decrease ruminal methane emissions. Lipids have been shown to have a negative impact on methane production through several processes, including enhancing propionate production, biohydrogenation, and protozoal inhibition (Johnson and Johnson, 1995). Czerkawski et al. (1966) infused the rumen of sheep with oleic, linoleic, or linolenic acid. All animals displayed decreased ($P < 0.01$) methane production by at least 13.8% with infusion of PUFAs (Czerkawski et al., 1966). The authors hypothesized that the reduction in methane was due to biohydrogenation of the double bonds by rumen microorganisms, and that the PUFA provided an alternative hydrogen sink to CO_2 (Czerkawski et al., 1966). However, the amount of metabolic H^+ used in the biohydrogenation of ethylene bonds is small (1%) compared to that used in the reduction of CO_2 to methane (48%), VFA synthesis (33%), and bacterial cell synthesis (12%; Czerkawski, 1986; Johnson and Johnson et al., 1995). Czerkawski et al. (1966) also noted a similar decrease in methane production from sheep infused with palmitate. Also, methane levels took as long as 8 d to return to level observed prior to infusion (Czerkawski et al., 1966). The authors hypothesized that this was due to the inhibition of methanogenic microorganisms in the rumen (Czerkawski et al., 1966). It was also noted that methanogenic populations were solely affected by the addition of lipid because general carbohydrate fermentation proceeded as expected even when methane levels were half their pre-infusion levels (Czerkawski et al., 1966). Other studies have revealed similar results with diets containing soybean oil and tallow compared with isocaloric controls (Swift et al., 1948; Haaland, 1978; Van der Honing et al., 1981). These studies attributed decreased methane production to encapsulation of feed particles

by lipid thereby limiting the opportunity for microbial attachment and decreasing the amount of fermentable substrate (Johnson and Johnson, 1995).

CONCLUSIONS AND IMPLICATIONS

Steers fed a corn-based control during the growing phase tended to be heavier at slaughter and produced heavier carcasses than those fed coproducts with 10% CDS inclusion. Increasing inclusion of CDS improved growing phase as well as overall ADG, and tended to increase HCW. Dietary fat inclusion from CDS increased predicted marbling scores via ultrasound but had no measureable impact on marbling at slaughter; however, it is possible that this is result of a small scale experiment that did not have sufficient statistical power to detect marbling differences. There were no adverse effects of including CDS up to 27% (9.5% fat) of the diet on DM or NDF digestibility, VFA production, or pH. These data indicate a difference in the behavior of fat from CDS in the rumen compared to other fat supplements available to ruminants. When diets are similar in terms of fat content, corn-based diets appear to be advantageous for enhancing gains and efficiency of growing calves. Increased growth performance with increased CDS inclusion and the lack of adverse effects on ruminal metabolism and carcass traits make CDS a viable option for beef cattle diets.

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TABLES AND FIGURES

Table 5.1. Dry matter composition and nutrient analysis of diets offered to early-weaned calves and fistulated steers fed corn or coproduct blends with increasing concentrations of fat from condensed distillers solubles (CDS).

	Growing Diets[1]					Finishing Diet
		CDS Inclusion				
Ingredient, % DM	Control	0%	10%	19%	27%	Finishing Diet
Corn Silage	20.0	20.0	20.0	20.0	20.0	20.0
Cracked Corn	52.0	-	-	-	-	45.0
Soybean Hulls	-	25.0	25.0	25.0	25.0	-
DDGS[2]	18.0	-	-	-	-	-
WDGS[3]	-	-	-	-	-	25.0
Dry Corn Gluten Feed	-	45.0	35.0	26.0	18.0	-
Condensed Distillers Solubles	-	-	10.0	19.0	27.0	-
Supplement, % Diet DM						
Ground Corn	5.80	7.30	7.30	7.30	7.30	7.30
Urea	1.50	-	-	-	-	-
Limestone	2.50	2.50	2.50	2.50	2.50	2.50
Trace Mineral Salt[4]	0.10	0.10	0.10	0.10	0.10	0.10
Rumensin 90[5]	0.017	0.017	0.017	0.017	0.017	0.017
Tylan 40[6]	0.011	0.011	0.011	0.011	0.011	0.011
Liquid Fat	0.075	0.075	0.075	0.075	0.075	0.075
Chemical Composition, % DM						
DM	67.7	77.5	73.0	68.9	65.2	67.7
CP	14.0	16.9	16.3	15.8	15.3	14.0
NDF	22.8	43.3	40.3	37.7	35.3	22.8
ADF	12.0	24.5	23.2	22.2	21.2	13.3
Ether Extract	5.5	3.4	5.6	7.7	9.5	5.5
Ca	0.95	1.47	1.48	1.48	1.49	1.37
P	0.40	0.61	0.65	0.68	0.71	0.56
S	0.23	0.34	0.41	0.47	0.53	0.20
Ash	5.2	7.0	7.5	7.9	8.3	5.8
NE_m, Mcal/kg[7]	1.77	1.68	1.63	1.72	1.75	1.53
NE_g, Mcal/kg[8]	1.15	1.07	1.02	1.10	1.13	0.94

[1] Growing phase diets for feedlot study (Exp.1) were also experimental diets for metabolism study (Exp. 2).
[2] Dried distillers grains with solubles: S = 0.74; NDF = 39.31; CP = 26.8
[3] Wet distillers grains with solubles: S = 0.40; NDF = 40.0; CP = 29.7
[4] Trace Mineral Salt = 5% Mg; 10% S; 7.5% K; 2% Fe; 3% Mn; 5,000 mg/kg; Cu; 250 mg/kg I; 40 mg/kg Co; 150 mg/kg Se; 2,204,600 IU/kg Vitamin A; 661,380 IU/kg Vitamin D3; 22,046 IU/kg Vitamin E
[5] Rumensin 198 g/kg (Elanco Animal Health, Greenfield, IN)
[6] Tylosin 88 g/kg (Elanco Animal Health, Greenfield, IN)
[7] Calculated based on BW and DMI using equations from NRC (1996)
[8] Calculated based on BW and DMI using equations from NRC (1996)

Table 5.2. Performance data for early-weaned calves fed corn control or coproduct blends with increasing concentrations of dietary fat from condensed corn distillers solubles (CDS).

	Diets						Contrasts		
		CDS Inclusion						P Value[1]	
Item	Control	0%	10%	19%	27%	SEM	Control vs 10%	Linear	Quadratic
n	7	8	8	7	7				
Initial BW, kg	190	183	184	191	192	10.14	0.65	0.47	0.96
d 106[2]									
BW, kg	406	350	347	392	385	17.03	0.03	0.07	0.92
ADG, kg	2.03	1.58	1.54	1.89	1.82	0.08	< 0.01	0.01	0.88
DMI, kg	9.33	8.20	8.56	9.20	8.69	0.44	0.23	0.28	0.40
G:F	0.22	0.19	0.18	0.21	0.21	0.01	< 0.01	0.01	0.09
d 196[3]									
BW, kg	558	502	506	535	537	18.05	0.06	0.11	0.96
ADG, kg	1.69	1.68	1.77	1.60	1.69	0.10	0.58	0.73	0.91
DMI, kg	12.88	11.75	12.22	12.14	13.36	0.43	0.31	0.38	0.79
G:F	0.13	0.14	0.15	0.13	0.14	0.01	0.13	0.29	0.85
Overall[4]									
ADG, kg	1.87	1.63	1.65	1.75	1.76	0.05	0.01	0.05	0.96
DMI, kg	10.96	9.83	10.24	10.55	10.38	0.38	0.20	0.25	0.50
G:F	0.17	0.17	0.16	0.17	0.17	0.01	0.21	0.51	0.65

[1]Pvalue: $P < 0.05$ indicates linear effect with increasing CDS inclusion; $P < 0.05$ indicates quadratic effect with increasing CDS inclusion

[2]d 106 = means generated at the end of growing phase after feeding of experimental diets

[3]d 196 = means generated at the end of the finising phase after feeding a common diet

[4]Overall = means calculated from weaning till slaughter

Table 5.3. Ultrasound data for early-weaned calves fed corn control or coproduct blends with increasing concentrations of dietary fat from condensed corn distillers solubles (CDS).

	Diets						Contrasts		
		CDS Inclusion						P value[1]	
Item	Control	0%	10%	19%	27%	SEM	Control vs 10% CDS	Linear	Quadratic
n	7	8	8	7	7				
d 106[2]									
Back Fat, mm	7.85	5.57	5.71	6.02	4.86	0.65	0.05	0.56	0.34
Marbling Score[4]	378	329	334	379	350	22.0	0.18	0.27	0.54
d 196[3]									
Back Fat, mm	13.16	12.29	10.78	11.46	10.53	1.29	0.20	0.26	0.80
Marbling Score	597	479	505	588	548	32.0	0.06	0.05	0.42

[1]Pvalue: $P < 0.05$ indicates linear effect with increasing CDS inclusion; $P < 0.05$ indicates quadratic effect with increasing CDS inclusion

[2]d 106 = means generated at the end of growing phase after feeding of experimental diets

[3]d 196 = means generated at the end of the finising phase after feeding a common diet

[4] 100=practically devoid, 200=traces, 300=slight, 400=small, 500=modest, 600=moderate, 700=slightly abundant, 800=moderately abundant

Table 5.4. Carcass data for early-weaned calves fed corn control or coproduct blends with increasing concentrations of dietary fat from condensed corn distillers solubles (CDS).

	Diets						Contrasts		
		CDS Inclusion						P value[1]	
Item	Control	0%	10%	19%	27%	SEM	Control vs 10%	Linear	Quadratic
Carcasses	7	8	8	7	7				
HCW, kg	347	305	312	335	334	13.0	0.07	0.08	0.88
LM area, cm^2	73.13	75.90	72.30	78.87	77.18	3.33	0.87	0.51	0.69
Marbling Score[2]	477	411	429	483	429	33.05	0.33	0.46	0.35
Back Fat, cm	1.11	1.18	1.09	0.87	0.97	0.16	0.93	0.26	0.63
KPH, %	2.0	2.3	2.2	2.1	2.1	0.10	0.14	0.17	0.69
Yield Grade	3.29	3.23	3.20	3.02	3.17	0.23	0.79	0.72	0.74
Select, %	29.0	50.0	29.0	29.0	29.0	0.18	1.00	0.38	0.55
$Choice^-$ or better, %	71.0	50.0	71.0	71.0	71.0	0.18	1.00	0.38	0.55
$Choice^0$ or better, %	43.0	13.0	14.0	43.0	14.0	0.15	0.20	0.58	0.38
Prime, %	0.0	0.0	0.0	14.0	0.0	0.06	1.00	0.53	0.28

[1]Pvalue: $P < 0.05$ indicates linear effect with increasing CDS inclusion; $P < 0.05$ indicates quadratic effect with increasing CDS inclusion

[2] 100=practically devoid, 200=traces, 300=slight, 400=small, 500=modest, 600=moderate, 700=slightly abundant, 800=moderately abundant

Table 5.5. Digestibility of dry matter, neutral detergent fiber, acid detergent fiber, and ether extract in steers fed corn control or coproduct blends with increasing concentrations of dietary fat from condensed corn distillers solubles (CDS).

	Diets						Contrasts		
		CDS Inclusion					P value[1]		
Item	Control	0%	10%	19%	27%	SEM	Control vs 10% CDS	Linear	Quadratic
n	5	5	5	5	5				
DMI, kg/d	10.04	11.39	11.53	10.97	10.62	0.86	0.24	0.48	0.74
Digestibility, %									
DM	77.58	67.91	71.74	73.84	72.45	1.41	0.01	0.02	0.11
NDF	69.63	63.73	65.45	65.94	63.97	2.05	0.17	0.86	0.39
ADF	71.57	65.90	67.65	66.91	69.38	3.07	0.38	0.49	0.91
Fat	83.91	76.01	87.35	87.97	87.04	1.25	0.07	< 0.01	0.02

[1]Pvalue: $P < 0.05$ indicates linear affect with increasing CDS inclusion; $P < 0.05$ indicates quadratic affect with increasing CDS inclusion

Table 5.6. Ruminal volatile fatty acid concentrations in steers fed corn control or coproduct blends with increasing concentrations of dietary fat from condensed corn distillers solubles (CDS).

	Diets								Contrasts		
		CDS Inclusion								CDS Inclusion	
	Control	0%	10%	19%	27%	SEM	Diet	Time	Diet × Time	Control vs. 10% CDS	Linear	Quadratic
Steers	5	5	5	5	5							
VFA												
Acetate, m*M*						4.40	0.55	< 0.01	0.47	0.72	0.13	0.83
0[1]	46.29	59.03	46.33	45.48	45.66							
3	62.21	64.57	61.52	61.18	55.14							
6	64.35	62.31	59.37	64.93	57.34							
Propionate, m*M*						4.52	0.70	< 0.01	0.66	0.60	0.22	0.96
0	25.37	21.18	18.31	17.92	16.65							
3	40.95	33.69	36.31	33.94	28.25							
6	41.26	30.56	33.97	36.38	31.20							
Total VFA, m*M*						9.46	0.70	< 0.01	0.66	0.60	0.22	0.96
0	86.81	99.87	79.39	76.17	78.17							
3	124.03	124.94	123.01	117.73	105.87							
6	125.62	117.93	115.92	122.79	112.67							
A: P Ratio[2]						0.27	0.55	< 0.01	0.51	0.23	0.80	0.83
0	2.00	2.92	2.87	2.92	2.85							
3	1.64	2.01	1.82	1.88	1.95							
6	1.68	2.08	1.90	1.97	1.87							

[1] Hours after feed delivery
[2]Acetate: Propionate Ratio

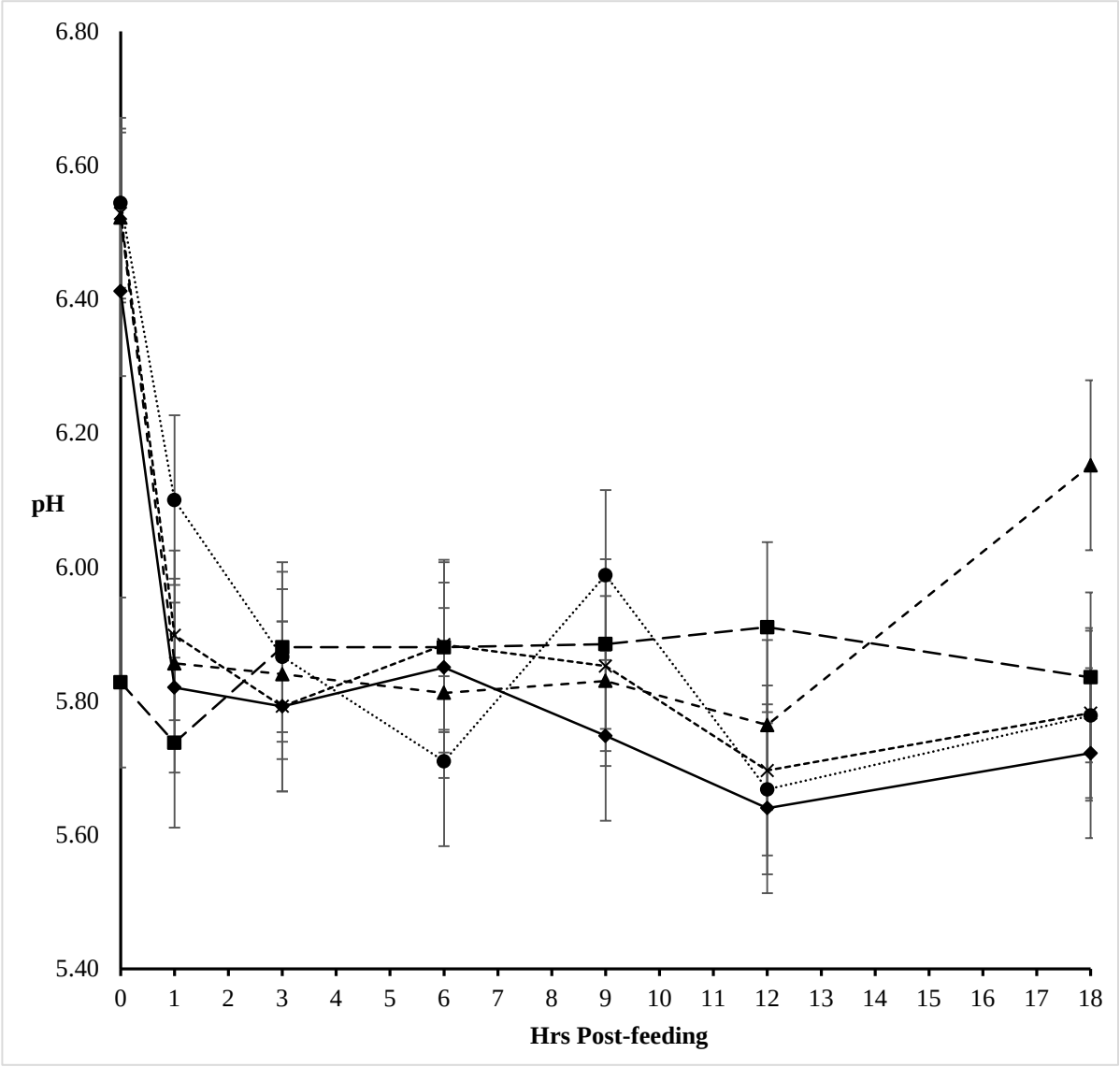

Figure 5.1. Ruminal pH from steers fed diets including corn control or coproduct blends with increasing concentrations of dietary fat from condensed corn distillers solubles (CDS). Diets fed to steers contained either a corn control (♦) or 0 (■), 10 (▲), 19 (×), or 27% (●) CDS. Ruminal pH decreased ($P < 0.01$) over time. No effects of treatment or treatment × time were detected ($P \geq 0.84$).

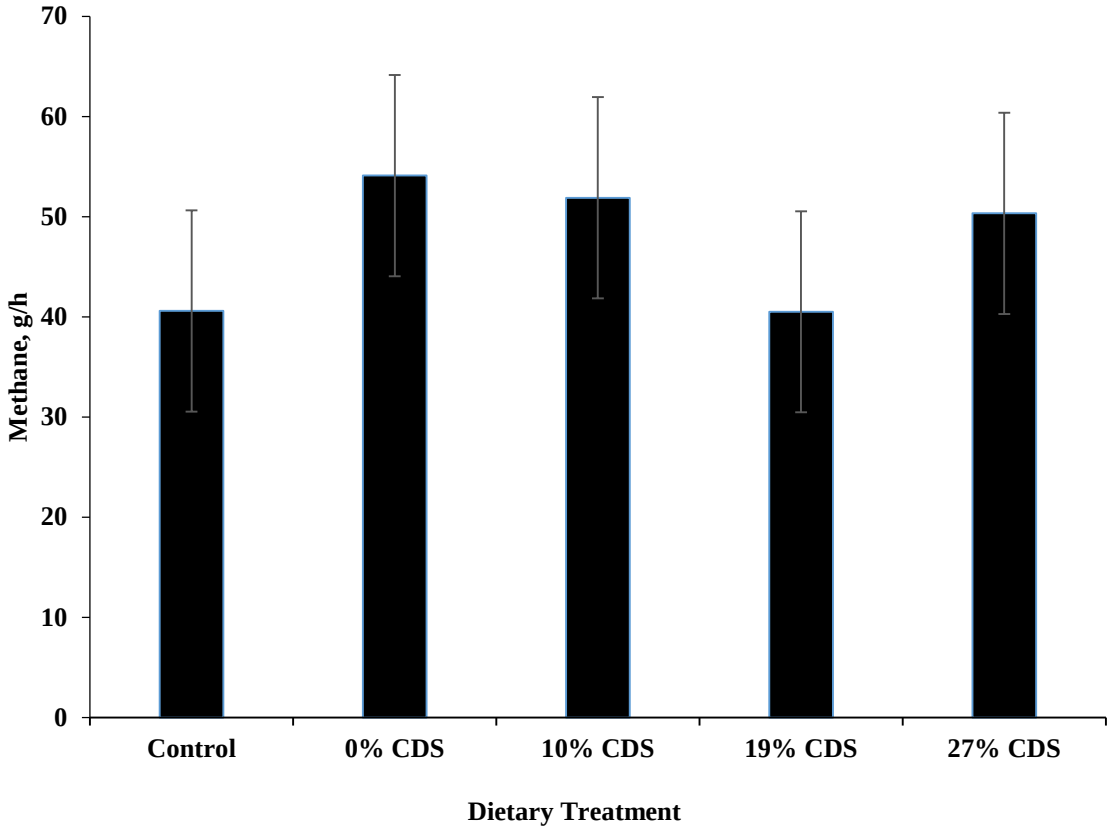

Figure 5.2. Ruminal methane emissions from steers fed diets including corn control or coproduct blends with increasing concentrations of dietary fat from condensed corn distillers solubles (CDS). Diets fed to steers contained either a corn control or 0, 10, 19, or 27% CDS. There was no effect ($P \geq 0.37$) of diet on ruminal methane emission.

CHAPTER 6
CONCLUSIONS AND IMPLICATIONS

In our initial experiment feeding corn during the growing phase increased ADG and decreased DMI thereby increase G:F compared to coproducts; however, there was no difference in BW at d 112 and performance was not different in the feedlot among calves fed differing growing phase diets indicating no negative effects of using coproducts diets during the growing phase of early-weaned calves. Also, coproducts with no corn fed during the growing phase resulted in carcasses with similar marbling scores to those fed corn-based growing diets suggesting that starch may not be necessary to produce high quality carcasses from early-weaned calves.

The combination of increased dietary protein and decreased dietary fat induced an increase in the expression several adipogenic and lipogenic precursors as well as serum leptin concentrations after cattle were acclimated to a common diet. The mechanism responsible for this interaction is unknown. This research provides insight into the effects of elevated protein and fat from corn coproducts on the molecular regulation of intramuscular fat development. Feeding differing levels of dietary fat and protein during the growing phase does affect intramuscular adipogenesis at the transcriptional level, but differences in gene expression were not sufficient to affect carcass quality among cattle fed coproducts.

In our examination of dietary fat inclusion form condensed distillers solubles (CDS), steers fed a corn-based control during the growing phase tended to be heavier at slaughter and produced heavier carcasses than those fed coproducts with similar fat concentration. This is important information for producers with an interest in exploring accelerated finishing systems

(i.e. early weaning) using coproducts. Increasing inclusion of CDS improved growing phase as well as overall ADG, and tended to increase HCW. Dietary fat inclusion from CDS had no measureable impact on marbling; however, it is possible that this is result of a small scale experiment that did not have sufficient statistical power to detect marbling differences. There were no adverse effects of including CDS up to 27% (9.5% fat) of the diet on DM or NDF digestibility, VFA production, or pH. These data indicate a difference in the behavior of fat from CDS in the rumen compared to other fat supplements such as corn oil. When diets are similar in terms of fat content, corn-based diets appear to be advantageous for enhancing gains and efficiency of growing calves. Increased performance with increased CDS inclusion and the lack of adverse effects on ruminal metabolism and carcass traits make CDS a viable option for beef cattle diets.