EFFECT OF ENERGY SOURCE, TIMING OF PROVISION, AND DAYS ON FEED ON FEED EFFICIENCY OF FINISHING BEEF CATTLE

A Thesis Submitted to the College of

Graduate and Postdoctoral Studies

in Partial Fulfillment of the Requirements

for the Degree of Doctor of Philosophy

in the Department of Animal and Poultry Science

University of Saskatchewan

Saskatoon, Saskatchewan

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ABSTRACT

The objective of this research was to evaluate if the decline in gain-to-feed ratio (**G:F**) during finishing in beef cattle could be due to a reduction in nutrient digestion, short chain fatty acid absorption, or post-absorptive nutrient utilization, and those responses were influenced by the dietary energy source or timing of provision. A high-lipid byproduct pellet (**HLP**) was used as a partial replacement for barley grain in a high concentrate finishing diet to partially replace starch with lipid as the energy source. Yearling steers were used for performance evaluations and ruminally cannulated Hereford crossbred heifers were used for nutrient metabolism studies. The dry matter (**DM**), organic matter (**OM**), crude protein (**CP**) and neutral detergent fibre (**NDF**) digestibility of HLP diets were lower than the barley-based control diet (**CON**). Utilizing a phase-feeding strategy and partially replacing barley grain and canola meal with a high-fibre high-lipid byproduct pellet in the latter part of the finishing period may improve carcass yield grade without affecting average daily gain and G:F. With advancing days on feed, diet DM digestibility *(P* = 0.02) and insulin resistance (*P* = 0.04) increase without changes in ruminal pH and plasma metabolite clearance rates. A marginal increase in forage inclusion with the HLP diet increased ADG (*P* = 0.04). Increasing dietary lipid supply up to 6% of DM using HLP did not affect the digesta flow and rumen fermentation parameters, therefore, increased lipid content is not associated with reduced feed efficiency of the HLP diet. In conclusion, decreasing feed efficiency in the later stages of finishing in beef cattle is most likely due to changes in the post absorptive nutrient metabolism, and these changes are not influenced by the dietary energy source. The small particle size of feed ingredients within the byproduct pellet may be the factor associated with decreased feed efficiency of HLP pellet rather than lipid content.

ACKNOWLEDGEMENTS

I thank Almighty God for all his blessings and giving this opportunity to work with a bunch of wonderful people at the Department of Animal Science, University of Saskatchewan as part of my Doctoral program.

I would like to extend my heartfelt gratitude to my supervisor Dr. Greg Penner for all his amazing support, guidance and encouragement throughout my study. I will always cherish his encouragement and support as an invaluable experience in my academic career. I thank my committee members Dr. John McKinnon, Dr. Steve Hendrick, Dr. Luis Burciaga and the graduate committee chair Dr. Fiona Buchanan for their continued assistance with my research project and thesis writing. My sincere appreciation to Dr. Pawel Górka, who patiently devoted his time for numerous discussions regarding this project.

A special thanks to Team Rumen, Gillian Gratton, Kasia, Coral, Katie, Dan, Silvia, Keshia, Rodrigo, Larissa, Jordan, Brittney, Liam, Tyler, Brittany, JK, Brittney Schurmann and numerous others for all their dedication and assistance with this research project. I would also like to extend my sincere thanks to the Manager and staff of Livestock Research Building and Beef Cattle Research and Teaching Unit at the University of Saskatchewan for assisting me with the sample collection. I also extend my gratitude to the Alberta Crop Industry Development Fund Ltd. (Lacombe, AB, Canada), Agriculture Development Fund administered through the Ministry of Agriculture in Saskatchewan (Regina, SK, Canada), and the Beef Cattle Research Council of Canada (Calgary, AB, Canada) for funding my projects. I thank Natalia, lab manager for her guidance with the laboratory work of this project.

I dedicate this work to my parents, Joy and Annamma, and my dear sisters for their constant motivation and strength in my academic career. I thank my dear wife Divya for always being there to support me in all the ups and downs of life, and instilling in me the confidence to go ahead and succeed in life. I also thank my son Enric for cooperating with my studies and writing and making my world more meaningful and beautiful each day.

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LIST OF ABBREVIATIONS

ADF	Acid detergent fibre
ADG	Average daily gain
ALP	Alkaline phosphatase
APE	Atom percent excess
BAA	β-adrenergic agonists
BAR	Barley-based finishing diet
BW	Body weight
Ca	Calcium
CaO	Calcium oxide
CBGA	Canadian Beef Grading Agency
CP	Crude protein
Cr	Chromium
CV	Coefficient of variation
DDGS	Dried distillers' grain with solubles
DM	Dry matter
DMI	Dry matter intake
DNA	Deoxyribonucleic acid
DOF	Days on feed
EDTA	Ethylenediaminetetraacetic acid
FAB	Fluid associated bacteria
FCR	Feed conversion ratio
FFA	Free fatty acids
FP	Fluid phase digesta fraction
G:F	Gain to feed ratio
GHG	Greenhouse gas
GIT	Gastrointestinal tract

HCW	Hot carcass weight
HF	High forage
HLP/HLHFP	High lipid high fibre byproduct pellet
IGF	Insulin like growth factor
IMF	Intramuscular fat
iNDF	Indigestible neutral detergent fibre
IU	International unit
Ka	Rate of absorption
Kc	Rate of clearance
Kp	Rate of passage
LCFA	Long chain fatty acids
LF	Low forage
LI	Large intestine
ME	Metabolizable energy
MP	Metabolizable protein
N	Nitrogen
NAN	Non-ammonia nitrogen
NANBN	Non-ammonia non-bacterial nitrogen
NaOH	Sodium hydroxide
NDF	Neutral detergent fibre
NEFA	Non-esterified fatty acids
NEg	Net energy of gain
NEm	Net energy of maintenance
NH_3	Ammonia
OM	Organic matter
P	Phosphorus
PAB	Particle associated bacteria

PDV	Portal drained viscera
PP	Particulate phase digesta fraction
RFI	Residual feed intake
RIG	Residual intake and gain
SCFA	Short chain fatty acids
SD	Standard deviation
SEM	Standard error of the mean
SI	Small intestine
VFA	Volatile fatty acids
WTP	Willingness to pay
Yb	Ytterbium

1.0 INTRODUCTION

The long-term growth of any industry depends on how it effectively utilizes its limited natural resources through far sighted planning and successful integration of technological innovations into applied production and marketing scenarios. The livestock industry, in general, has grown many folds over the last few decades, through improvements in animal genetics, a better understanding of nutritional physiology, availability of cheap and nutritious feed ingredients, and innovations in food preservation, processing, and marketing technologies. This is true across all food animal industries such as chicken, dairy, pork, and beef production. A common trend over the years is a decrease in animal numbers, and small farms, and a concurrent increase in the individual animal production and number of large farm units. This trend has helped to increase the profitability of the industry while decreasing the reliance on natural resources. This is particularly important when considering an exponentially increasing world population pushing with increasing protein demand, and, diminishing land resources pushing up the prices of agricultural produce.

The profitability of the beef industry is highly influenced by fluctuations in the feed grain prices. Considering feed as the primary input for beef production, this has resulted in exorbitant beef prices driving away consumers to other cheaper alternatives. Limited land resources for grain production and diversion of grain for bioethanol and biofuel industries has only aggravated the situation. On the other hand, without livestock, byproducts from agricultural and food processing industries would be disposed of in landfill sites, leading to wastage of resources and posing an environmental challenge. One main challenge related to the utilization of agricultural byproducts in the animal feed industry has been the nutritional inconsistency of the byproducts, where they oversupply and undersupply some nutrients limiting the ability to use them as the sole animal feed. Blending of multiple byproducts to achieve a palatable final product with desired nutrient composition was the focus of research in the last decade. The beef cattle industry was at the helm of such experiments due to the capability of the ruminant stomach to convert cellulose into energy and protein. Several byproduct pellets with different combinations of ingredients and energy sources and density were developed, but none were fully successful in meeting the desired outcome in terms of improving livestock performance and feed efficiency.

Improving feed efficiency is another critical factor for the sustainability and profitability of the beef industry. The beef industry and supporting scientific community has attained considerable

progress in the development of intensive beef production, especially in North America, but the ever-increasing global population exerts more pressure for further improving efficiency. It was understood that efficiency of production decreases with advancing days of growth and multiple factors has been attributed to this decreased efficiency. Thorough understanding of all the factors leading to changes in feed efficiency with advancing days on feed is important for devising strategies to improve the efficiency of gain.

2.0 LITERATURE REVIEW

2.1 Feeding management in North America

Nearly 24% of the global production of beef and veal occurs within the United States, Mexico, and Canada (USDA 2018). While located on the same continent, there is considerable regional diversity within and across countries regarding the structure of the beef industry in North America. Conventional beef production can be broadly divided into cow-calf, backgrounding/stocker, and finishing sectors (NASEM 2016). The cow-calf and backgrounding/stocker operations are more diverse and are distributed more broadly from a geographical perspective across North America when compared to finishing operations. According to NASEM (2016), small farms and ranches predominate in the eastern and southern regions of US and Canada, while large ranches for cow-calf operations and feedlots predominate in the western areas.

The diversity in beef finishing operations in Canada is evident when comparing eastern operations (Ontario and Quebec) versus those in the Prairies. Factors contributing to diversity include size of operation, use of grazing, calving period, and forage management. Finishing operations often rely on harvesting forages before full bloom because of the requirement of higher quality forage by finishing animals compared to breeding animals (Sheppard et al., 2015). The primary feed grain used in finishing operations in western Canada is barley while in eastern Canada it is corn. Eighty percent of the feedlot operations surveyed by Shepperd et al., (2015), fed feed supplements to finishing cattle, even though the survey captured only 1 to 2% of the Canadian beef farms. Less than 4% of finishing operations in the Prairie-region relied on summer pasture grazing for finishing their cattle, while the number of such operations was greater in the Atlantic region. As per the survey, the use of ionophores or hormonal implants was less in Canadian feedlots (80%; Shepperd et al., 2015) compared to their U.S. counterparts (90%; Capper and Hayes, 2012) and the authors claim that lower adoption rates of ionophores and implants may provide export opportunities in the future due to increased demand for non-implanted cattle in European countries.

A survey of practicing nutritionists conducted in US reported that grain inclusion in finishing diets has decreased in recent years (Samuelson et al., 2016). In 2007, Vasconcelos and

Galyean reported that 93.1% of the feedlot nutritionists surveyed included at least 60% grain on DM basis in diets for finishing cattle. Using the same questionnaire, Samuelson et al. (2016) reported that only 78.3% of nutritionists surveyed used diets of at least 60% grain. The apparent reduction of cereal grain in finishing diets may be in part due to greater byproduct availability and use in response to rapid growth of the grain, ethanol, and oilseed industries. Inexpensive energy-rich cereal, ethanol, and oilseed byproducts provide alternative energy sources compared to costlier cereal grains (Zenobi et al., 2014; Johnson et al., 2018). Use of high-energy byproducts has allowed to achieve high dietary NEg concentrations despite decreased grain inclusion. In fact, Samuelson et al., (2016) reported that 97.1% of the nutritionists surveyed incorporated some grain byproducts in their finishing diets and this trend has increased by 17% since the study of Vasconcelos and Galyean (2007).

Common byproducts used by the nutritionists surveyed include wet distiller's grains, dried distiller's grains, wet corn gluten feed, and dry corn gluten feed. On average, byproducts were reported to be included at a rate of 10 to 20% of DM in finishing diets (Vasconcelos and Galyean, 2007; Samuelson et al., 2016). In addition to the cereal grain and byproducts, forage sources are included and account for 8 to 10% of the DM in finishing diets. The main roughage sources used in finishing diets among these nutritionists were corn silage and corn stalks.

Supplemental lipid in finishing diets was used by 54% of the clients of nutritionists surveyed; however, this trend appears to be decreasing, possibly due to higher cost of lipid relative to other energy sources and the contribution of lipids from some of the byproducts used in diet formulation. When lipid was added, tallow was the primary source followed by fat blends, yellow grease, and corn oil (Samuelson et al., 2016).

Arthur et al. (2004) reported that profitability in the beef industry is a function of revenue and costs, of which feed is a major variable cost. With the feedlot sector, and the beef industry in general, functioning with tight margins in North America, emphasis on improving profitability by increasing feed efficiency and using cost effective feed resources is critical.

2.2 Feed efficiency in feedlot finishing diets

Feed efficiency is an important component of profitability in the feedlot sector. It is expected that a 5% decrease in feed-to-gain ratio will have four to eight times more economic impact than a similar percentage increase in daily gain (Gibb and McAllister, 1999). In addition, increasing feed costs and growing environmental awareness (Herd et al., 2003) make more efficient cattle desirable.

Considerable progress has been made in the last three decades towards improving feedlot cattle performance and efficiency, largely due to advancements related to growth promoting implants, ionophores, genetic predictors, vaccines, antibiotics, and repartitioning agents (NASEM 2016). From the feedlot data compiled from 1990 to 2011, Reinhart and Waggoner (2012) reported an upward trend in feed efficiency from 6.6 to 5.8 kg feed/kg gain in steers and 6.7 to 6.2 kg feed/kg gain in heifers (NASEM 2016).

Several measures have been used in the literature to compare the feed efficiency of feedlot cattle. The commonly used indexes include residual feed intake (RFI; Koch et al., 1963), feed conversion ratio (FCR), gain-to-feed ratio (G:F), residual BW gain (RG) and residual intake and BW gain (RIG; Berry and Crowley 2012). While RFI is commonly evaluated in research, there are several concerns including: that RFI measurement does not account for potential differences in sorting or dominance at the feed bunk and that one feed bunk is used for numerous cattle; that re-ranking of cattle for RFI is substantial between consecutive measurement periods (Durunna et al., 2011); and that all herds/groups of cattle have a mean RFI score of 0 thereby eliminating potential to compare among groups. In addition, a regression study by Cruz et al. (2010) reported that G:F alone or DMI and ADG together explained 98% of the variance in cost of BW gain for finishing cattle, while RFI alone explained only 18%. Those authors concluded that RFI was less useful than G:F as an indicator of feed efficiency and profitability. As a result, combined with the need for measurement of individual feed intake, important terms used to describe feed efficiency in the feeding sector include FCR or G:F. Nevertheless, evaluation of RFI data can help improve the knowledge of feed efficiency for feedlot cattle.

2.2.1 Patterns of feed efficiency

The energetic efficiency for the conversion of feed into BW gain is influenced by numerous external (environmental conditions, diet composition) and internal/inherent factors including, but not limited to breed, days on feed, body composition, and body weight. A comparison of different beef breeds and their crosses for growth rate and efficiency of meat production has been an area of interest since the 1960's (Taylor, 1971), and it was well understood that breed differences occur for the efficiency of production. Gregory et al. (1994) published findings from an elaborate study evaluating nine different beef breeds and their production efficiencies at constant time (DOF), constant gain, and constant carcass weight as endpoints, and reported that the breeds with smallest mature weight tended to be more efficient in weight gain at a constant weight endpoint, while breeds with a greater rate of gain were more efficient with a gain constant. When a retail product end point was used for comparison, breeds with a greater dressing percentage and percentage of retail product were most efficient. These data suggest that while breed/frame size can affect efficiency, the reference point of consideration imposes a major influence on which breeds will be deemed most efficient.

Ferrell and Jenkins (1998a) reported that cattle from sires of different breeds with the same height and BW can have different body composition in terms of the percentage of water, protein, and fat. When analyzing dam and sire breed effects, Ferrell and Jenkins (1998a) found that sire breed prominently influences the longissimus area, fat thickness, quality and yield grade, while dam breed influenced DM and ME intake and organ weights. Ferrell and Jenkins (1998b) also reported that maintenance energy requirement as well as efficiency of energy use for weight gain differed among sire breeds. In another study, six breeds of beef bulls in Ontario bull test stations from 1991 to 2000 were evaluated and the authors reported that breeds ranked differently based on RFI when adjusted for production and back fat thickness (Schenkel et al., 2004). This study reported that among the breeds studied, Blonde d'Aquitaine and Limousin were most efficient owing to their high dressing percentage and lean yield of the carcass, while Angus remained least efficient. In a comparative study of temperate beef breeds (Limousin and Simmental) with indigenous Chinese breeds within a Chinese beef production system, it was found that the Limousin breed possessed the highest G:F compared to all other breeds in the study (Xie et al., 2012). A finishing study comparing RFI of Simmental and Angus reported that Simmental cattle

had a more desirable RFI (Retallick et al., 2013) and in a study evaluating Irish performance tested bulls, Limousin and Charolais were the most efficient breeds in terms of FCR or RFI (Crowley et al., 2010). Martinez et al. (2010) reported that the double muscled genotype of a Spanish beef breed exhibited greater feed efficiency compared to other genotypes and breeds under the study. Despite the varied breed comparisons and production scenarios evaluated, these breed comparison studies have resulted in a common conclusion that breed indeed is a major factor in determining feed efficiency in beef cattle. However, these breed differences in efficiency of gain can be attributed to several other breed specific traits and characteristics such as initial body weight, body composition, growth rate, organ weight, and/or double muscling genotype.

Body composition as an important factor influencing feed efficiency has been another area of study since the 1970's. It is understood that different breeds were able to deposit fat in body tissues and fat depots at different rates and amounts (Hedrick, 1972). Kelly et al. (2010) reported that less efficient (high RFI) heifers fed a finishing diet had greater lumbar fat thickness and fat gain compared with the more efficient low RFI heifers. They also reported that the rump fat accretion tended to be greater in high RFI cattle. In a breed comparison study, Ferrell and Jenkins (1998a) found that Angus/Hereford sired steers contained more body fat and energy but tended to contain less protein and water than Belgian Blue or Piedmontese sired steers. Breeds of cattle with a greater rate or quantity of fat deposition were considered less efficient than those depositing leaner tissue, because of the high energy content of fat compared to protein and water. Supporting the relationship of RFI and efficiency, selection for low RFI cattle results in less subcutaneous fat (Richardson et al., 2001; Arthur and Herd, 2008). Weak positive phenotypic and genotypic correlations between RFI and body fat content were reported indicating that the greater the body fat content the less efficient the cattle (Richardson et al., 2001, Basarab et al., 2003, Schenkel et al., 2004). Similarly, Herd and Bishop (2000) reported negative phenotypic and genotypic associations between RFI and carcass lean content. On the other hand, heavier cattle or breeds were considered less efficient than lighter cattle and breeds because of the greater maintenance energy requirement due to their greater BW. This theory is further exacerbated by the greater maintenance energy cost associated with body protein than with body fat (Pullar and Webster, 1977; Ferrell et al., 1979).

As cattle mature, more energy is diverted towards fat accretion as it is 1.6 times more energetically efficient compared to protein accretion, due to greater protein turnover (Owens et al., 1995). However, on a BW basis, due to the water content of muscle, protein accretion is more efficient. Another hypothesis states that variation in RFI in beef cattle is a result of different rates of protein degradation and total protein gain (Richardson and Herd, 2004), indicating that low RFI cattle have more efficient protein deposition or decreased protein degradation rates (Bonilha et al., 2013). Weak genetic correlations have also been reported between RFI and BW (Herd and Bishop, 2000; Schenkel et al., 2004), even though no such relationships were established in the studies of Arthur et al. (2001a,b) and Nkrumah et al. (2004).

Splanchnic tissues have a considerable impact on metabolizable energy (ME) use and contribute to 40 to 50% of whole-body heat production (McLeod and Baldwin, 2000). On average, the gastrointestinal tract (GIT) accounts for 7% of empty BW and 20% of whole-body energy expenditure, while the liver accounts for 2% of empty BW and 20% of whole-body energy expenditure (McBride and Kelly, 1990). Ferrell and Jenkins (1985) and Ferrell (1988) suggested that maintenance requirements and efficiency of gain are more closely associated with weight and metabolic activity of visceral organs like the GIT and liver rather than body composition or composition of gain. The greater maintenance requirement is evident as splanchnic tissues have greater O_2 consumption per unit mass than non-splanchnic tissues, indicating greater metabolizable energy expenditure (Baldwin and Sainz, 1995). The greater maintenance cost of splanchnic tissues is inherent to their high cell turnover rate, secretory function of the GIT, and the high metabolic rate required to facilitate nutrient absorption and metabolism. In fact, the amount of absorbed nutrients and metabolic demand is a major factor influencing liver mass, while the forestomach and intestinal mass respond to dietary fibre and the amount of absorbed nutrients (Sainz and Bentley, 1997; Hersom et al., 2004b). Supporting this theory, high milk producing cattle with high feed intake are reported to have increased visceral organ weight to support higher nutrient demand, which in turn has been linked to greater maintenance energy requirement (Ferrell and Jenkins, 1984). Similarly, in steers fed a high concentrate finishing diet, mesenteric/omental fat increased as the empty BW of steers increased (Sainz et al., 1995). Basarab et al. (2003) reported that the main difference between high and low RFI steers was that low-RFI steers had less body cavity fat.

The changes in visceral tissue weight are not only restricted to the forestomach and liver, but also influence the lower GIT. Differences in organ mass can affect maintenance energy requirements of beef cattle and might influence feed efficiency during finishing. Based on serial slaughter, steers predicted to have lower liver weights at the start of finishing tended to have greater G:F during finishing period than steers with greater predicted liver weight (Sharman et al., 2013a). Visceral organ mass of cattle at entry into the finishing phase may have a greater influence on finishing efficiency compared with carcass composition (Sharman et al., 2013b). However, there are inconsistent reports in the literature regarding the association between feed efficiency, carcass composition, and visceral organ mass. Some studies have reported a lack of differences in visceral organ weight or body composition between divergent RFI groups (Sainz et al., 2006; Bonilha et al., 2013). Nevertheless, it is clear that the splanchnic tissues play an important role in the overall efficiency in finishing beef cattle including delivery of nutrients and a disproportionate use of energy relative to their weight. However, more studies are required to confirm the extent of splanchnic tissue's influence and how they impact feedlot efficiency.

2.2.2 Importance of feed efficiency in sustainability

The main concern of feeding the expanding global population is the lack of arable land for food production (Lambin and Meyfroidt, 2011). Hertel (2011) explained that the concern should be the cost of land rather than the quantity of land, because a vast proportion of the land on the earth's surface is not suitable for cultivation for production of food for humans. There is direct competition for arable land between animal feed and human food production. However, much of this discussion focuses on crop production approaches. According to the Food and Agriculture Organization of the United Nations, around 70% of the agricultural land on earth is covered by grass lands (FAO, 2012). While much of this could be considered non-arable, ruminants have the ability to convert forages and crop residues into high quality animal protein (NASEM, 2016). Thus, strategies to enhance the quantity of beef produced per unit land area and to ensure efficient utilization of non-cultivatable land should be developed or improved on (Schroeder et al., 2000; Tonsor et al., 2010; White and Capper, 2013).

Based on a study conducted in the Netherlands, Elferink and Nonhebel (2007) reported that beef production required more land per unit of meat produced when compared to chicken and

pork production. While acknowledging the fact that all the land used for beef production cannot be used for human food production (Oltjen and Beckett, 1996), even after removing the non-tillable land from the land use assessment, the land requirement for beef was still greater than the metrics for pork and chicken. Greater land use for beef production relative to poultry and swine include differences in the G:F ratio between different species of animals and that forage yields from non-tillable land may not be equivalent to that with tilled land. That said, those authors did not consider the conversion of non-human edible feeds which give ruminants an inherent advantage of non-ruminant species. However, the importance of reducing the pressure on land resources for efficient meat production cannot be over emphasized.

Every production system has attributes that support and challenge the sustainability triad of economic, social, and environmental goals. There are frequent trade-offs between the components of this triad and no single production system will satisfy all aspects of sustainability simultaneously (Stern et al., 2005). Cooprider et al. (2011) stated that technologies that work to improve efficiency and do not have any deleterious effects on the environment will have sustainability benefits. Expressing comparisons of different production systems in terms of a unit of output is important to avoid practices that satisfy sustainability goals at the expense of productivity (Beauchemin et al., 2010; Place and Mitloehner, 2010). White and Capper (2013) reported that improving the ratio of feeder cattle to the consumer population, by improving finishing BW has a greater impact on all three attributes of sustainability (economic, environmental and social attributes), than reducing days from birth to slaughter.

2.2.2.1 Environmental considerations

With the expansion of the global population, the demand for meat products is anticipated to increase (Tilman et al., 2002). Cattle with poor feed efficiency have a greater impact on the environment (Nkrumah et al., 2006). Ruminants produce higher greenhouse gas emissions (GHG) per kilogram of meat produced when compared to poultry and pork (Phetteplace et al., 2001; Beauchemin et al., 2010) and require more land and energy than any other livestock species (Gerber et al., 2013). Enteric methane emissions from beef cattle alone account for nearly 18% of the total global man-made methane emissions (USEPA, 2015). Approximately 15% of total CO_2 emissions from the beef sector originate from the feedlot sector (Phetteplace et al., 2001).

Minimizing the dietary inefficiencies of feedlot cattle can significantly reduce adverse environmental impacts (e.g. improving starch utilization, minimizing days on feed, reducing methane production). Adopting mitigation measures such as dietary modifications can reduce GHG emissions up to 45% (Del Prado et al., 2010). Feeding programs using small grains like barley and wheat were reported to have the greatest soil and land use impact due to their low yield per hectare and higher physical footprint for farming when compared to high yielding grains like sorghum and corn (Mekonnen and Hoekstra, 2010). Hengen et al. (2016) reported that a well-balanced diet can reduce enteric methane, decrease manure solids, and increase digestibility. Additionally, lower-energy diets for feedlot cattle will decrease the per kilogram feed cost with a lower environmental burden.

Adopting technology in management systems has resulted in the doubling of output over the last 50 years while farm animal numbers increased only marginally. These achievements were made possible by employing management practices and technologies that improve efficiency of production and reducing environmental impact per unit of output (Capper et al., 2009). In a comparison study of conventional versus organic (Never Ever 3) cattle, Cooprider et al. (2011), reported that conventional cattle spent fewer days on feed, and had 28% less emissions of CO_2-equilant/kg of feedlot gain compared to organic fed cattle. The improved efficiency (15% improvement) in beef cattle was due to lower feed consumption, land use, water use, and reduced the carbon footprint by 6.4%, 3.2%, 12.3% and 11.7%, respectively when compared to a control (White and Capper, 2013). The same study also reported that an increase in feed efficiency to achieve 15% greater finishing weight had decreased feedstuff consumption, water use, land use, and total greenhouse gas emissions by 12.1%, 9.2%, 15.5% and 14.7%, respectively. It has also been reported that removing growth enhancing technologies will result in a 10% increase in greenhouse gas emission per unit of beef produced (Capper and Hayes, 2012).

In a recent Canadian study comparing changes in greenhouse gas emissions arising from beef production between 1981 and 2011, Legesse et al. (2016) reported a 14% decline in methane emissions, 15% decline in N_2O emissions, and a 12% decline in CO_2 emissions from fossil fuel, for the same amount of slaughter weight. These improvements were attributed to improved reproductive efficiency, ADG, final slaughter weight, decreased DOF, and a shift towards high grain finishing diets. Growth enhancing technologies, besides increasing productivity, also alter

the microbial profile in the rumen leading to increased nitrogen retention and reduced greenhouse gas, volatile organic compounds, and ammonia emissions from feedlot cattle (Stackhouse-Lawson et al., 2013). They reported that animals supplemented with β-adrenergic agonists (BAA) had lower CH_4, and NH_3-N emissions per kilogram of hot carcass weight than non-supplemented cattle.

2.2.2.2 Economic considerations

Less feed efficient animals are associated with greater costs of production (Crews, 2005). In beef operations, feed costs account for nearly 80% of the total variable costs (Arthur et al., 2004). Out of the total dietary energy supply, approximately 75% is used for maintenance energy requirements. Studies evaluating the economic impact of adopting technologies to improve efficiency in feedlot operations have shown that cattle raised with growth promoting technologies like β agonists and feed additives resulted in 17% less feed and lowered the cost of production per kilogram of feedlot BW gain (Cooprider et al., 2011). This was supported by another study by Fernandez and Woodward (1999) where a conventional finishing treatment using growth implants and ionophores improved ADG and feed efficiency and reduced the cost of BW gain by 39% over an organic feeding system. Even though the economic drawbacks of the less efficient organic beef production system might be partly compensated by the premium revenue generated from its niche market, such cattle were also under the risk of further setbacks from possible incidences of rumen acidosis, liver abscesses, adhesions, and associated performance loss or carcass trimming. White and Capper (2013) stated that income over cost in beef production is dependent on socioeconomic scenario. According to those authors, when the efficiency of gain or final BW was increased by 15%, it resulted in increased feedlot profits ranging from 37% to 134% when compared to average US production. Wileman et al. (2009) reported that in feedlot operations, an improvement in feed efficiency by 9% or a 0.2 kg/kg increase in G:F from anabolic implants maximized resources and increased profitability.

2.2.2.3 Public perception

Efficient and sustainable beef production practices appeal to the public and result in more social acceptability. But, the use of technology or metabolic modifiers to improve efficiency has been challenged by the general public. According to a US survey in 2010, natural and organic beef sales constituted 1.6% of all fresh beef sales, representing 2.5% of the total beef value (NCBA, 2010). Consumers of organic beef were paying a premium of up to 39% over conventional beef (USDA, 2019). Thilmany et al. (2006) conducted a survey of beef consumers to identify the reasons for their willingness to pay a premium for organic beef and found that 48% prefer organic beef for personal benefits (nutrition, quality and safety), 24% for public health concerns (antibiotic resistance, hormone residues), 23% based on broad social benefits (support to local agriculture, environmental benefits) and 5% based on other concerns. Health and environmental concerns are contributing factors driving the demand and creating a value-added market for organic beef production (Cooprider et al., 2011) and this necessitates developing strategies to improve feed efficiency that align with organic beef production systems. Cooprider et al. (2011) concluded that using metabolic modifiers in a conventional feedlot production system satisfies both the economic and environmental attributes of sustainable beef production, while the social attributes were opposed. The 'willingness to pay' (WTP) was used as measure of social acceptability of any beef production system. When beef was marketed as more efficiently produced, WTP improved by 10% (White and Capper, 2013). However, when beef was marketed on production efficiency using growth enhancing technology, WTP decreased by 12%. Economic and social impacts of improved efficiency thus depend heavily on consumer and producer awareness, education, and behavioral responses to the use of technology that results in efficiency improvements.

2.2.3 Physiological factors affecting feed efficiency

Several hypotheses are available in the literature explaining the physiological basis of feed efficiency including factors such as: intermediary metabolism, ruminal metabolism, methane production, protein metabolism, and stress responses. According to Richardson and Herd (2004) differences in empty body and carcass composition account for only 5% of the variation in net feed efficiency measured based on RFI. There might be several other factors that play a role in feed efficiency like digestibility, feeding patterns, metabolic heat production, physical activity,

protein turnover, tissue metabolism and stress (Bonilha et al., 2013). The phenotypic manifestation of feed efficiency could be a result of complex interactions of any of these factors. Enhanced feed efficiency is also reported to be linked to lower activity levels in cattle (Pitchford, 2004). The BW of cattle also influences feed efficiency, as heavier cattle require more net energy for maintenance (NEm) and have greater metabolizable protein (MP) requirements (NASEM 2016). Feed efficiency is also affected by stage of growth, as the composition of gain changes with advancing DOF (NASEM 2016).

2.2.3.1 Digestive factors

Digestion contributes to variation in feed efficiency in cattle (Simeone and Beretta, 2005). Ruminal digestion is influenced by factors like DMI, rumen pool size, chewing activity, and regulation of outflow from the rumen. Cattle with large rumen volume have longer retention times, greater digestibility, and greater methane emissions (Waghorn et al., 2006) which in turn can influence the efficiency of production. Nkrumah et al. (2006) reported a 5% difference and Richardson et al. (1996) reported a 1% difference in DM digestibility between high and low RFI cattle that ultimately accounted for 14% of the variation in feed efficiency. This was further supported by the finding that low RFI cattle had greater apparent total tract digestibility of DM and CP (Nkrumah et al., 2006) and lower partitioning of feed N to fecal N. Divergence in hindgut fermentation may also contribute to differences in feed efficiency (Gressley et al., 2011; Khiaosa Ard and Zebeli, 2014). Difference in starch digestion among high and low efficiency cattle has been documented (Channon and Rowe, 2004; Channon et al., 2004) and is assumed to be the result of greater starch digestion in the small intestine in more efficient cattle, rather than in the rumen, and reduced loss of energy in the form of methane.

It has been reported that for ruminants fed a low digestible diet, there is a positive correlation between voluntary DMI and digestibility. However, when fed a highly digestible finishing diet, a negative correlation exists between DMI and apparent digestibility (Blaxter et al., 1961; Conrad et al., 1964). In experiments with beef cattle fed ad libitum vs. restricted high concentrate diets, an increase in DMI was associated with decreased digestibility (Galyean et al., 1979) and decreased feed efficiency (Sainz et al., 1995; Rossi et al., 2001). Restricting DMI is also associated with decreased ADG (Hicks et al., 1990; Rossi et al., 2001) and decreased ME intake.

However, restricting DMI without restricting protein and energy intake relative to ad libitum feeding results in an increase for G:F, ADG (Schmidt et al., 2005), and DM digestibility (Clark et al., 2007). Schmidt et al. (2005) explained that improved performance with moderate feed restriction was due to increased DM digestibility. Based on regression models, DMI accounted for 67% of the variation associated with cattle performance while DM digestibility only accounted for 2%. In contrast, initial BW accounted for 31% of the variation in cattle performance (Davis et al., 2014). These data suggest that DM digestibility likely only plays a minor role separating beef cattle performance. These data further suggest that other physiological processes such as post-absorptive metabolism may also contribute to variation in animal performance.

Splanchnic tissues are considered metabolically active and their efficiency is important to support whole-body efficiency. Ferrell et al. (1986) reported that as DMI increases, the weight of the visceral organs and their maintenance energy requirement increase. Studies have shown that steers with restricted intake had smaller livers compared to steers fed ad-libitum (Sainz and Bentley, 1997). The difference in size was primarily due to a reduction in size of hepatocytes rather than a reduction in number of liver cells/kg BW. Baldwin and Sainz (1995) reported that visceral organs such as the GI tract, liver, and kidneys have greater O_2 consumption per unit mass than non-visceral tissues, indicating a greater metabolizable energy expenditure in the visceral organs compared to non-visceral organs. In fact, the portal drained viscera accounts for 24% of the total energy expenditure in sheep (Johnson et al., 1990), and the liver accounts for 20 to 26% of energy expenditure by the portal drained viscera. Energy costs accounted to liver and the GIT are estimated to be around 25% of whole-body oxygen consumption (Reynolds et al., 1991) and there might be opportunities to improve overall feed efficiency by improving energetic efficiency of these critical organs. Krehbiel et al. (2016) reported that the liver serves as a 'hub' of intermediary metabolism for the entire animal, and that splanchnic tissues (PDV and liver) accounts for 40 to 60% of the oxygen consumption of the whole ruminant.

The dietary forage-to-concentrate ratio also plays a role in energetic efficiency. In a study conducted in growing beef heifers fed isonitrogenous and isoenergetic pelleted diets containing either 75% alfalfa or 75% concentrate, heifers fed a 75% concentrate diet produced less heat energy and retained more tissue energy compared to those fed the 75% alfalfa diet. Those authors reported an increased blood flow to portal drained viscera for the alfalfa-based diet compared to

the concentrate-based diet. Greater oxygen uptake by portal drained viscera accounted for a 72% decrease in retained tissue energy for heifers fed 75% alfalfa pellets compared to those fed 75% concentrate pellets (Reynolds et al., 1991a). In a study conducted in dairy cows, Dong et al. (2015) reported an increase in the maintenance energy requirement with increasing proportion of forage in the diet (from 30% to 100%), and partially attributed this to increased heat production per unit of ME intake. In an integrative metabolomics and proteomics study in dairy heifers fed either 80% or 20% forage, enhanced hepatic pathways were found for heifers consuming high forage diets indicating further rationale for greater energy demand and possibly reduced feed efficiency (Zhang et al., 2019).

Energy rich cereal grains are the major component of finishing diets for cattle. Increasing the dietary starch content in finishing diets at the expense of forage inclusion has implications in the site of digestion in the GIT of cattle. Ruminal digestibility of starch in beef cattle is approximately 80% and decreases with increasing starch intake (Moharrery et al., 2014). In conditions of high starch intake and reduced feed particle size, especially if pelleted feeds are fed, a considerable amount of starch escapes ruminal fermentation due to increased passage rate. Owens et al. (1986) reported that about 18 to 42% of the dietary starch fed to cattle reaches the small intestine (SI) for digestion. Enzymatic starch digestion in the SI is more energetically efficient over ruminal starch digestion due to the 13 to 18% loss of gross energy during ruminal fermentation (Owens et al., 1986; Harmon and Mcleod, 2001). However, the energetics do not consider benefits provided by ruminal fermentation, such as the microbial protein supply. Even though increased flow of starch into the SI can result in increased pancreatic secretions, the total amount of pancreatic α-amylase remains constant (Swanson et al., 2004), posing limitations to the amount of starch that could be digested in the SI. Other factors like time and surface exposure could also limit SI starch digestion (Owens et al., 1986).

Casein supplementation to the SI has been reported to increase α-amylase secretion, but casein stimulation is ineffective in the presence of starch (Richards et al., 2003; Swanson et al., 2002a). Supplementing leucine in diets for dairy cattle also increases the secretion of α-amylase and improves SI starch digestion (Liu et al., 2015). Developing strategies to improve SI digestion of starch is important because digestive efficiency of starch in the large intestine (LI) is poor (Harmon and Mcleod 2001). Besides that, microbial fermentation of carbohydrates in the hind gut

can result in hindgut acidosis and other health disorders (Gressley et al., 2011) that could further negatively affect performance and feed efficiency of beef cattle.

Methane and SCFA produced in the rumen are viewed as important factors of digestive efficiency. Efficiency could be improved by decreasing methane emissions and enhancing production, absorption, and metabolism of SCFA (Khiaosa Ard and Zebeli, 2014). Khiaosa Ard and Zebeli (2014) further reported that the diversity of rumen microbial communities and difference in the immune response to nutritional challenges were some factors that lead to divergence in feed efficiency. The improvement in production efficiency achieved in cattle over the last decades is primarily by the dilution of the energy used for non-productive purposes like methane production, maintenance, and heat production (Capper et al., 2009). Methane formed in the rumen represents considerable energy losses in ruminants (Khiaosa-ard and Zebeli, 2012). As much as 8.4% of total dietary gross energy could be lost as methane when cattle are fed on pasture (Harper et al., 1999). Low methane emissions have been linked with improved feed efficiency in cattle and genetic selection for improved feed efficiency has been proposed as a means for mitigating methane emissions (Hegarty, 2004; Hegarty et al., 2007). Nkrumah et al. (2006) observed that low RFI steers had fewer and shorter visits to the feed bunk per day, and less frequent feeding can increase propionate production and amplify shifts in ruminal pH between feedings (Sutton et al., 1986). Methanogenesis is further influenced by ecology of the methanogen (Zhou and Hernandez-Sanabria, 2009), host breed genetics (King et al., 2011), feed type, and quality (Jones et al., 2011). Even the methanogenesis pathway used by methanogens can lead to variation in energy loss (Zhou et al., 2010).

The divergence of bacterial communities between low and high feed efficiency steers and the penchant for specific bacterial species for efficient steers has been reported (Guan et al., 2008). The same research also reported differences in metabolic activity of microbes and end products of fermentation (higher butyrate production in efficient steers) contributing towards the differences in feed efficiency. However, this study was based on RFI values and the differences in the total feed intake and frequency of feeding observed between high RFI and low RFI cattle can influence the microbiome. Additionally, the overlap in activity between bacterial species could be a limitation in ascertaining different metabolic activity with differing microbiome composition. Host genetics can play a role in determining the rumen microbiome, and cattle revert to their original

microbiome even after exchange of microbiota between animals (Weimer et al., 2010). This uncertain relationship between rumen microbial adaptation and feed efficiency can lead to another hypothesis that rather than microbes associated with rumen contents, the rumen wall associated microbes might have a major role in determining feed efficiency (Li et al., 2012). In addition, to some extent, dietary factors like forage to concentrate ratio, energy density of the diet, and forage type might have an influence on determining the effect of feed efficiency through rumen microbial adaptation. Future studies are needed to build the knowledge base on the composition of the microbiome and their activity before ascertaining a definite relationship between feed efficiency in cattle and the rumen microbiome.

2.2.3.2 Absorptive factors of SCFA and other nutrients

In response to increased SCFA production, the rumen epithelium adapts to increase SCFA absorption through coordinated changes in epithelial proliferation, cellular function, and tissue permeability (Penner et al., 2011). Increased absorption of SCFA increases the energy supply to the host for enhanced production (Aschenbach et al., 2011). Efficient absorption of SCFA across the rumen epithelium is not only important from an energy source standpoint, but also for welfare and health as SCFA uptake is critical for regulation of ruminal pH and prevention of acidosis and systemic disorders (Penner et al., 2009a, Khiaosa Ard and Zebeli, 2014). Morphological adaptations of the ruminal epithelium influence the absorptive response to acid load in the rumen (Bannink et al., 2010), and individual variation in the absorptive capacity between cattle is one of the major factors determining their susceptibility to metabolic disorders (Penner et al., 2009). Rumen epithelial proliferation is further influenced by the amount and type of SCFA produced. Butyrate may stimulate SCFA absorption by promoting epithelial proliferation through its indirect effects on the release of hormones and growth factors (Gorka et al., 2009; Penner et al., 2011)

2.2.3.3 Intermediary metabolism and markers for feed efficiency

Beef cattle are raised to maximize lean tissue accretion and excessive fat accumulation can result in wastage (Du et al., 2013). The goal of a finishing program for feedlot cattle is to maximize lean tissue accretion coupled with appropriate intramuscular fat deposition. The palatability of

beef depends on the marbling and tenderness: two quality issues for the beef industry (Garcia et al., 2008). Marbling is associated with juiciness, tenderness, and palatability of beef (Wheeler et al., 1994). Intramuscular fat (IMF) deposition associated with marbling is an important variable affecting quality grades for beef cattle in North America; however, excessive deposition of other fat depots like visceral fat and subcutaneous fat decrease production efficiency and induce lower dressing percentage (Louveau et al., 2016). Selection of cattle for high rates of lean growth, harvesting at increasingly younger ages, and the use of growth promoting implants can also reduce intramuscular fat deposition (Albrecht et al., 2011; Du et al., 2013).

Studies have shown that myocytes, adipocytes, and fibroblasts are all derived from a common progenitor cell type during embryonic development (Du et al., 2013). Bonnet et al. (2010) reported that both adipose tissue and muscle tissue in cattle grow by hyperplasia during the fetal stages. While the myocyte number is set by the end of the fetal stages, the number of adipocytes is never set (Bonnet et al., 2010) or is set upon reaching adolescence (Goessling et al., 2009). In growing cattle, hypertrophy resulting from nutrient storage in fully differentiated myocytes and adipocytes is thought to be the main mechanism of tissue accretion (Bonnet et al., 2010; Cianzio et al., 1985).

Generally, fat deposition in farm animals increases with weight and age and the development of adipose depots are not uniform from a quantitative or a temporal standpoint (Arana et al., 2006). From studies in lambs, Joy et al. (2008) reported that on quantitative terms, the importance of intramuscular (IM) fat depots are less compared to other adipose tissues in the carcass. Visceral fat depots are the first to develop, followed by intermuscular and subcutaneous fat depots, and lastly the intramuscular adipose depot develops (Louveau et al., 2016; Urrutia et al., 2018). Since adipose depot tissues grow at different times and at different rates, the adipocyte size (Schiavetta et al., 1990; Mendizabal et al., 1999) and the lipogenic activity (Eguinoa et al., 2003) also will be lowest for IM fat depots compared to subcutaneous or visceral fat depots. Different fat depots are also different metabolically, where subcutaneous adipocytes primarily use acetate as a carbon source while intramuscular adipocytes mainly use glucose and lactate as carbon sources (Smith et al., 2009). Even though the progenitor cells for tissue accretion for cattle are common, the successive waves of myogenesis and adipogenesis result in significantly different proportions of muscle and fat with advancing age. As the cattle deposit more adipose tissue with

increasing age, more and more energy is partitioned to deposit fat (Welegedera et al., 2012). Because the energy content per unit of fat is greater than that of protein, with advancing age and increased fat accretion, the energetic efficiency of BW gain in finishing cattle decreases drastically.

Understanding the metabolism of nutrients following their absorption from the GIT helps in understanding the barriers towards efficient nutrient utilization. The three major end products of ruminal fermentation: acetate, propionate, and butyrate are known to undergo metabolism differently in the ruminal epithelium, liver, and peripheral tissues (van Houtert, 1993). About 90% of the absorbed butyrate is metabolised by the ruminal and omasal epithelium, and converted to ketone bodies like acetoacetate and β-hydroxybutyrate or oxidized as a source of energy. While a portion of absorbed propionate is metabolised to lactate or oxidized to carbon dioxide in the ruminal and omasal epithelia, the majority of the absorbed propionate enters portal blood flow, is transferred to the liver, and is the primary substrate for gluconeogenesis (Pennington and Sutherland, 1956b; Leng et al., 1967; Bergman and Wolff, 1971). Activation of short-chain fatty acids (SCFA) by acyl-CoA synthetase is an important mechanism for the utilization of SCFA by different tissues (Stangassinger and Giesecke, 1986). Acetate is the only SCFA reaching the peripheral tissue in considerable amount and is mainly utilized by muscle and adipose tissue in non-lactating ruminants (van Houtert, 1993). Acetate is mainly oxidised to CO_2 in the muscle cell (Pethick et al., 1981), for the generation of ATP in mitochondria, a process which requires oxaloacetate. Acetate is also used as a carbon source for long chain fatty acid (LCFA) synthesis in adipose tissues (Hanson and Ballard, 1967; Hood et al., 1972). For adipogenesis from acetate, presence of sufficient glucose is important. Acetate requires oxidation of glucose in the pentose phosphate pathway to generate the NADPH for fatty acid synthesis. Glucose also provides the carbon for glycerol required for the esterification of LCFA into a triglyceride (Hood et al., 1972; Vernon, 1981). Because propionate is the main gluconeogenic precursor in ruminants, there is a minimum requirement of propionate relative to acetate, above the requirement for protein accretion and tissue maintenance, for lipogenesis. Limited supply of propionate and thereby the glucose supply will lead to energetically inefficient pathways for acetate utilization in adipose tissue (van Houtert 1993). It has already been reported that a negative correlation exists between the proportion of acetate in SCFA and the efficiency of energy retention in ruminants (Elliot and

Loosli, 1959; Blaxter, 1967) and that this extends beyond differences in efficiency of fermentation from hexoses to SCFA.

Several blood metabolites are associated with feed efficiency in ruminants. Identifying those blood metabolites has been an area of interest in several studies to use it as a suitable marker associated with feed efficiency for selection purposes. Identification of biomarkers is challenging considering that feed intake, diet composition, and physical activity are the primary determinants of blood metabolite concentration rather than genotype (Beeby et al., 1988; Spicer et al., 1990). Identifying the functional dynamics and kinetics of these metabolites could help in understanding how metabolites interact with each other and with differing physiological status of cattle, and eventually affect feed efficiency.

Past studies by Richardson et al. (2004) and Brown (2005) have reported a higher concentration of circulating insulin in high-RFI steers during finishing, that has been attributed to a decrease in leanness and increase in fat deposition. Insulin is known to reduce lipolysis and promote lipogenesis in adipose tissue. This agrees with the finding that circulating blood glucose was greater in inefficient steers (Kolath et al., 2006). Other studies by Kelly et al. (2010) reported that plasma insulin concentration was unrelated to performance or feed efficiency traits. The glucose:insulin ratio is considered as an indicator of glucose metabolism and based on RFI, this indicator is unaffected (Kelly et al., 2010). However the glucose:insulin was negatively correlated with FCR, indicating that more efficient cattle may have altered glucose metabolism.

Kelly et al. (2010) reported a positive relationship of leptin with feed conversion ratio. In agreement, Foote et al. (2016) has reported that mean leptin concentration over an 83-d finishing period was negatively associated with G:F and positively associated with RFI, indicating that more efficient cattle had lower leptin concentrations. However, these authors did not observe an association of leptin with G:F towards the latter half of the finishing period, even though the leptin concentration was increased from d 1 to d 83. They also reported that plasma leptin concentrations can explain the variation in body composition, especially body fat content. Leptin is produced from adipose tissue and influences appetite, body composition, energy expenditure, and nutrient partitioning (Chilliard et al., 2005). However, Bourgon et al. (2017) reported a greater blood leptin concentration in cattle with improved feed efficiency, when they have used an RFI model adjusted for carcass composition.

Blood urea concentrations were found to be greater in less efficient animals (Richardson et al., 1996, 2004). This has been attributed to high protein intake in high RFI animals, a greater protein degradation rate, or a variation in the efficiency of microbial protein production in the rumen (Lush et al., 1991; Kahn, 2000). Lobley (2003) reported that younger animals have lesser blood urea compared to older ones, suggesting greater efficiency to convert nitrogen into amino acids and proteins, partially attributable to changes in growth curve or body composition. However, Kelly et al. (2010) did not find any difference in urea concentrations when comparing RFI ranking. Moreover, Santana et al. (2013) observed a positive correlation between RFI and urea in bulls, but the relationship disappeared when the RFI model was adjusted for body composition. This also suggests the importance of adjusting for body composition when selection is completed for feed efficiency to avoid undesirable changes in carcass composition (Montanholi et al., 2009; Schenkel et al., 2004).

Triglycerides are usually stored in adipose tissue as an energy reserve (Vernon and Houseknecht, 2000) and their presence in plasma could be used to indicate the energy status ruminants. Circulating plasma triglycerides are often used by muscle tissue as a fuel source, enabling energy supply for protein synthesis (Cameron, 1992). High RFI steers (less efficient) had less circulating plasma triglyceride concentrations than low RFI steers (Richardson et al., 2004). The low plasma triglyceride concentration was attributed to accretion in adipose tissue and greater fat content in high-RFI cattle and greater energy requirement by muscle tissue due to greater protein turnover rate. This was supported by the findings of Kelly et al. (2010), where NEFA was greater in the low RFI group. They also reported a positive relationship for circulating β-hydroxybutyrate with RFI, FCR, and DMI.

Blood cholesterol, due to its more stable relationship with RFI, is considered a better indicator of energy efficiency in cattle. Cholesterol plays a major role in lipogenesis and lipid transport in cattle (Van Soest, 1982) as well as serving as a precursor for steroid hormones. Synthesis of cholesterol from acetate in ruminant hepatic tissue is an energetically expensive process (Christie, 1981). Thus, lower circulating cholesterol may indicate lower cholesterol production, decreased lipogenesis, decreased lipid transport, and overall decreased energy expenditure. Moreover, mean blood cholesterol levels were reduced in efficient bulls, indicating its potential as an indicator of feed efficient animals (Bourgon et al., 2017).

Blood alkaline phosphatase (ALP) is a protein that is secreted from liver and bone tissues and is positively correlated with feed intake in cattle (Richardson et al., 2014). Lancaster et al. (2014) has reported that an elevated hepatic mitochondrial respiration is associated with improved feed efficiency. There have been inferences that greater mitochondrial respiration in efficient bulls will result in lesser blood ALP (Zhong et al., 2011; Bourgon et al., 2017), rendering it as another candidate for selection on feed efficiency.

Blood IGF-1 in growing bulls increases in concentration initially from 238 to 350 d, followed by a decrease thereafter (Brito, 2007). Although some past studies have reported decreased IGF-1 with improved efficiency in beef cattle (Arthur et al., 2004; Moore et al., 2005), others observed no correlation between them (Lancaster et al., 2008). When using IGF-1 as a selection tool for feed efficiency, age of the animal is an important factor to be accounted for. Due to the variation of IGF-1 between age groups, IGF-1 may not be an accurate indicator of feed efficiency, especially in older cattle (Bourgon et al., 2017).

Circulating thyroid hormones were also studied to define their role in determining feed efficiency. Although the association of T4 with feed efficiency is ambiguous from past studies (Walker et al., 2015; Bourgon et al., 2017), lower T3 levels in blood are associated with greater efficiency. Greater T3 was reported to be associated with high maintenance energy requirements (Iossa et al., 2001) by increasing energy expenditure and feed intake (Hulbert, 2000). Circulating T3 could be used as a proxy for selection based on RFI when dealing with bulls from similar age group.

Several circulating compounds in the blood contribute to the blood osmolality. In ruminants, glucose concentration in blood is less when compared to non-ruminants (VI Baldwin et al., 2004), and hence a greater influence on osmolarity is exerted by circulating urea and sodium for ruminants than monogastrics. More efficient bulls exhibited lower blood osmolality, suggesting a lower concentration of circulating solutes (Gennari, 1984), indicating less energy expenditure for protein turnover and ion transport (Baldwin et al., 1980). This indicates a decreased maintenance energy requirement in efficient animals. Further, a lack of difference in the osmolality between divergent efficiency groups on the day of slaughter is attributed to a higher stress level on the day of slaughter, which is associated with changes in ion transport (Minka and Ayo, 2009), electrolyte balance, and osmolality (Schaefer et al., 1997; Bourgon et al., 2017).

Energy and nutrients might be diverted from productive processes to support the innate immune system in stress responses (Klasing and Iseri, 2013) and this loss of energy and nutrients can affect performance (Adams, 2008). Evidence suggest that less efficient animals exhibit higher oxidative stress (Chen et al., 2011) and have more activated detoxification processes (Chen et al., 2012a, 2012b), indicating increased energy requirement to deal with metabolic stress. Supporting this notion, Richardson et al. (2004) reported that, in beef steers, plasma cortisol was negatively correlated to RFI, and insulin and leptin positively correlated to RFI. Elsasser et al. (2008) reported that when growing animals encounter stress, the activation of a cascade of pro-inflammatory mediators like cytokines, prostaglandins, superoxide anions, and nitric oxide will override the regulatory signals normally ascribed for growth and anabolic tissue accretion. They also reported that the efficiency of growth rate in these animals will decrease due to diversion of nutrients for the immune functions.

Several other factors contribute to the complexity of interpreting the metabolic profiles, including the homeostatic control mechanisms and factors governing rumen function, leaving the causal-effect relationships difficult to explain (Kelly, 1997; 2010). The blood parameters commonly analyzed as phenotypic markers of feed efficiency are often influenced by age, time of sampling, and stress. The complex biochemical pathways through which these blood metabolites are associated with feed efficiency are still vague and is constantly evolving.

2.2.3.4 Insulin and feed efficiency

As discussed in the previous section, circulating blood hormones can influence glucose metabolism. Among several metabolites and hormones studied for their correlation with feed efficiency traits, one important hormone is insulin. Insulin is secreted from the islets cells of the pancreas in response to circulating levels of metabolites, primarily glucose. Association of insulin with feed efficiency was reported by Richardson et al. (2004), where high RFI steers tended to have greater insulin concentrations than low RFI steers when fed a finishing diet.

Insulin resistance has been studied extensively in transition dairy cattle associated with their negative energy balance. The anabolic hormone promotes uptake of glucose, reduces catabolism of protein and lipid, and can influence feed efficiency. Considering that most of the

circulating glucose originates from hepatic gluconeogenesis and that gluconeogenesis is an energy consuming reaction, the effect of dietary energy source towards glucose and insulin responses are important. When corn and hay fed steers were studied, Rhoades et al. (2007) found that glucose supply and tissue utilization of glucose in response to insulin was influenced by the dietary energy source. However, a past study had reported that there were no changes in insulin sensitivity among steers based on dietary energy density when fed a similar diet fed for 140 d (Vasconcelos et al., 2009). These data suggest that rather than the dietary energy content, the energy source, has a major impact on glucose availability, insulin response, and glucose metabolism.

Kelly et al. (2010) reported that the glucose:insulin ratio was negatively correlated with FCR and thus, according to this index, more efficient cattle have altered glucose metabolism. However, the FCR was not affected by RFI. Richardson et al. (2004) reported that high RFI steers exhibited increased insulin concentrations due to increased fat deposition, as insulin reduces lipolysis and stimulates lipogenesis. Hocquette et al. (1999) reported a positive relationship between plasma insulin concentration and carcass adipose tissue. McCann and Reimers, (1986) and McCann et al. (1986) reported that low RFI cattle with an increased leanness might have greater insulin sensitivity of muscles resulting in increased glycolytic energy metabolism, thereby explaining the reduced insulin concentration. Meanwhile, high RFI steers might have reduced muscle sensitivity to insulin, resulting in reduced muscle protein catabolism and subsequently greater release of insulin from the pancreas thereby promoting adipogenesis and carcass fatness (Trenkle and Topel, 1978). However, a cause-effect relationship between insulin concentration and tissue adiposity is difficult to derive, as the underlying molecular mechanisms in ruminants are still to be elucidated.

De Koster and Opsomer (2012) discussed that many modern-day metabolic states in humans such as pregnancy and obesity are similar to insulin resistance observed in cattle. Even though there are only limited number of studies that evaluate the mechanisms underlying insulin resistance in beef cattle with increasing adiposity, a considerable number of studies have been undertaken for humans, exploring the mechanism of insulin resistance associated with obesity. Obesity has been associated with increased circulating NEFA and insulin resistance in humans (Reaven et al., 1988; Boden, 1997). There is strong evidence linking the concentration of circulating NEFA with the development of insulin resistance in ruminants (Oikawa and Oetzel,

2006; Pires et al., 2007). In ruminants, an increase in circulating NEFA is often associated with negative energy balance and is well documented in transition dairy cattle. Studies on fatty acid digestion in humans have shown another source of circulating NEFA, commonly referred as "spill over", originating from inefficient fatty acid uptake by adipose tissue postprandially (Evans et al., 2002; McQuaid et al., 2011). Chylomicrons and triglycerides undergo lipolysis by lipase before their uptake by the adipose tissue. In obese individuals, this lipase mediated uptake of triglycerides is impaired (Potts et al., 1995; Sadur et al., 1984; McQuaid et al., 2011). Even though the dietary fat content in ruminants is considerably lower than for humans, the contribution of spill-over NEFA due to reduced lipase mediated uptake by adipose tissues in finishing cattle could be a contributing factor to insulin resistance. Studies using human subjects showed that subcutaneous fat is the main source of systemic NEFA in circulation when compared to other adipose depots (Nielsen et al., 2004), and in ruminants, subcutaneous fat depots develop in parallel to the development of insulin resistance. Increased NEFA delivery or decreased intracellular fat metabolism could lead to intracellular accumulation of fat intermediate molecules that can activate a cascade of reactions leading to insulin resistance in humans (Shulman, 2000). The association of NEFA in circulation and the development of insulin resistance has been established in both species (human and bovine), even though the cause-effect relationship and the exact molecular mechanisms are still vague.

While circulating NEFA has been associated with insulin resistance, there is feedback inhibition on NEFA production per unit of fat mass with increasing adiposity in humans (Karpe et al., 2011). This feedback can reduce the amount of NEFA secreted per unit of fat, but the overall secretion of NEFA into the blood stream in obese individuals is increased over time. However, this expected increase in NEFA in the blood stream has not always been reported. Possible reasons might include the short half-life of NEFA and high standard deviation for plasma NEFA concentrations, even within the same individuals (Eaton et al., 1969). In the absence of a consistent increase in circulating NEFA associated with insulin resistance, other mechanisms possibly leading to insulin resistance have been evaluated. One of them is increased ectopic lipid deposition (Yki-Jarvinen, 2002), where fat is deposited in tissues other than adipose tissues and the associated impairment in fat metabolism. There is strong link between intra-myocellular triglyceride

accumulation and insulin resistance in humans (Perseghin, 1999; Kelley, 2005). More studies are needed to find how these factors are associated with insulin resistance in ruminants.

The distribution of fat across the body is also as important as the level of whole-body adiposity and contributes to the development of insulin resistance. Studies in humans have shown that individuals with more peripheral distribution of fat are more insulin sensitive than individuals with central or visceral fat deposition (Carey, 1996; Kahn, 2006). The quantity of proteins secreted by adipocytes also varies depending on the type of fat depot. This is particularly true with adiponectin secretion where omental adipocytes secrete more adiponectin than subcutaneous adipocytes (Motoshima et al., 2002). Adiponectin is an insulin sensitizer and will lead to fatty acid oxidation. Visceral fat is more lipolytic and less sensitive to the anabolic effect of insulin than its peripheral counterpart (Montague and O'Rahilly, 2000), thereby exposing the hepatic tissue to more NEFA than peripheral tissues due to its proximity. A reversal of insulin resistance was observed in rats (Catalano et al., 2010), with reduction of mesenteric fat and hepatic triglycerides. Sinclair (2010) explained that differences in regional body fat deposition and insulin resistance affect ruminant production primarily through its influences on liver metabolism and hepatic lipidosis. Even though in ruminants, the rate of hepatic free fatty acids (FFA) synthesis and hepatic entry of FFA from circulation are comparatively low (Vernon, 2005), high circulating concentrations of SCFA are more potent insulin stimulators than glucose (Brockman, 2005). Considering the differential substrate preferences among various adipose depots in ruminant systems (Smith and Crouse, 1984), understanding the substrate preferences of visceral fat and changes in blood metabolites in the portal vein may hold the key for better understanding of insulin resistance in finishing beef cattle.

2.2.4 Strategies to increase feed efficiency

Improved animal performance can be achieved by increasing efficiencies through improved nutrition, reproduction, genetics, and management (Boadi et al., 2004). Several studies have demonstrated that considerable genetic variation exists in feed efficiency, both within and across breeds (Archer et al., 1999, Renand and Krauss 2002). Moreover, advances in technology have also resulted in a better understanding of complex physiological processes and have helped in developing growth modifiers to improve efficiency.

2.2.4.1 Dietary management

Recent advances in our understanding of the role of nutrition in modulating the ruminal microbiota or at least their end-products and consequently the physiology of cattle has provided nutritionists with the tools to formulate diets maximizing efficiency. Feed efficiency can partly be attributed to dietary energy supply and digestibility of nutrients. As a general concept, high-grain diets are considered more efficient than forage-based diets (Beauchemin et al., 2001). Similarly, among roughage sources, the undigested NDF (uNDF) content is a major determinant of forage digestibility and efficiency (Sniffen et al., 1992) and highly lignified roughage sources and byproduct feeds can decrease digestibility and efficiency compared to good quality forages (Thompson et al., 2002). High lipid products in diets in association with high fibre concentrations can impact microbial fibre digestion in the rumen decreasing digestibility of fibre (Górka et al., 2013). However, the importance of fibre digestion for finishing cattle has been questioned (Górka et al., 2013). Highly fermentable finishing diets can cause a rapid decline in ruminal pH that can also adversely affect ruminal fibre digestion and the resulting ruminal acidosis can initiate a local and systemic pro-inflammatory response (Kent-Dennis et al., 2019). Both the reduction in pH and initiation of a low-grade systemic immune response can consequently decrease feed efficiency, necessitating mitigation strategies to reduce the incidence and severity of ruminal acidosis (Castillo-Lopez et al., 2014). Thus, while cereal grain processing such as dry-rolling or steam-flaking can improve the nutritive value and increase digestibility, over processing also can increase risk for ruminal acidosis. Others have suggested that reducing the starch content could be beneficial as Russel (2016) reported that growing and finishing steers using roughage sources along with byproduct feeds had improved ADG when compared to other conventional dietary management strategies.

2.2.4.2 Management strategies with growth enhancing technology

Growth promoting technologies such as implants, β-adrenergic agonists, antibiotics, and ionophores are broadly used to improve performance, reduce ruminal disorders, and improve feed efficiency (Wileman et al., 2009, Samuelson et al., 2016). Ionophores such as monensin and antibiotics such as tylosin are included in the finishing diets of beef cattle to improve animal health

and feed efficiency. The single largest improvement in cattle performance is ascribed to anabolic implants that increase final BW and promote greater lean tissue accretion relative to a non-implanted steer (Guiroy et al., 2002). In contrast, β-adrenergic agonists are incorporated into finishing diets during the last 20 to 40 d before harvest to improve efficiency of weight gain and increase the proportion of lean muscle (Avendano-Reyes et al., 2006; Vasconcelos et al., 2008; Montogomery et al., 2009). Chung and Johnson (2008) reported that the enhanced lean tissue growth observed with β-adrenergic agonists was due to enhanced contribution of satellite cell nuclei as a source of DNA for muscle fibres thereby promoting muscle hypertrophy.

The β-adrenergic agonists used for finishing cattle include zilpatrol hydrochloride (ZH) and ractopamine hydrochloride (RH). Ractopamine, which will increase lean muscle proportion by increasing protein deposition and hypertrophy of muscle fibres, has been banned in 160 countries since 2013. Even though the addition of ZH did not increase G:F, there was an increase in HCW, which was presumably due to repartitioning of body mass from non-carcass components to carcass tissues or differences in tissue deposition rates for carcass and non-carcass components (Montogomery et al., 2009; Holland et al., 2010). Thus, when corrected for carcass, β-adrenergic agonists generally improve carcass adjusted gain and carcass-adjusted feed efficiency. Due to the repartitioning of body mass, there was an increase in dressing percentage and LM area (Avendano-Reyes et al., 2006; Vasconcelos et al., 2008; Montogomery et al., 2009). Chung and Johnson (2008) reported that supplementation with β-adrenergic agonists results in stimulation of β-adrenergic receptors on cell surfaces that increase the skeletal muscle mass, cross-sectional area of individual muscles or both, and this increase in muscle mass increased N requirements resulting in less urinary N excretion.

2.3 Alternative diets in feedlot cattle

With the aim of reducing the dependency on conventional fossil fuels, in early 2000, more attention was given to the production of biofuels from feed grains. Government policy focusing on renewable fuel sources increased the proportion of the total grain supply in the US and Canada that was directed towards ethanol production rather than being used for human food or the feed industry (Mabee and Saddler, 2010). This diversion has resulted in tighter supply of cereal grains

for the livestock sector, significantly contributing to the increased market price of cereal grains. This has resulted in the search for viable energy rich alternatives to be used in the feedlot sector.

2.3.1 Advantages of single byproduct substitution

The high cost of cereal grains has motivated the beef industry to search for viable energy-rich alternatives that could allow for at least partial replacement of cereal grains. Studies evaluating the incorporation of various byproducts from the grain, oil-seed, and bioethanol industries into feedlot diets based on barley grain have demonstrated that comparable carcass quality and ADG can be attained at a lesser cost, even though the rate of incorporation plays a vital role (Pylot et al., 2000; Li et al., 2011). A study by Li et al. (2011) demonstrated that wheat DDGS can be used to substitute for barley grain and barley silage in finishing diets at 25 to 35% of the dietary DM. In a similar study conducted by Wierenga et al., (2010) triticale DDGS was included at 20 to 30% on a DM basis by replacing barley grain and barley silage with no negative consequences on ADG and carcass characteristics. In a study where sunflower seeds were included at 9 to 14% o of the dietary DM by replacing barley grain for finishing steers, Gibb et al., (2004) reported a linear increase in DMI, ADG, G:F ratio, and dressing percentage. Felton and Kerley (2004) reported that including whole raw soybean in finishing diets of feedlot steers had little effect on carcass quality, ADG, and feed efficiency. These studies emphasize the considerable amount of work that has been conducted to evaluate energy sources other than traditional cereal grains, so that at least part of the cereal grain can be replaced in feedlot diets in order to reduce feed cost.

2.3.2 Disadvantages of byproducts in feedlot diets

The inclusion of byproduct feeds in feedlot diets has been limited for several reasons. The dustiness and difficulty in handling byproducts like soyhulls, oat hulls, and rice bran are factors that restrict their utilization. Because of their low density, costs associated with transportation and storage can be greater than the cost of the feed. Another factor liming the use of byproducts is the high proportion of phosphorus and sulfur in some of these ingredients, leading to greater risk for toxicity such as for polioencephalomalacia. For example, corn DDGS used in feedlot diets can

have a high sulfur content ranging from 0.35 to 1.04% (DM basis; He, 2016b) that can affect the Cu homeostasis along with increasing risk for sulfur induced polioencephalomalacia.

Some byproducts may contain toxic components (gossypol in cotton seed and ergot in grains) that restrict their use in large quantities in cattle diets. Byproducts arising from the oil industry, like whole canola seed (off-grade or heat damaged), canola meal, and soybean meal have high concentrations of protein and whole canola and soybean seeds are rich in fat. Feeding byproducts rich in fat content may limit the DMI and fibre digestibility in rumen. Feeding a single byproduct at high inclusions can often lead to overfeeding of some nutrients and less efficient feed utilization (Amat et al., 2012; Yang et al., 2012). Overfeeding (e.g. CP) can lead to greater nutrient cost and loss of nutrients to the environment. Moreover, the nutrient composition of byproducts are dependent on several factors like species and strain of crop used, climate, geographical location, year, crop management, stage of harvest, and type and severity of processing. The unpredictability in the nutrient composition of byproducts, between batches and across sources (Marx et al., 2000) is a challenge for the nutritionist to formulate a balanced diet.

Most of the byproducts arising out of biofuel, oil, and grain industries are high in fibre content and possess a lower dietary energy value and energy density relative to the ingredient that they replace (Marx et al., 2000). One strategy to overcome reduced energy density arising from byproduct incorporation could be to include ingredients rich in lipids (Zinn and Jorquera, 2007; Hess et al., 2008) like off-grade, frost damaged, or heat damaged canola which have become increasingly available (Pylot et al., 2000).

2.3.3 Blended byproducts

The most efficient strategy to avoid the drawbacks of single byproduct utilization and eliminate overfeeding is to formulate a strategic combination of different byproducts to optimize ruminal and postruminal energy and protein availability (Zenobi et al., 2012). Blending strategies also reduce the risk of overfeeding or underfeeding particular nutrients (Amat et al., 2012; Yang et al., 2012). Górka et al. (2013) combined off-grade canola, pea screenings, and oat hulls in a pelleted form with wheat included as a binder and reported comparable ADG to that obtained with a barley-based control diet. Górka et al. (2013) reported that despite the additional cost, pelleting confers the advantage of allowing for precise ingredient inclusion and mixing and rapid analysis

of feeds before mixing using near-infrared spectroscopy, thereby allowing changes in ingredient inclusion rate to minimize variation in nutrient composition of final product. Moreover, the pellet can provide a means to deliver minerals, vitamins, and other feed additives. Pelleting will also reduce the dustiness, increase the bulk density of individual ingredients, and reduce the wastage and cost associated with handling, storage, and transport. The feed offered can be better controlled by pelleting when compared to feeding unprocessed individual ingredients (Thomas and van der Poel, 1996).

However, the fine physical structure of byproducts and the reduction in particle size associated with pelleting can negatively affect the G:F (Abouheif et al., 2012). With a greater proportion of NDF and finer particle size, byproduct pellets likely increase the passage rate of digesta and reduce ruminal retention time and digestibility (Rodrigue and Allen, 1956; Abouheif et al., 2012; Górka et al., 2013). Digestibility of structural carbohydrates, especially lignified carbohydrates from byproducts like oat hulls, is less than non-structural carbohydrates (Beauchemin et al., 2001; Thompson et al., 2002).

2.3.4 Rumen fermentation and feed efficiency with byproduct diets

Despite being energy dense, lipid supplements can reduce ruminal fibre digestibility (Hess et al. 2008) in finishing cattle and shift the site of starch and fibre digestion to the small and large intestine (Plascencia et al., 2003). However the effect of lipid supplementation on OM digestibility in ruminants is often inconsistent and depends on the source and type of lipid used for supplementation (Hess et al., 2008).

Experiments designed to evaluate alternative energy sources have reported many inconsistent findings. Firstly, the feed efficiency of fat rich byproducts as a substitute for cereal-based concentrate has been shown to be influenced by various factors such as the source of byproduct, level of incorporation (Zinn, 1989; Walter et al., 2012), nature of processing (for example, pelleted or rolled; Williams et al., 2008), degree of ruminal biohydrogenation of fat (Plascencia et al., 1999), and the cereal present in the basal diet. A study using cannulated heifers (Walter et al., 2012) indicated that varying the level of incorporation of corn DDGS and wheat DDGS had differential effects on DMI and digestibility affecting the meat characteristics. Williams et al. (2008) reported that pelleted barley blended with canola meal results in improved

feed conversion when compared to rolled barley and canola meal for steers. Plascencia et al., (1999) reported that decreasing ruminal biohydrogenation using formaldehyde protected fat minimizes the detrimental effect of fat on digestibility of fibre. Thus, it appears that a variety of feed ingredients may be included in as energy sources for feedlot cattle; however, the impact of differing energy sources and their inclusion rate on performance and feed efficiency outcomes need to be considered.

To study the performance of cattle fed fat rich diets based on byproduct pellets during the finishing stage, Górka et al., (2013) used high-lipid byproduct pellets as a partial replacement for barley grain. In that study, feeding cattle with 60% high-lipid pellet-based diets (5.5% crude fat) resulted in a less favourable G:F ratio relative to the control diet. But, from a partial economical assessment, they reported that it was more economical to feed the high-lipid byproduct pellets (HLP) when cereal grain prices are high. It was expected that this lower cost of gain would outweigh negative effects on the G:F ratio based on the fact that carcass yield and grade were not affected. Moreover, marked variation among treatments in the G:F ratio were observed throughout the feeding period, where initially cattle fed the HLP had poor feed conversion, but G:F was not different than barley fed cattle near the end of the finishing period. Understanding the cause for this variation in feed efficiency could help to develop strategies that enhance feed efficiency and the utilization of low-cost alternative energy sources.

The exact reasons for difference in feed efficiency between the cereal grain-based diet and diets containing high-fat high-fibre pellets have not been thoroughly investigated. Furthermore, there is a paucity of data describing factors affecting the changes in feed efficiency throughout the finishing period. It is commonly accepted that feed efficiency is less favourable with advancing days on feed (NRC, 2000; NASEM, 2016). The reduction in G:F is generally attributed to the increased energy required per unit gain with fat compared to muscle protein (Welegedara et al., 2012), and that cattle are approaching a mature body weight (NRC, 2000). While these explanations may partially explain this phenomenon, it must be acknowledged that factors responsible for changes in the G:F ratio may also be attributable to pre-absorptive factors (total tract digestibility), absorptive capability (SCFA absorption), and post-absorptive nutrient utilization (intermediary metabolism). A thorough understanding of the changes in the digestive physiological processes during the course of the finishing stage may lend the possibility to mitigate

the decreased efficiency through nutrition or management. No comprehensive studies, to my knowledge, have evaluated changes in feed digestibility, nutrient absorption, or post-absorptive nutrient utilization with advancing days on feed. Some individual, but short-term studies in this area have shed some light on the fact that other reasons like repeated episodes of ruminal acidosis which may increase in severity with subsequent exposure (Dohme et al., 2008) can contribute to the reduced feed efficiency with advancing DOF (Penner et al., 2010; Wilson et al., 2012), which may be mitigated by substituting highly fermentable cereal grain with lipid pellets at later stages (Gorka et al., 2013). This also suggests the importance of developing and evaluating phase feeding programs using feeds with varying energy substrates to negate the economic impact of decreased feed-efficiency in late finishing stages.

Moreover, the NRC (2000) and NASEM (2016) evaluation of feed energy is based on short-term feeding trials and chemical analysis whereas, the energy requirement of the animal is determined mainly based on long-term feed trials associated with comparative slaughter study approaches. Thus, the efficiency of feed utilization and increased requirement for gain with changing tissue proportions (increased fat relative to protein per unit of empty body gain) is confounded with days on feed. Thus, it is possible that the importance of the changes in energetic losses or efficiency of feed utilization before the contribution of feed towards retained energy, associated with increasing days on feed (eg. losses associated with digestion, nutrient absorption and utilization) have been underemphasized.

2.4 Global hypothesis and objectives

The decline in G:F during finishing can be partially accounted for by reductions in short-chain fatty acid absorption and changes in the post-absorptive utilization and is influenced by dietary energy source and timing of provision.

Objectives:

1) To determine whether phase-feeding programs can be used to optimize the delivery and use of energy substrates during the finishing period;

2) To determine if days on feed and the dietary energy source affect apparent total tract digestibility, short-chain fatty acid absorption, and post-absorptive utilization of glucose and acetate (2 major energy substrates for ruminants);

3) To determine whether the level of forage inclusion affects total tract digestibility and growth performance of growing beef heifers fed diets containing a high proportion of HLP;

4) To determine if increasing levels of fat with non-forage fibre sources will alter the rumen passage rate, site of digestion, and hence the fat and fibre digestibility.

3.0 EVALUATION OF A PHASE-FEEDING STRATEGY UTILIZING A HIGH-LIPID HIGH-FIBRE BYPRODUCT PELLET IN DIETS FOR FEEDLOT STEERS[1]

ABSTRACT: Two studies were conducted to evaluate the timing of provision of a high-lipid high-fibre byproduct pellet when used as a partial replacement (60% in Study 1 and 30% in Study 2; HLP) for barley grain and canola meal in a barley-based finishing diet (BAR). The HLP was fed for the last 49, 98, or 147 d (HLP49, HLP98, and HLP147, respectively) in Study 1, and for the last 60 d or 120 d in Study 2 (HLP60 and HLP120, respectively) or the last 60 d with additional canola oil (HLP60CO). In study 1, steers fed BAR147 had the greatest ADG (P = 0.009) and G:F (P = 0.010). The HLP147 had the greatest DMI during the first 49 d but least during the last 49 d of the finishing phase (treatment × period; P = 0.003). Hot carcass weight for BAR147 and HLP49 were the heaviest (P = 0.036). In Study 2, DMI and ADG were not affected but hot carcass weight was greater for BAR120 and HLP60 than for HLP120 and HLP60CO (P = 0.01). Partially replacing barley grain and canola meal with a high-fibre high-lipid byproduct pellet in the latter part of the finishing period may improve carcass yield grade without affecting ADG and G:F.

[1]A version of this chapter has been published: Joy, F., P. Górka, J. J. McKinnon, S. Hendrick, L. O. Burciaga-Robles, and G. B. Penner. 2016. Evaluation of a phase-feeding strategy utilizing high-lipid high-fibre byproduct pellets in diets for feedlot steers. Can. J. Anim. Sci. 96: 232-242.

3.1. Introduction

Feed grain prices in western Canada have been volatile over the past decade. Some factors contributing to the volatility include yearly variation in crop yield, quality, and availability, as well as regulatory decisions to support the bioethanol and biodiesel industries (Ministry of the Economy, Government of Saskatchewan, 2013). As a consequence of increased grain prices, feedlot operators have been searching for viable alternatives to cereal grains as energy sources for finishing cattle. Studies evaluating the use of byproducts from the cereal grain, oilseed, and bioethanol industries for finishing cattle have demonstrated that comparable carcass quality and ADG can be attained, relative to barley grain, although the level of incorporation of the byproducts in the diets could affect performance (Pylot et al., 2000; Amat et al., 2012; Yang et al., 2012). Most previous studies have investigated byproduct inclusion in isolation rather than a combination of various byproducts. However, recent studies have evaluated the use of strategically blended byproduct pellets that incorporate the benefits of individual byproducts while avoiding overfeeding of individual nutrients as occurs with single byproduct inclusion strategies (Górka et al., 2013; Zenobi et al., 2014). The use of strategically blended byproduct pellets also minimizes difficulty associated with handling multiple ingredients on farm and increases feed density.

To maintain caloric density as a substitute for cereal grains, byproduct pellets often depend on byproducts from the oilseed industry as a cheaper source of energy substrate (Górka et al., 2013). Hence the incorporation of byproducts from the oilseed industry (e.g. off-grade canola) can be associated with a partial shift in the dietary energy source from starch to lipid. Such a shift has been reported to be beneficial with regard to ruminal pH, even though it is also associated with reduced apparent total tract diet digestibility (Górka et al., 2015), especially when replacing more than 60% of the barley grain on a DM basis.

Some individual, but short-term studies focusing on ruminal pH have indicated that exposure to ruminal acidosis may increase the risk and severity of subsequent ruminal acidosis bouts (Dohme et al., 2008). Exposure to ruminal acidosis can contribute to reduced feed efficiency (Castillo-Lopez et al., 2014) and the risk for digestive disorder related morbidity increases towards the later stages of the finishing period (Castillo-Lopez et al., 2014; Xu and Ding 2011). One approach to limit digestive associated morbidity linked to ruminal acidosis could be to partially replace barley grain with high-lipid, high-fibre byproduct pellets. Shifting from a starch source to

a lipid source may also provide more precursors for fat deposition and fatty acid biosynthesis (Nayananjalie et al., 2013). Collectively, the above-listed information suggests that there may be an opportunity to evaluate phase-feeding programs using feeds with varying energy substrates for finishing beef cattle.We hypothesized that using HLP in a phase-feeding program in which the dietary energy source is altered at different stages of finishing will result in similar production performance relative to steers fed a cereal-grain based diet.

3.2. Materials and methods

All experimental procedures were reviewed and approved by the University of Saskatchewan Animal Research and Ethics Board before initiation of the studies described below.

3.2.1 Study 1

A total of 288 crossbred steers were purchased from a local auction market (mean BW ± SD, 351.5 ± 20.4 kg). Upon arrival, all steers were treated with Ivermectin pour-on against endo- and ecto-parasites (Bimectin® Pour-on, Bimeda-MTC Animal Health Inc., Cambridge, ON) and were vaccinated against *Pasturella haemolytica* and *Hemophilus somnus* (Somnu-Star Ph®, Novartis Animal Health Canada Inc., Mississauga, ON) and also against infectious bovine rhinotracheitis, bovine viral diarrhea Type I and II, para-influenza-3, and bovine respiratory syncytial virus (Starvac® 4 Plus, Novartis Animal Health Canada Inc.). Steers were also vaccinated against eight different strains of clostridium prevalent in Canada (Covexin® Plus, Schering-Plough Animal Health, Pointe Claire, QC) and were also given a dose of broad-spectrum antibiotic (Liquamycin® LA-200®, Pfizer Canada Inc., Kirkland, QC). After initial processing, steers were implanted with 200 mg of trenbolone acetate and 40 mg of estradiol (Revalor XS, Revalor Implants, Merck, Kirkland, QC). All steers were housed in pens measuring 12 × 24 m with 3.3-m high windbreak (20 cm m^{-1} porosity) fencing. After an initial acclimatization of 21 d, steers were stratified by BW and randomly allotted to one of 24 pens (12 steers/pen and 6 pens/treatment). Diets included a barley-based (processing index (wt/v) = 80%) diet (BAR) or a diet where high-lipid high-fibre byproduct pellets were used to replace 60% of the rolled barley grain and canola meal. The high-lipid high-fibre byproduct pellets contained (% inclusion on DM basis): wheat

(29.7), off-grade canola (14.9), wheat screenings (26.4), oat hulls (11.2) and pea screenings (17.8; Table 3.1). The high-lipid byproduct pellets were produced at West Central Pelleting Ltd. (Wilkie, Saskatchewan, Canada) and were similar to that reported by Gorka et al. (2013). When the high-lipid byproduct pellets were included as a partial replacement for barley grain and canola meal, the high-lipid high-fibre byproduct pellets-containing diets (HLP) contained (DM basis) 51.2% high-lipid high-fibre byproduct pellets, 34.1% rolled barley grain, 8% mineral-vitamin pellets, 6% barley silage and 0.7% limestone (Table 3.1). The diets were formulated to be iso-nitrogenous and iso-caloric and to target an ADG of 1.8 kg d^{-1} based on NRC (1996).

In addition to the diets, the 147-d finishing phase was divided equally into three periods of 49 d each, namely P1 (d 1 to d 49), P2 (d 50 to d 98) and P3 (d 99 to d 147). Treatments were a combination of experimental diet and the timing (periods described above) and duration for when diets were fed (Table 3.2). Pens assigned to the control (BAR147) treatment were fed the barley-based finishing diet throughout the 147-d finishing period. The remaining treatments were used to evaluate whether the duration and timing of feeding the high-lipid high-fibre byproduct pellets affect DMI and production responses. Thus, pens were assigned to the HLP147 (HLP diet fed throughout the 147 d), HLP98 (BAR fed during P1and HLP fed during P2 and P3) and HLP49 (BAR fed during P1 and P2, and HLP diet during P3) as described in Table 3.2. The study was designed as a completely randomized design (pen as the experimental unit) with repeated measures, where, the periods (P1, P2 and P3) were the repeated data points. Monensin and tylosin phosphate (Elanco Animal Health, Indianapolis, IN) were included in the mineral and vitamin pellets for all diets to target a final dietary concentration of 33 ppm and 11 ppm, respectively. Throughout the study, steers were fed a total mixed ration once daily at 1030 h and feed bunks were assessed before the morning feeding for the amount of residual feed. The amount of feed provided was designed to target 5% residual feed on a daily basis. At the start of study, steers averaged 378.4 ± 22.71 kg (mean ± SD) and the target final live weight was 650 kg.

The weights of individual steers were measured on two consecutive days at the start and end of the study to determine the initial and final body weight.

Table 3.1 Dietary ingredient and chemical composition of the barley-based (BAR) and high-lipid byproduct pellets (HLP) based diets used in Study 1.

Item	Diet	
	BAR	HLP
Ingredient, % DM		
Barley silage	6.0	6.0
Rolled barley grain	75.2	34.1
Canola meal	9.8	0.0
High-lipid high-fibre byproduct pellets[1]	0.0	51.2
Barley-based vitamin and mineral pellets[2]	8.0	8.0
Limestone	1.0	0.7
Chemical composition[3], % DM basis		
DM, %	85.0 ± 1.10	85.7 ± 1.26
OM, % DM	95.0 ± 0.28	94.0 ± 0.30
CP, % DM	15.5 ± 0.48	14.7 ± 0.38
Starch, % DM	45.5 ± 0.92	38.2 ± 0.79
Ether extract, acid hydrolysed,, % DM	3.2 ± 0.25	7.3 ± 0.76
NDF, % DM	22.6 ± 0.64	25.5 ± 0.67
ADF, % DM	10.4 ± 0.76	14.0 ± 1.17
Lignin, % DM	2.5 ± 0.14	3.4 ± 0.27
Ca, % DM	0.96 ± 0.048	0.90 ± 0.043
P, % DM	0.48 ± 0.016	0.42 ± 0.024
NE_m[4], Mcal kg of DM^{-1}	1.83 ± 0.017	1.93 ± 0.058
NE_g[4], Mcal kg of DM^{-1}	1.21 ± 0.016	1.29 ± 0.051

[1]Ingredient composition of high-lipid high-fibre byproduct pellets: 29.7% wheat, 14.9% off-grade canola, 26.4% wheat screenings, 11.2% oat hulls and 17.8% pea screenings.
[2]On DM basis contained 2.5% of NaCl, 5% of Ca, 0.46% of P, 2.0% of Mg, 1.96% of K, 2.0% of S, 5.06 mg/kg of Co, 161.0 mg/kg of Cu, 8.8 mg/kg of I, 494.8 mg/kg of Fe, 370.6 mg/kg of Mn, 2.5 mg/kg of Se, 345.2 mg/kg of Zn, 44052.8 IU/kg of vitamin A, 16519.8 IU of vitamin D, 330.4 IU of vitamin E, 901.4 mg/kg of choline, 442.7 mg/kg of monensin and 148.2 mg/kg of tylosin phosphate.
[3]Chemical analysis is average of three composite samples from three periods of the study.
[4]Net energy calculated from feed samples from NRC (2001) equation.

Table 3.2 Timing and duration of diet provision for steers in Study 1.

Treatment	Periods		
	P1 (d 1 to 49)	P2 (d 50 to 98)	P3 (d 99 to 147)
BAR147	BAR[1]	BAR	BAR
HLP147	HLP[2]	HLP	HLP
HLP98	BAR	HLP	HLP
HLP49	BAR	BAR	HLP

[1]BAR: Barley based finishing diet (75.2% rolled barley grain, 6% barley silage, 9.8% canola meal 8% vitamin- mineral pellets and 1% limestone on DM basis).
[2]HLP: High-lipid high-fibre byproduct pellets-based diet (34.1% rolled barley grain, 6% barley silage, 51.2% high-lipid high-fibre byproduct pellets, 8% vitamin-mineral pellets and 0.7% limestone on DM basis).

In addition, steers were weighed on a single day every two weeks. The weight change between consecutive weighing days was used to calculate ADG. Feed bunks were cleaned every two weeks corresponding to BW measurement and the residual feed was weighed, sampled for DM, and discarded. The difference in weight between the DM offered and DM of residual feed measured at the time of bunk cleaning was used to determine pen DMI.

Weekly representative feed ingredient samples were collected for barley silage and biweekly samples were collected for barley grain, high-lipid high-fibre byproduct pellets, mineral and vitamin pellets and canola meal. All samples of feed as well as samples of refusals were dried in a forced-air oven at 55°C for 72 h for DM determination. The DM content of each ingredient was used to ensure that the as fed ingredient provision met DM inclusion specifications. Subsequently, the dried feed ingredient samples were ground to pass through a 1-mm screen using a hammer mill (Christie-Norris Laboratory Mill, Christie-Norris Ltd. Chelmsford, UK). Samples were then composited by period and sent to Cumberland Valley Analytical Services (CVAS, Hagerstown, MD) for chemical analysis as described by Rosser et al., (2013) except ether extract, which was determined with acid hydrolysis (AOAC, 2005; Methods 922.06 and 954.02) because of the higher lipid content in feed ingredients and greater processing it undergone. Net energy values of feed were calculated by the commercial lab using a summation equation (NRC, 2001) and were also calculated based on animal performance as described by Zinn and Shen (1998) and Zinn et al. (2002).

At the end of the finishing period, steers were transported to a federally inspected abattoir (XL Foods, Brooks, AB). Hot carcass weight, back fat thickness, and rib eye area between the 12th and 13th rib were measured at the processing plant. The Canadian Beef Grading Agency yield grades and quality grades were determined using the Computer Vision Grading System (VBG 2000 e+v Technology GmbH, Oranienburg, Germany). Carcass adjusted G:F and ADG were calculated from a carcass adjusted final body weight, which in turn is calculated by dividing the hot carcass weight with a common herd dressing percentage (60%) calculated based on shrunk weight (Shipping weight × 0.96).

3.2.2 Study 2

Two hundred sixty-four crossbred steers were procured from a local auction market (mean BW ± SD, 424.7 ± 28.6 kg). The receiving protocol was the same as described for Study 1 with the exception that steers were implanted with 36 mg of zeranol (Ralgro®, Shering-Plough Animal Health) at the start of the study and then re-implanted with 40 mg of trenbolone acetate and 8 mg of estradiol (Revalor-G®, Hoechst-Roussel Agri-Vet, Somerville, NJ) 65 d after the initial implant. After an initial acclimatization of 21 d, steers were stratified by BW and randomly allotted to one of 24 pens (11 steers/pen).

Diets consisted of a 1) barley-based diet (BAR) similar to that in Study 1, 2) a diet where high-lipid high-fibre byproduct pellets were included at 30% (HLP**)**, or 3) a diet containing 30% high-lipid high-fibre byproduct pellets with added canola oil (HLP+CO; Table 3.3). Canola oil was sprayed into the mixing wagon to ensure uniform distribution of oil. The BAR and HLP diets were formulated to be iso-nitrogenous and iso-caloric targeting an ADG of 1.7 kg/d while the HLP + CO provided additional predicted net energy that would improve performance. The high-lipid high-fibre byproduct pellet composition was the same as described in Study 1 (Table 3.1). The 120-d finishing period was divided into two halves, P1 (first 60 d of study) and P2 (last 60 d of study). Pens were assigned to 1 of 4 treatments (Table 3.4) using a combination of diet and duration that the diet was fed. Treatments included; 1) the control that was fed BAR throughout the 120-d finishing phase (BAR120), 2) a treatment group that received HLP for 120 d (HLP120), 3) a treatment group where BAR was fed for P1 (i.e. 60 d) and HLP was fed for the last 60 d (HLP60), or 4) a treatment group where BAR was fed for P1 and the HLP+CO diet was fed for the last 60 d (HLP60CO). Body weight at the start of the study was 441.3 ± 27.2 kg (mean ± SD), with a targeted final weight of 650 kg. Data and sample collection and analysis were conducted as described in Study 1.

Table 3.3 Dietary ingredient and chemical composition of a barley-based finishing diet (BAR) and high-lipid pellets based diet (HLP) and the HLP diet with added canola oil (HLP+CO) (Study 2).

	Diet[1]		
	BAR	HLP	HLP+CO
Ingredient, % DM			
Barley silage	6.2	6.2	6.2
Rolled barley grain	83.1	58.0	54.7
Canola meal	5.2	0	1.0
High-lipid high-fibre byproduct pellets[2]	0	30.4	30.4
Barley-based vitamin and mineral pellet[3]	5.5	5.4	5.4
Canola oil	0	0	2.3
Chemical composition[4]			
CP, % DM	14.2 ± 0.35	13.4 ± 0.22	13.4 ± 0.21
Starch, % DM	46.7 ± 1.03	43.0 ± 0.84	41.3 ± 0.80
Ether extract, acid hydrolysed, % DM	3.5 ± 0.13	5.1 ± 0.13	7.4 ± 0.13
NDF, % DM	25.9 ± 1.51	28.2 ± 1.00	27.7 ± 0.94
ADF, % DM	10.9 ± 0.55	13.5 ± 0.30	13.4 ± 0.29
Lignin, % DM	2.5 ± 0.11	3.0 ± 0.26	3.0 ± 0.26
Ash, % DM	5.4 ± 0.18	5.8 ± 0.11	5.8 ± 0.11
Ca, % DM	0.69 ± 0.027	0.74 ± 0.018	0.75 ± 0.018
P, % DM	0.45 ± 0.014	0.40 ± 0.013	0.40 ± 0.012
NE_m[5], Mcal kg of DM^{-1}	1.84 ± 0.019	1.85 ± 0.020	1.91 ± 0.020
NE_g[5], Mcal kg of DM^{-1}	1.20 ± 0.012	1.22 ± 0.018	1.27 ± 0.017

[1]Diets: BAR diet: Finishing feedlot diet consisting mainly of barley grain and canola meal; HLP diet: A diet where high-lipid high-fibre byproduct pellets was included at 30 % of the total diet; HLP+CO diet: A diet similar to HLP diet with added canola oil.

[2]Ingredient composition of high-lipid high-fibre byproduct pellets: 29.7% wheat, 14.9% off-grade canola, 26.4% wheat screenings, 11.2% oat hulls and 17.8% pea screenings.

[3]On DM basis: 2.5% of NaCl, 5% of Ca, 0.46% of P, 2.0% of Mg, 1.96% of K, 2.0% of S, 5.06 mg/kg of Co, 161.0 mg/kg of Cu, 8.8 mg/kg of I, 494.8 mg /kg of Fe, 370.6 mg/kg of Mn, 2.5 mg/kg of Se, 345.2 mg/kg of Zn, 44052.8 IU/kg of vitamin A, 16519.8 IU of vitamin D, 330.4 IU of vitamin E, 901.4 mg/kg of choline, 442.7 mg/kg of monensin and 148.2 mg/kg of tylosin phosphate.

[4]Chemical composition is the average of four composite samples collected at different time points.

[5] Net energy calculated from feed samples on NRC (2001) equation.

Table 3.4 Timing and duration of diet provision for steers in Study 2.

Treatment	Periods	
	P1 (d 1 to 60)	P2 (d 61 to 120)
BAR120	BAR[1]	BAR
HLP120	HLP[2]	HLP
HLP60	BAR	HLP
HLP60CO[3]	BAR	HLP

[1]BAR: Barley-based finishing diet (83.1% rolled barley grain, 6.2% barley silage, 5.2% canola meal and 5.5% vitamin-mineral pellet).
[2]HLP: High-lipid high-fibre byproduct pellets based diet (58% rolled barley grain, 6.2% barley silage, 30.4% high-lipid, high-fibre byproduct pellets and 5.4% vitamin-mineral pellet).
[3]HLP+CO: Diet similar to HLP with added canola oil to increase energy density (54.7% rolled barley grain, 6.2% barley silage, 1% canola meal, 30.4% high-lipid, high-fibre byproduct pellets, 2.3% canola oil and 5.4% vitamin-mineral pellet).

3.2.3. Statistical analysis

Data from Study 1 and 2 were analyzed separately. For both studies, pen was used as the experimental unit and statistical analyses were performed using the mixed model of SAS (SAS version 9.2; SAS Institute, Inc. Cary, NC) with the fixed effect of treatment. When appropriate (for variables measured over time) the fixed effects of period and the treatment × period interaction were included in the model with period included as a repeated measure. For repeated measures, covariance error structures were tested to select the best-fit model for each variable based on least Akaike's and Bayesian information criterion values. For continuous variables with a single measurement time point, the model included the fixed effect of treatment. Yield grade, quality grade, and marbling score were analyzed using the GLIMMIX procedure of SAS (SAS version 9.2, SAS Institute, Inc. 2002) with binominal error structure and logit data transformation. For all statistical analyses, significance was declared when $P \leq 0.05$ and trends were discussed when $0.05 < P \leq 0.10$. When the F-test was significant, means were separated using the Tukeys method.

3.3. Results

3.3.1. Study 1

The BAR and HLP diets were formulated to be isonitrogenous and isocaloric, however the NE_m (calculated from NRC equations; NRC, 2001) was numerically greater (1.93 vs. 1.83 Mcal/kg) and CP numerically less (14.7 vs. 15.5 %CP) for the HLP diet compared to the BAR (Table 3.1). The difference between formulated and achieved dietary composition reflects a challenge with using byproduct feeds and is likely related to the variation in the nutritive value of the byproducts.

Overall, DMI increased with advancing days on feed ($P < 0.001$) from 9.43 kg d^{-1} in P1 to 12.22 kg d^{-1} in P3 (Fig. 3.1). Steers fed the HLP147 treatment had the greatest DMI during P1 but the least DMI in P3 (treatment × period interaction $P = 0.003$). The ADG was greater in P2 and P3 than P1 ($P < 0.001$; Table 3.5) and was greater for BAR147 than HLP treatments (1.96 vs 1.83 kg d^{-1}; $P = 0.009$). A treatment × period interaction ($P = 0.008$) was reported for G:F (Fig. 3.2), following a similar response as reported for DMI.

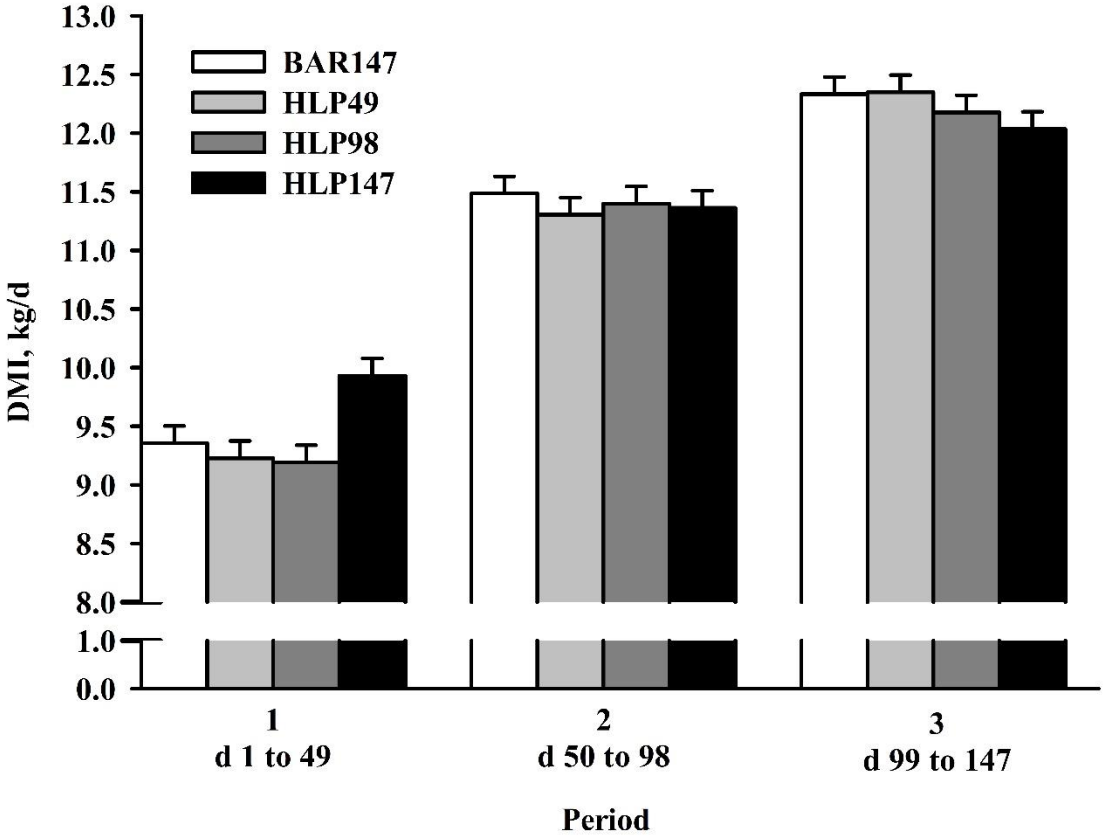

Figure 3.1 Treatment × period interaction for DMI (P = 0.003) for finishing feedlot cattle when fed with four different treatments. BAR147: BAR diet fed for 147 d, HLP147: HLP diet fed for 147d, HLP98: BAR followed by HLP diet fed for the last 98d, HLP49: BAR followed by HLP diet fed for the last 49d (Study 1). Within a period, the only difference among treatments was between HLP49 and HLP147 during P1. Pen was considered as the experimental unit (n = 6/treatment) and 3 consecutive periods per treatment.

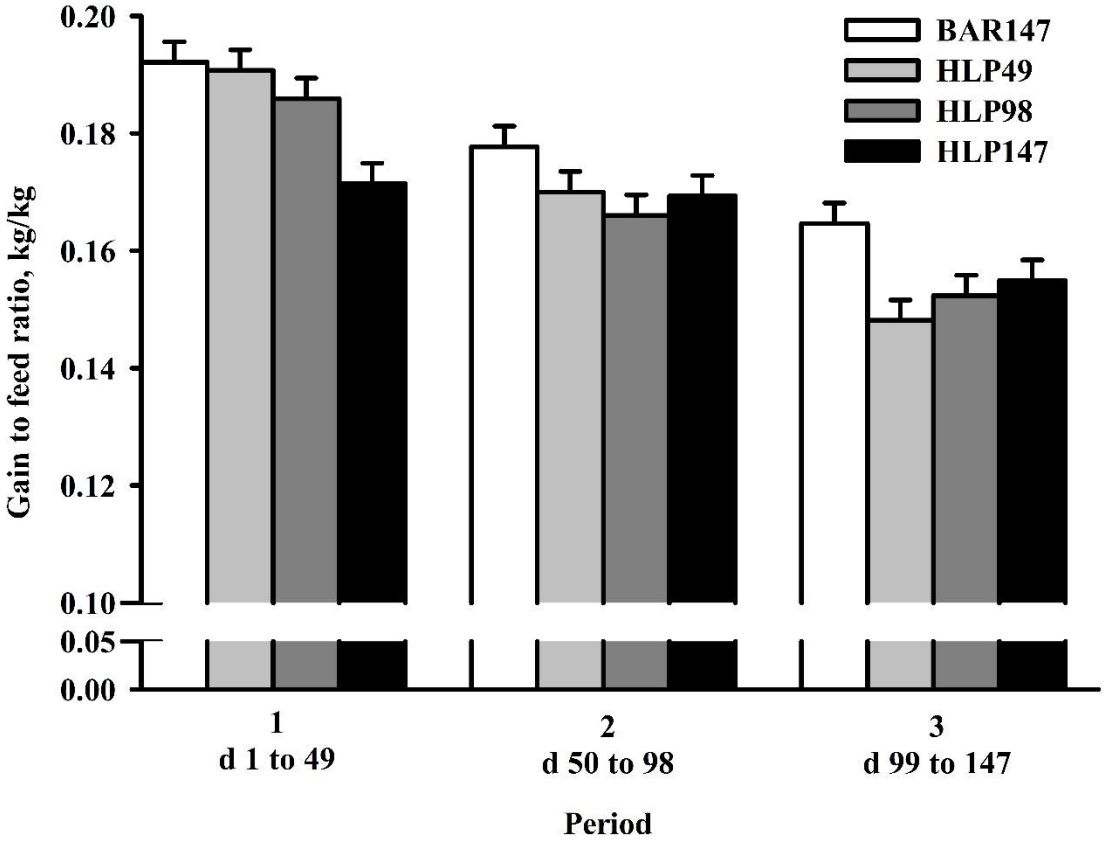

Figure 3.2 Treatment × period interaction in gain to feed ratio (P = 0.008) of finishing feedlot cattle when fed with four treatments. BAR147: BAR diet fed for 147 d, HLP147: HLP diet fed for 147d, HLP98: BAR followed by HLP diet fed for the last 98d, HLP49: BAR followed by HLP diet fed for the last 49d (Study 1). Within a period, only HLP147 had reduced gain to feed relative to BAR147 and HLP49 during P1. Pen was considered as the experimental unit (n = 6/treatment) and 3 consecutive periods per treatment.

Table 3.5 Effect of the timing of provision and duration of feeding high-lipid high-fibre byproduct pellets as a partial (60%) replacement for barley and canola meal on average daily gain (ADG), dry matter intake (DMI) and gain:feed (G:F) of steers during finishing period (Study 1).

	Treatment[1]					Period[2]				*P* value		
	BAR147	HLP49	HLP98	HLP147	SEM[3]	P1	P2	P3	SEM[3]	Trt[1]	Per[2]	Trt×Per
Initial BW, kg	378.1	379.1	378.5	377.9	0.44					0.31		
Final BW, kg	665.6*a*	649*b*	645.6*b*	646.6*b*	4.18					0.01		
DMI, kg d^{-1}	11.1	11.0	10.9	11.1	0.11	9.43*c*	11.39*b*	12.22*a*	0.073	0.63	<0.001	0.003
DMI, % of BW	2.15	2.15	2.15	2.20	0.018	2.24*a*	2.23*a*	2.02*b*	0.013	0.11	<0.001	<0.001
ADG, kg d^{-1}	1.96a	1.84*b*	1.82*b*	1.83*b*	0.029	1.74*b*	1.94*a*	1.89*a*	0.020	0.009	<0.001	0.60
G:F[4], kg kg^{-1}	0.178*a*	0.170*ab*	0.168*ab*	0.165*b*	0.003	0.185*a*	0.171*b*	0.155*c*	0.002	0.01	<0.001	0.008
NE_m[5],Mcal kg^{-1}	1.97*a*	1.91*ab*	1.89*b*	1.87*b*	0.018	1.86*c*	1.91*b*	1.97*a*	0.013	0.006	<0.001	0.001
NE_g[5],Mcal kg^{-1v}	1.32*a*	1.26*ab*	1.25*b*	1.23*b*	0.016	1.22*c*	1.26*b*	1.31*a*	0.011	0.006	<0.001	0.001

[1]Treatment: BAR147= barley grain and canola based diet fed throughout the 147 days; HLP49= HLP diet fed during the last 49 days of finishing; HLP98= HLP diet fed during the last 98 days of finishing; HLP147= HLP diet fed throughout the 147 days.

[2]Period: P1= day1 to day 49; P2 = day 50 to day 98; P3 = day 99 to day 147.

[3]Standard error of mean. Pen was considered as the experimental unit (n = 6/treatment) and for each experimental unit there were 3 consecutive periods.

[4]Gain:Feed (ADG kg d^{-1} : DMI kg d^{-1}).

[5]Calculated based on the performance data over the entire study period (Zinn and Shen 1998; Zinn et al., 2002).

Means followed by same alphabets are not significantly different.

The interaction for G:F was a result of HLP147 having less ADG than BAR147 during P1 without differences between treatments in P2 and P3. The cumulative G:F for the entire study was greater for BAR147 than HLP147 (0.178 vs 0.165 kg gain/kg DMI; $P = 0.01$), with the other treatments being intermediate. As expected, the G:F decreased ($P < 0.001$) with advancing days on feed irrespective of the dietary treatment (0.185, 0.171, and 0.155 for P1, P2, and P3). Based on steer BW, growth, and DMI, the calculated NE_g (Zinn and Shen 1998; Zinn et al., 2002) for the high-lipid high-fibre byproduct pellets was reduced as the duration of HLP feeding increased.

Steers fed BAR147 had a greater ($P = 0.04$) hot carcass weight when compared to the HLP98 and HLP147 treatments (382.8 vs. 370.6 and 373.3 kg respectively) while HLP49 was intermediate (Table 3.6). Dressing percentage tended to differ among treatments ($P = 0.08$) with HLP49 being the greatest. Carcass adjusted ADG and G:F were greater for BAR147 compared to HLP98 and HLP147 while HLP49 did not differ from the other treatments ($P \leq 0.02$). Differences were not observed for back fat thickness, longissimus dorsi muscle area, quality grade and marbling score among the treatment groups ($P \geq 0.10$). However, the proportion of carcasses grading yield grade 1 tended to be greater ($P = 0.07$) for HLP49 than the other treatments.

3.3.2. Study 2

The CP concentration was numerically greater for the BAR than the HLP diets (14.2 vs 13.4; Table 3.3). However, the NE_m and NE_g were similar between the BAR and HLP diets with the HLP+CO having energy values that were numerically greater than the other treatments (1.84, 1.85 and 1.91 MCal/kg DM respectively).

Overall DMI did not differ between treatments, averaging 12.5 kg d^{-1} (Table 3.7), but DMI of steers fed HLP120 was greatest in P1 and intermediary in P2 when compared to other treatments (Fig. 3.3; treatment × period interaction, $P < 0.001$). Likewise, ADG was not affected by treatment although a treatment × period interaction was also observed for ADG (Fig. 3.4) with HLP120 steers having the greatest ADG in P1 and the least ADG in P2 ($P = 0.02$). The G:F ratio for HLP120 was least ($P < 0.001$) when compared to all other treatment groups (0.147 vs 0.158).

Table 3.6 Effect of high-lipid high-fibre byproduct pellets as a partial (60%) replacement of barley and canola meal for different durations on carcass quality of finishing steers (Study 1).

	Treatment[1]				SEM[2]	*P* value
	BAR147	HLP49	HLP98	HLP147		
Hot carcass, kg	382.8*a*	376.8*ab*	370.6*b*	373.3*b*	3.09	0.04
Back fat thickness, cm	0.93	0.87	0.88	0.98	0.039	0.21
Longissimus muscle area, cm^2	89.0	91.1	88	88.4	1.20	0.25
Dressing % on shrunk wt[3]	59.9	60.5	59.8	60.1	0.19	0.08
Carcass adjusted ADG, kg d^{-1}	1.76*a*	1.69*ab*	1.63*b*	1.66*b*	0.028	0.02
Carcass adjusted G:F, kg kg^{-1}	0.160*a*	0.154*ab*	0.149*b*	0.150*b*	0.0021	0.007
Yield Grade, %[4,5]						
CBGA 1	69.5	78.3	61.4	55.6	5.5	0.07
CBGA 2	26.8	20	31.4	31.9	5.3	0.43
CBGA 3	3.7	1.7	5.7	11.1	2.6	0.17
Quality Grade, %[4,5]						
Prime	0	0	1.4	0	0.4	1.00
CBGA AAA	31.7	28.3	31.4	36.1	5.5	0.82
CBGA AA	67.1	68.3	61.4	58.3	5.7	0.58
CBGA A	1.2	3.3	4.3	4.2	2.1	0.71
CBGA B	0	0	1.4	1.4	0.7	1.00
Marbling score, %[4,6]						
Modest	2.4	1.7	4.3	4.2	1.7	0.79
Small	34.1	30	20	31.9	5.7	0.29
Slight	63.4	66.7	71.4	58.3	5.4	0.44
Trace	0	1.7	4.3	5.6	2	0.75

[1]Treatment: BAR147 = finishing diet based on barley grain fed for the entire study duration of 147 days; HLP49 = high-lipid high-fibre byproduct pellets included to replace 60% of the barley grain and canola meal and fed for the last 49 days of finishing; HLP98 = similar to HLP49 but fed for last 98 days of finishing; HLP147= similar to HLP49 but fed for 147 days.

[2]Standard Error of mean. For yield grade, quality grade and marbling score: standard error.

[3]Calculated based on shipping weight × 0.96.

[4]Percent of total carcasses in each category.

[5]According to Canadian Beef Grading Agency (CBGA).

[6]According to United States Department of Agriculture (USDA) where 500 to 599 = modest; 400 to 499 =small; 300 to 399 =slight; 200 to 299 = trace.

Means followed by same alphabet are not significantly different.

Table 3.7 Effect of including high-lipid high-fibre byproduct pellets as a partial replacement (30% DM) for barley and canola meal for different durations on average daily gain (ADG), dry matter intake (DMI) and gain:feed (G:F) in finishing steers (Study 2).

	Treatment[1]					Period[2]			*P* values		
	BAR120	HLP60	HLP60CO	HLP120	SEM[3]	P1	P2	SEM[3]	Trt[1]	Period	Trt × Period
Initial BW, kg	441.3	441.2	441.2	441.6	0.41				0.88		
Final BW, kg	676.4	680.0	679.2	667.6	4.74				0.26		
DMI, kg d^{-1}	12.2	12.7	12.5	12.7	0.18	12.8*a*	12.2*b*	0.10	0.18	< 0.001	< 0.001
DMI, % of BW	2.16	2.25	2.21	2.23	0.028	2.49*a*	1.94*b*	0.015	0.13	< 0.001	< 0.001
ADG, kg d^{-1}	1.96	1.99	1.98	1.88	0.0390	2.45*a*	1.46*b*	0.026	0.22	< 0.001	0.02
G:F[4] kg kg^{-1}	0.160*a*	0.156*a*	0.158*a*	0.147*b*	0.0018	0.191*a*	0.119*b*	0.0019	< 0.001	< 0.001	0.07
NE_m[5], Mcal kg^{-1}	1.92*a*	1.87*a*	1.89a	1.81*b*	0.013	1.99*a*	1.75*b*	0.014	< 0.001	< 0.001	0.08
NE_g[5], Mcal kg^{-1}	1.27*a*	1.23*a*	1.25a	1.18*b*	0.012	1.34*a*	1.13*b*	0.012	< 0.001	< 0.001	0.08

[1]Treatment: BAR120= barley grain and canola based diet fed throughout the 120 days; HLP60= high-lipid high-fibre byproduct pellets based diet fed during the last 60 days; HLP60CO= HLP diet fed during the last 60 days along with canola oil; HLP120= HLP diet fed throughout the 120 days of finishing.

[2]Period: P1= day1 to day 60; P2 = day 61 to day 120.

[3]Standard error of mean. Pen was considered as the experimental unit (n = 6/treatment) and 2 consecutive periods per treatment.

[4]Gain:Feed (ADG kg d^{-1} : DMI kg d^{-1}).

[5]Calculated based on the performance data over the entire study period (Zinn and Shen 1998; Zinn et al., 2002).

Means followed by same alphabet are not significantly different.

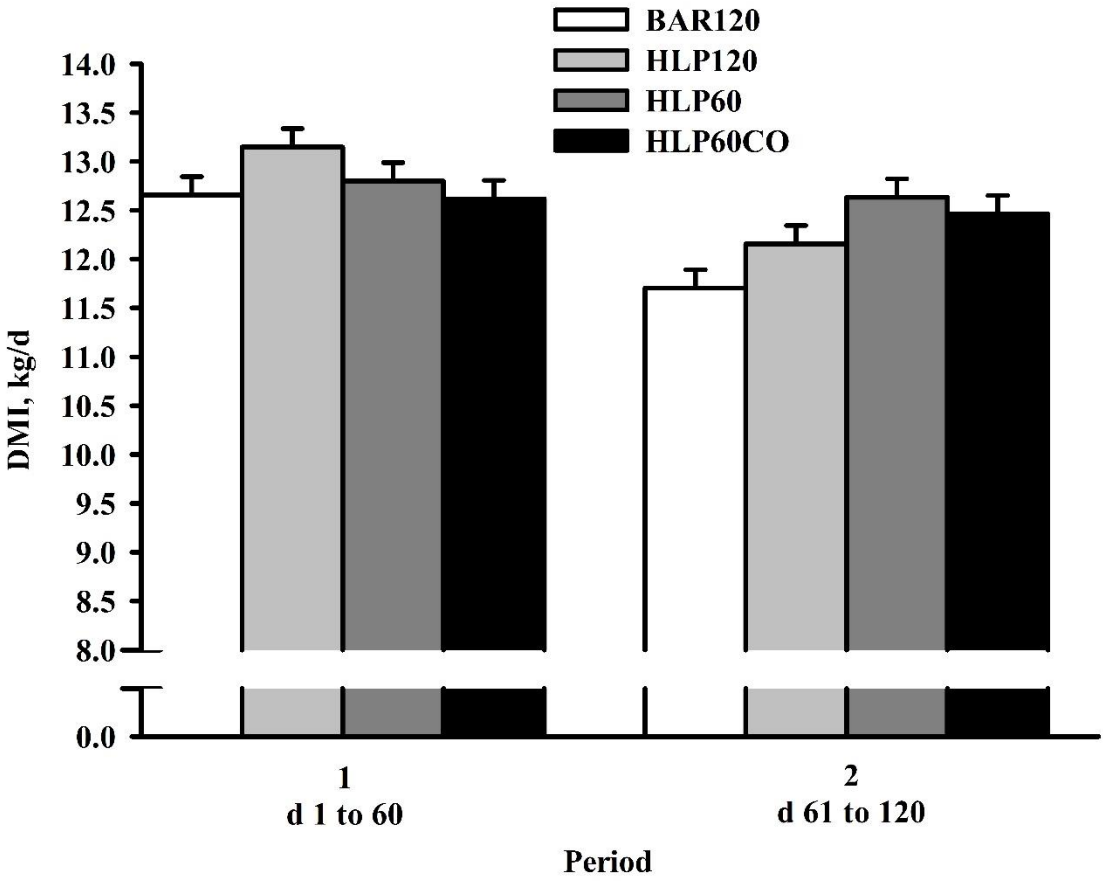

Figure 3.3 Treatment × period interaction of DMI in Study 2 ($P < 0.001$). BAR120: BAR diet fed for 120 d, HLP120: HLP diet fed for 120d, HLP60: BAR followed by HLP diet fed for the last 60 d, HLP60CO: BAR followed by HLP diet fed for the last 60d with additional canola oil. Within a period, only HLP60 had greater DMI than BAR120 during P2. Pen was considered as the experimental unit (n = 6/treatment) and 2 consecutive periods per treatment.

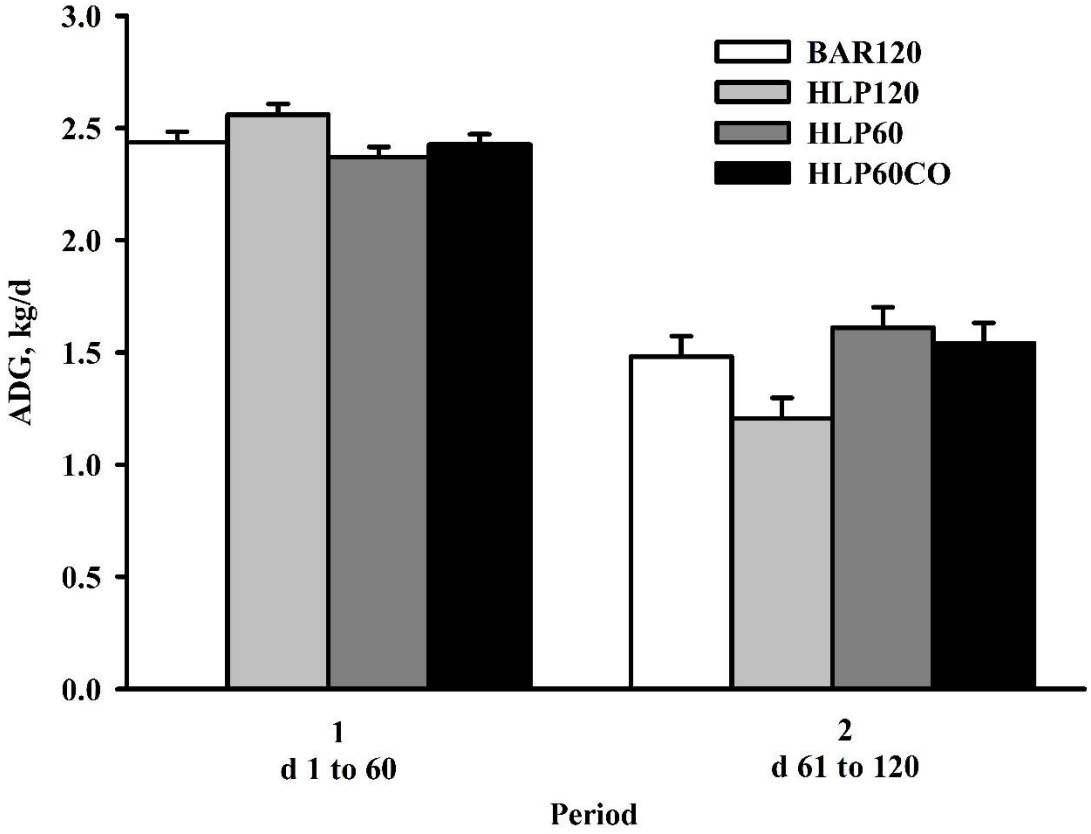

Figure 3.4 Treatment × period interaction of ADG in Study 2 (*P* = 0.015). BAR120: BAR diet fed for 120 d, HLP120: HLP diet fed for 120d, HLP60: BAR followed by HLP diet fed for the last 60d, HLP60CO: BAR followed by HLP diet fed for the last 60d with additional canola oil. Although a significant interaction was detected, means within a period were not different among treatments. Pen was considered as the experimental unit (n = 6/treatment) and 2 consecutive periods per treatment.

Hot carcass weight of steers fed BAR120 was heavier (P = 0.01) than the HLP120 and HLP60CO steers (387.6 vs 376.6 and 377.8 kg, respectively) while the HLP60 (384.4 kg) differed only from the HLP120 treatment (Table 3.8). Dressing percentage tended (P = 0.06) to be greatest for BAR120 and least for HLP120. Carcass adjusted ADG and G:F were greatest for BAR120, least for HLPCO while HLP60 did not differ from BAR120 or HLP120. Back fat thickness and the longissimus dorsi muscle area were not affected nor were quality grades and marbling score ($P \geq$ 0.10). However, the proportion of carcasses grading yield grade 1 tended to be greatest (P = 0.06) for HLP120 and HLP60 (61.5% and 56.9 %) with HLP60CO tending to have the least (37.9%).

3.4. Discussion

The objective of the studies reported above were to determine whether the timing and duration for feeding a high-lipid high-fibre byproduct pellets would influence feed intake, growth performance, and carcass characteristics for finishing steers. Past studies have demonstrated that G:F may be reduced with the inclusion of high-lipid high-fibre byproduct pellets in diets for finishing steers (Gorka et al., 2013). However, that study used a continuous inclusion of high-lipid high-fibre byproduct pellets throughout the finishing phase. Our studies support that of Gorka et al. (2013) where steers fed the high-lipid high-fibre byproduct pellets for 147 or 120 d had reduced G:F relative to steers fed a barley-based finishing diet. However, feeding the high-lipid high-fibre byproduct pellets during the latter part of finishing period (49 d in Study 1, and 60 d in Study 2) did not negatively influence DMI, G:F, ADG, or carcass characteristics. This suggests that phase-feeding may be a viable option to utilize high-lipid high-fibre byproduct pellets in feedlot settings. The use of high-lipid high-fibre byproduct pellets could be particularly beneficial when cereal grain costs are high.

One consistent result in the current study and that of Gorka et al. (2013) was that steers fed high-lipid high-fibre byproduct pellets throughout finishing had reduced G:F. Reduced G:F would not have been predicted based on the energy values determined using chemical analysis. However, energy values calculated using mean BW, DMI, and ADG indicate a lower energy value than expected for HLP diets.

Table 3.8 Effect of including high-lipid high-fibre byproduct pellets as a partial replacement (30% DM) for barley and canola meal for different durations on carcass quality of finishing steers (Study 2).

	Treatment[1]				SEM[2]	*P* value
	BAR120	HLP60	HLP60CO	HLP120		
Hot carcass (kg)	387.6*a*	384.4*ab*	377.8*bc*	376.7*c*	2.37	0.01
Back fat thickness (cm)	1.07	1.05	1.10	0.98	0.056	0.50
Longissimus muscle area (cm^2)	84.3	83.5	82.0	84.0	1.17	0.52
Dressing % on shrunk wt[3]	61.7	60.5	59.9	60.3	0.44	0.06
Carcass adjusted ADG, kg d^{-1}	1.71*a*	1.66*ab*	1.57*bc*	1.56*c*	0.034	0.02
Carcass adjusted G:F, kg kg^{-1}	0.140*a*	0.131*ab*	0.125*b*	0.123*b*	0.0032	0.006
Yield Grade, %[4,5]						
CBGA 1	47.6	56.9	37.9	61.5	6.1	0.06
CBGA 2	38.1	35.4	44	24.6	5.9	0.17
CBGA 3	14.3	7.7	18.2	13.8	4.2	0.41
Quality Grade, %[4,5]						
Prime	0	0	1.5	0	0.4	1.00
CBGA AAA	61.9	70.8	69.7	63.1	5.9	0.63
CBGA AA	36.5	29.2	28.8	36.9	5.8	0.63
CBGA A	1.6	0	0	0	0.4	1.00
CBGA B	0	0	0	0	0	1.00
Marbling score, %[4,6,7]						
Modest	6.3	12.3	13.6	9.2	3.7	0.56
Small	47.6	52.3	51.5	60	6.2	0.57
Slight	46	35.4	34.8	29.2	5.9	0.29
Trace	0	0	0	1.5	0.4	1.00

[1]Treatment: BAR120 = finishing diet comprised of barley grain and canola meal fed for 120 days;HLP60 = HLP diet fed for last 60 days; HLP60CO = HLP diet + canola oil fed for the last 60 days; HLP= HLP diet fed for 120 days.

[2]Standard error of mean. For yield grade, quality grade and marbling score: standard error.

[3]Calculated based on shipping weight × 0.96.

[4]Percent of total carcasses in each category.

[5]According to Canadian Beef Grading Agency (CBGA).

[6]According to United States Department of Agriculture (USDA).

[7]Where: 500 to 599 = modest; 400 to 499 =small; 300 to 399 =slight; 200 to 299 = trace.
Means followed by same alphabet are not significantly different.

This is likely attributed to lower digestibility of the byproduct feeds composing the high-lipid high-fibre byproduct pellets (Gorka et al., 2015). The primary reasons for the lower digestibility are not known and could be attributed to; 1) high lignin content in some of the byproduct feeds, 2) small particle size of the feeds within the high-lipid high-fibre byproduct pellets and 3) negative associative effects of the lipid on rumen fermentation. Similar findings were also seen previously (Pylot et al., 2000) where canola screenings were used to replace a substantial portion of barley grain resulting in lower ADG and G:F.

As stated above, it is possible that the high lipid content (7.3% on DM basis) of the high-lipid high-fibre byproduct pellets and resulting diet may have reduced microbial efficiency and fibre digestibility (Jenkins, 1993; Hess et al., 2008). Supporting this suggestion, Gorka et al. (2015) reported reduced OM and NDF digestibility with increasing inclusion of high-lipid high-fibre byproduct pellets in finishing diets although the digestibility of CP, ADF, starch, and crude fat were not affected. However, not all studies have reported a reduction in NDF digestibility even when the diet contained up to 9.4% fat (Kucuk et al., 2004). It should also be noted that in Study 2, the dietary fat concentration was only 5.1% for the HLP diet and steers fed this diet still had reduced ADG for the HLP120 treatment. Past research has suggested that similar concentrations of dietary fat did not have a negative effect on fibre digestibility (Plascencia et al., 2003). While a reduction in NDF digestibility is a plausible explanation, given the relatively high starch and lipid content of the diets, the energetic contribution of NDF for feedlot steers is questionable. The barley silage contributing to the NDF fraction used in our studies were only 6% of the total dietary dry matter. This implies that reduced performance associated with high lipid diets may not only be due to a reduced efficiency of microbial fibre digestion. This low proportion is also important from feed efficiency stand point as it has been shown that a barley silage incorporation of 3-6% of diet (DM basis) will contribute to maximum G: F (Koenig and Beauchemin, 2011).

The complete fermentation and utilization of nutrients in the rumen largely depends on how long feeds are retained in the rumen, which in turn partially depends on the feed particle size and density (Welch, 1986). The high-lipid high-fibre byproduct pellets may be prone to faster disintegration into smaller particles in the rumen due to previous grinding and processing at the feed mill, which can result in lower retention time and digestibility (Mohamed et al., 2012). This may be further exacerbated for diets that contain a low proportion of structural fibre (Zebeli et al., 2007), as is the case for the finishing diets used in these studies. Incorporation of high-lipid high-

fibre byproduct pellets, similar to that used in the current studies, has been reported to reduce ruminal digesta mass and result in greater omasal OM flow with increasing inclusion of high-lipid high-fibre byproduct pellets into finishing diets (Gorka et al., 2015). A structured rumen mat plays a vital role in enhancing particle retention time, thus allowing more complete rumen fermentation by the rumen microbial communities. Future research is needed to further understand limitations to efficient high-lipid high-fibre byproduct pellet utilization and to evaluate strategies to enhance transfer of energy from byproduct feeds to productive responses.

Feeding the HLP diet throughout the finishing stage at both the 60% and 30% level of incorporation decreased G:F and hot carcass weight. As discussed earlier, factors responsible for curtailing the availability of dietary energy from the HLP diet may have contributed to the reduced performance. However, the phase feeding strategy where the HLP diet is fed during the later stages of the finishing period mitigated the negative effects of a full high-lipid high-fibre byproduct pellets feeding regimen. In fact, in Study 1, steers fed the HLP49 had similar DMI, G: F, and hot carcass weight relative to BAR147. Similarly, in Study 2, steers fed HLP60 had similar performance as steers fed BAR120 for DMI, ADG, G:F and hot carcass weight. Thus, altering the timing and limiting the duration of high-lipid high-fibre byproduct pellets feeding could be an effective strategy to reduce feed costs without affecting overall performance and potential revenue.

3.5. Conclusion

The outcomes from these two studies indicate that use of high-lipid high-fibre byproduct pellets can be an effective alternative to barley grain and canola meal in diets for finishing steers. However, reduced G:F, ADG, and hot carcass weights may occur when feeding the high-lipid high-fibre byproduct pellets throughout the finishing period. Reducing the duration and delaying the timing of provision can mitigate the negative effects of feeding the high-lipid high-fibre byproduct pellets at a lower inclusion rate.

4.0 EFFECT OF DURATION ON FEED AND ENERGY SUBSTRATE ON DIGESTIBILITY, RUMINAL CLEARANCE, GLUCOSE TOLERANCE TEST , AND INSULIN RESPONSE IN FINISHING FEEDLOT CATTLE[2]

Lessons learned so far:

Use of HLP can be an effective partial alternative to barley grain. However feeding HLP throughout the finishing period may negatively affect ADG, G:F, and hot carcass weight. Reducing the duration and delaying the timing of provision mitigates the negative effects of feeding the HLP when used at lower inclusion rates. The current study discussed in chapter 4 was designed to delineate the reasons for decreased feed efficiency with advancing days on feed that are intrinsic to the ruminant digestive system, based on the energy source.

ABSTRACT: The objective of this study was to determine the effect of dietary energy substrate and days on feed (DOF) on apparent total tract digestibility, ruminal fermentation, short-chain fatty acid (SCFA) absorption, plasma glucose and acetate clearance rates, and insulin responsiveness. Eight ruminally cannulated, cross-bred growing heifers were randomly allocated to 1 of 2 dietary treatments. The control (CON) diet consisted of 75.2% barley grain, 9.8% canola meal, 9% mineral and vitamin supplement, and 6% barley silage (DM basis). To evaluate the effect of energy source, a high-lipid high-fibre byproduct pellet was included in the diet by replacing 55% of the barley grain and 100% of canola meal (HLHFP). The study consisted of 4 consecutive 40-d periods with data and sample collection occurring in the last 12 d of each period. Dry matter intake did not differ among periods but HLHFP heifers tended to eat less (P = 0.09). The ADG of

[2]A version of this chapter has been published: Joy, F., J. J. McKinnon, S. Hendrick, P. Gorka, and G. B. Penner. 2017. Effect of dietary energy substrate and days on feed on apparent total tract digestibility, ruminal short-chain fatty acid absorption, acetate and glucose clearance, and insulin responsiveness in finishing feedlot cattle. J. Anim. Sci. 95: 5606-5616.

CON was greater than HLHFP during P1 and P4 (treatment × period; $P = 0.02$). Heifers fed HLHFP tended to have greater mean ruminal pH (6.10 vs. 5.96; $P = 0.07$) than CON, but pH was not affected by period. The CON heifers had a greater digestibility for DM, OM, CP and NDF ($P \leq 0.03$) and the digestibility for DM and OM increased linearly ($P = 0.01$) and CP, NDF and starch increased ($P \leq 0.04$) quadratically with advancing period. Ether extract digestibility for CON generally increased with period, while that of HLHFP decreased (treatment × period; $P = 0.03$). Total SCFA concentration in the rumen was greater ($P = 0.006$) for CON (141.5 vs 128.08 m*M*) than HLHFP. The molar proportion of acetate and isobutyrate increased and valerate decreased ($P \leq 0.05$) linearly with advancing periods. The rate of valerate absorption tended to increase ($P = 0.06$) and rate of rumen passage rate of chromium tended to decrease ($P = 0.08$) with advancing period. The arterial clearance rate of acetate tended to increase ($P = 0.06$) with period while clearance rate of glucose was not affected by treatment or period. Both fasting plasma insulin and the area under the insulin curve in response to glucose infusion increased ($P \leq 0.04$) linearly with period. These data suggest that partially replacing a barley diet with high lipid byproduct pellets negatively affects total tract digestibility and performance. Moreover, with advancing DOF, digestibility and insulin resistance increased without changes in ruminal pH and plasma metabolite clearance rates.

4.1 Introduction

Byproduct feeds can be a cost-effective alternative to cereal grains (DiConstanzo et al., 2012) and blending byproducts can help overcome limitations associated with single-byproduct inclusion (Górka et al., 2013; Zenobi et al., 2014). One strategy to increase the energy density of blended byproduct feeds has been to use byproducts from the oilseed industry (Górka et al., 2013). While the effects of lipid supplementation are variable, Górka et al. (2013) and Joy et al. (2016) demonstrated that high-lipid byproduct pellets can be a viable alternative to barley grain; however, a reduction in G:F has been observed.

In addition to a diet-related cause, the reduction in G:F with advancing days on feed (**DOF**) is attributed to increased energy required per unit gain (Welegedera et al., 2012) and that cattle are approaching a mature body weight (NASEM, 2016). That said, it may be possible that other factors are involved. For example, the incidence of digestive related mortalities is greater in the latter part of the finishing period (Smith, 1998) corresponding to increased prevalence and severity of ruminal acidosis (Castillo-Lopez et al., 2014). Low ruminal pH can reduce fibre digestibility (Russell and Wilson, 1996), short-chain fatty acid (**SCFA**) absorption (Schwaiger et al., 2013), and may lead to systemic inflammation (Gozho et al., 2005). All of the previously mentioned factors could reduce G:F. However, we are not aware of previous studies that have evaluated changes in digestibility, SCFA absorption, and post absorptive nutrient metabolism with advancing DOF and whether dietary energy substrate influences the response.

We hypothesized that the inclusion of high-lipid high-fibre byproduct pellets will alter ruminal fermentation, improve the SCFA absorption, and metabolite clearance rates in finishing heifers. It was further hypothesized, that benefits arising from the high-lipid high-fibre supplementation would be most prominent towards the latter part of the finishing period.

4.2 Materials and methods

4.2.1 Heifer Management

All procedures involving heifers were pre-approved by the University of Saskatchewan Animal Research Ethics Board (protocol number 20100021) and followed the guidelines of the

Canadian Council on Animal Care (2009). Eight forage-fed 18-m old Hereford heifers with an initial BW of 454 ± 15 kg (mean ± SD) were fitted with a ruminal cannula (model 9C, Bar Diamond Inc., Parma, ID) before the start of the study. Upon arrival, all heifers were treated with Ivermectin pour-on endecto-paraciticide (5 mg/mL; Alberta Veterinary Laboratories, Calgary, AB) by topical application. Throughout the study, heifers were housed at the Livestock Research Building at the University of Saskatchewan in individual pens (9 m^2) fitted with rubber mats as bedding. Pens were scraped and washed daily.

4.2.2 Dietary treatments, feeding and experimental design

This study was conducted as a generalized complete block design. Heifers were blocked by BW into 2 blocks to facilitate the labor-intensive sampling protocol (blocks initiated the study at different times), and within block randomly assigned to treatments (2 animals/treatment/block). Dietary treatments consisted of a barley grain and canola meal-based finishing diet (**CON**) or a diet where 55% of the barley grain and 100% of canola meal were replaced with a high-lipid high-fibre byproduct pellet (**HLHFP**; Table 4.1). The HLHFP was formulated using byproducts from the cereal grain and oilseed sectors and was similar to that used by Górka et al. (2013; 2015) and Joy et al. (2016). Canola meal was used in the CON diet to balance the CP concentration between treatments and limestone was added to adjust the Ca:P ratio. Diets were formulated to be iso-caloric and iso-nitrogenous and contained melengestrol acetate at 0.4 mg/heifer/d to prevent estrus.

The study was conducted over 160 d including a 21-d dietary transition. Heifers were initially fed a diet consisting of 92% grass hay and 8% of a vitamin and mineral supplement pellet with barley grain as a carrier. Feed was offered ad libitum once daily at 0830 h to allow for feed refusals equating to 5% of the weight offered on an as fed basis. Heifers had free access to water throughout the study. To evaluate the effect of DOF, the 160-d study period was divided into four 40-d periods (**P1**, **P2**, **P3** and **P4**). The first period also included the 21-d dietary transition from a forage diet to a high grain diet in 7 steps of sequential increases of the concentrate component (35, 45, 54, 62, 70, 76 and 82 % of the diet on DM basis) replacing the forage component, with each diet fed for 3 d. Performance, ruminal fermentation, and post absorptive nutrient metabolism data were collected in each of the 4 periods.

Table 4.1 Ingredient and chemical composition of a barley-based diet (CON) or a high-lipid byproduct-based diet (HLHFP) fed to finishing heifers.

	Diet	
Item	CON	HLHFP
Ingredient, % of DM		
Barley silage	6.0	6.0
Rolled barley grain	75.2	34.1
Canola meal	9.8	0.0
High-lipid byproduct pellet[1]	0.0	51.2
Vitamin-mineral pellet[2]	8.0	8.0
Limestone	1.0	0.7
Chemical composition, Mean ± SD		
n	8	8
DM, %	85.3 ± 1.2	85.0 ± 1.2
CP, % of DM	15.5 ± 0.3	13.6 ± 0.3
Starch, % of DM	46.6 ± 0.8	39.5 ± 0.9
Ether extract, % of DM	3.8 ± 0.2	5.7 ± 0.3
NDF, % of DM	20.2 ± 1.2	26.4 ± 1.4
ADF, % of DM	9.1 ± 0.3	14.3 ± 0.7
Lignin, % of DM	2.6 ± 0.1	3.5 ± 0.3
Ash, % of DM	5.4 ± 0.4	6.9 ± 0.2
Ca, % of DM	0.94 ± 0.01	0.88 ± 0.02
P, % of DM	0.53 ± 0.13	0.43 ± 0.09
NE_m[3], Mcal kg of DM^{-1}	1.87 ± 0.02	1.81 ± 0.02
NE_g[3], Mcal kg of DM^{-1}	1.23 ± 0.02	1.18 ± 0.02

[1]Ingredient composition of HLHFP pellet: 29.7% wheat, 14.9% off-grade canola, 26.4% wheat screenings, 11.2% oat hulls and 17.8% pea screenings on DM basis.
[2]Contained (DM basis): 2.5% of NaCl, 5% of Ca, 0.46% of P, 2.0% of Mg, 1.96% of K, 2.0% of S, 5.06 mg/kg of Co, 161.0 mg/kg of Cu, 8.8 mg/kg of I, 494.8 mg /kg of Fe, 370.6 mg/kg of Mn, 2.5 mg/kg of Se, 345.2 mg/kg of Zn, 44052.8 IU/kg of vitamin A, 16519.8 IU of vitamin D, 330.4 IU of vitamin E, 901.4 mg/kg of choline, 442.7 mg/kg of monensin and 0.68 mg/kg of melengestrol acetate.
[3]Net energy calculated based on a summation equation (Weiss, 1998).

4.2.3 Feed Intake and ADG

Heifers were weighed upon arrival and at the start and end of P1, P2, P3 and P4 by taking the average of BW from 2 consecutive days. The change in weight between the start and end of each 40-d period was used to determine ADG. Feed intake and feed refusals were measured daily with samples of feed (bi-weekly composites) and refusals (during sampling days) being analyzed for DM content. The DM offered and DM refused were used to calculate DMI and the ingredient DM values were used to ensure the formulated diet composition was achieved. Feed and refusal samples were dried in a forced air oven at 55ºC for 72 h and were composited by period (feed) and heifer (refusals). Before compositing, samples were ground using a hammer mill with a 1-mm screen (Christy and Norris Ltd., Chelmsford, UK). Ground samples were submitted to Cumberland Valley Analytical Services (Hagerstown, MD) and analyzed for CP, NDF, ADF, lignin, ash, starch, ether extract (acid hydrolysis), Ca, and P as described by Rosser et al. (2013).

4.2.4 Ruminal fermentation

Ruminal pH was measured in the ventral sac every 5 min from d 29 to 33 of each period using the Lethbridge Research Centre Ruminal pH Measurement System (LRCpH; Model Dascor, Escondido, CA) as described by Penner et al. (2006). The pH systems were standardized before being inserted into and after removal from the rumen using standard pH buffers 7.0 and 4.0 at 39°C. Data were transformed from mV recordings to pH using beginning and ending linear regressions while assuming linear drift in measurements over time. A pH threshold of 5.5 was used to define subacute ruminal acidosis, and pH below 5.2 for acute ruminal acidosis (Penner et al., 2007; Aschenbach et al., 2011). The mean, minimum, and maximum pH, and the area (AREA) and duration **(**DUR) that ruminal pH was < 5.5 were also calculated.

On d 36, 37, and 38 of each period, 8 samples of ruminal digesta were collected starting at 0800 h on d 36 with 9-h intervals between sampling points. For each of the 8 samples corresponding to 8 time-points, ruminal digesta was collected from the anterior, ventral, and posterior regions of the rumen (250 mL/region) and placed in a common container. Digesta samples were then strained through 2-layers of cheese cloth and two 10-mL aliquots of filtrate were transferred into 15-mL tubes. One sample was added 2 mL of 25% (wt/vol) metaphosphoric

acid and kept for the analysis of SCFA using gas chromatography and the other sample kept as a spare. All samples were sealed and stored at -20°C until analysis. Composite rumen fluid samples representative of each period was used for the determination of SCFA using gas chromatography (Agilent 6890 plus GC system, Agilent Technologies, Santa Clara, CA) as described by Albornoz et al. (2013).

4.2.5 Short-chain fatty acid absorption and liquid passage rate

The fractional rate of SCFA absorption was measured using the Cr-EDTA/n-valeric acid technique (Allen et al., 2000; Resende-Júnior et al., 2006; Penner et al., 2009) from d 34 to 36 of each experimental period. Briefly, 500 mL of Cr-EDTA/n-valeric acid solution (20 m*M* of valerate adjusted to pH of 6.0 with NaOH solution and 1 g/100 mL of Cr) was pulse-dosed into the rumen and digesta was manually mixed for 1 min. Representative rumen fluid samples were collected at 0 (pre-infusion), 60, 120, 240, 480, 960, 1440, 2880, and 4320 min post infusion. Samples of ruminal fluid were mixed with 25% (wt/vol) metaphosphoric acid (ratio of 5 mL rumen fluid: 1 mL metaphosphoric acid) and immediately frozen at -20°C. The concentration of Cr (by atomic absorption spectrophotometry; model iCE 3300 spectrometer, Thermo Scientific, Waltham, MA) and valerate (by gas chromatography; Agilent 6890 plus GC system, Agilent Technologies, Santa Clara, CA) were determined in the ruminal fluid samples at each time-point. The exponential decay of Cr and n-valeric acid was determined according to Penner et al. (2009). The rate of passage (Kp) was determined according to the clearance of Cr. The clearance rate (Kc) of valerate was assumed to include both passage and absorption. Thus, the fractional rate of valerate absorption (Ka) was determined by difference: (Kc – Kp) when corrected for baseline concentrations.

4.2.6 Plasma glucose, and insulin measurements

Indwelling jugular catheters (14 gauge, MILA International, Erlanger, KY) were inserted into each heifer 1 d before initiation of the sampling period (d 35) for collection of composite blood samples as well as nutrient clearance experiments (described below). Catheter patency was ensured by infusing 5 mL of heparinized physiological saline (10 IU/mL) twice daily. Blood samples were collected using vacutainers on the same days and at the same time points used for determining SCFA concentration and processed to separate plasma (148 IU of Li-heparin; Becton

Dickinson, Franklin Lakes, NJ) and serum (silica coated clot activator; Becton Dickinson, Franklin Lakes, NJ). For plasma, whole blood was placed on ice until being centrifuged at 2500 × *g* for 15 min at 4°C, whereas, for serum, samples were allowed to sit at room temperature for 1 h before centrifugation. All samples were stored at -20°C until analysis. For glucose and insulin measurements, plasma samples collected at 9 h intervals over 3 d were composited by period, before analyses.

Plasma glucose was determined by enzymatic oxidation of glucose to gluconic acid and the subsequent enzymatic oxidation of o-dianisidine in the presence of glucose oxidase and peroxidase enzymes (PGO Enzymes; Sigma, MO) as described by Penner and Oba (2009). Oxidized o-dianisidine was detected by absorption at 450 nm (Spectramax Plus384; Molecular Devices Inc, Sunnyvale, CA). Plasma insulin was determined by using a commercial kit (Bovine Insulin ELISA, Mercodia, Uppasala, Sweden) with an intra-assay CV of 2.52% and inter-assay CV of 2.56%.

4.2.7 Post-absorptive nutrient clearance

Clearance rates of acetate and glucose were used as an indicator for post-absorptive nutrient utilization (Benschop and Cant, 2009). Before measurements, heifers were fasted overnight for 12 h, but had ad libitum access to water. On d 39 of each period, the clearance rates of acetate and glucose were determined with a 1-h interval between last and first measurements of consecutive metabolites with acetate measured before glucose. Glucose and acetate were chosen due to the reliance on glucose as energy source during growth for intramuscular fat accretion with acetate and glucose both contributing to lipogenesis during the late finishing stage (Smith and Crouse, 1984). The acetate solution for infusion was prepared from sodium acetate (Sigma Aldrich, 3*M*, 5.2 pH), adjusted to pH 7.4 using NaOH, sterile filtered (0.22 µm filter), and infused at a dose rate of 2.18 mmol/kg $BW^{0.75}$. The infusion was accomplished over a 1 min time period with a constant flow rate. Blood samples were collected at -10, 0 (immediately after completion of the infusion), 2, 4, 6, 8, 10, 15, 20, 25, 30 min post-infusion into a vacutainer containing 148 IU of Li-heparin (Becton Dickinson). Blood samples were placed on ice and then centrifuged at 2,500 × *g* for 15 min for separation of plasma. The plasma was frozen until being analyzed for acetate concentration using a commercial kit (K-ACETRM 07/12, Megazyme International Ireland, Wicklow, Ireland).

To evaluate the arterial glucose clearance rate, a 2.78 *M* solution of glucose was used for infusion. Glucose was infused at a dose rate of 7.57 mmol/kg $BW^{0.75}$. The solution was infused over a 2 min duration and blood was collected at -10, 0, 5, 10, 15, 20, 25, 30, 45, 60, 90, 120 and 180 min post-infusion. The blood collected in vacutainer was immediately placed on ice, centrifuged as described above, and the plasma was frozen until glucose and insulin was measured. Urine was collected for 24 h post-glucose infusion using indwelling urinary catheters (Bardex Foley Catheter, C. R. Bard Inc. Covington, GA), and urinary glucose excretion was analyzed as described above.

4.2.8 Apparent total tract digestibility

Total tract digestibility was determined based on measurements of total fecal DM mass excreted and the amount of feed DM offered and refused. Collection of feed and feed refusals was described previously. Feces were collected off the pen floor and placed in clean plastic containers every 4 h starting from 0800 h on d 36 and finishing on d 38 of each period. The weight of the feces was recorded and a representative sample equating to 5% of the wet weight was collected and composited across the 72-h measurement. The composite fecal sample was stored at -20°C until being used to determine DM content and for chemical analysis. Twenty-four hours before to the start of total collection, urinary catheters were inserted and urine was collected to avoid urinary contamination of feces. Representative samples of feed refusals were also collected during the 3 d of total collection and were composted by period for each heifer. Refusals and feces were sent to Cumberland Valley Analytical Services (Hagerstown, MD) for chemical analysis as described above.

4.2.9 Statistical analysis

All data were tested for normality using graphical representation and the Shapiro-Wilk test. All data except apparent total tract starch digestibility and time to peak insulin concentration following the glucose infusion were normally distributed. Not normally distributed data were transformed using the BoxCox method. *P*-values arising from the transformed data analysis were reported. All variables were analyzed considering a repeated measure structure of data using the mixed procedure of SAS (SAS version 9.2; SAS Inc., Cary, NC) as described by Wang and

Goonewardene (2004), with period as the repeated statement. Block was removed from the model wherever it was not significant. The best covariance structure was chosen based on the structure that yielded the lowest Akaike and Bayesian Information Criterion. The model used was as follows:

$Yijk=\mu+D_i+T_k+DT_{ik}+E_{ikl}$

Where, μ = Overall mean

D_i = fixed effect of diet (CON vs. HLHFP)

T_k = fixed effect of period (P1, P2, P3 and P4)

DT_{ik} = fixed effect of the diet × time interaction

E_{ikl} = random error

The data analysis for 'time to peak' insulin post-glucose infusion was conducted using PROC GLIMMIX of SAS using the model described above. For all analyses, mean separation was completed using Tukey's test. Significance were declared when $P \leq 0.05$ and tendencies were reported when $0.05 < P \leq 0.10$.

4.3 Results

4.3.1 Diet composition

No statistical analysis was conducted on the diets (Table 4.1) and thus the results are means ± SD. Both the dietary treatments were formulated to be iso-energetic and iso-nitrogenous; however, the CP content of CON diet was greater (15.5%; Table 4.1) than the HLHFP diet (13.6%). Nevertheless, both treatments met the minimum requirements for all nutrients according to NASEM (2016). Because of the greater inclusion rate of barley grain, the starch content of the CON diet (46.6%) was greater than for the HLHFP diet (39.5%). The HLHFP diet was formulated to be greater in ether extract content than the CON diet (5.7 vs 3.8%). The byproducts incorporated in the pellets such as grain screenings and oat hulls resulted in a greater NDF and ADF concentration in the HLHFP diet relative to the CON (26.4 vs 20.2% and

14.3 vs 9.1%, respectively). Overall, the diet formulation succeeded in providing two diets differing in the energy substrates.

4.3.2 DMI and ADG

There was a treatment × period interaction ($P = 0.02$; Table 4.2) for ADG with the CON heifers gaining more than HLHFP heifers during P1 and P4 (Fig. 4.1). Despite having a similar transition protocol to CON diet, the high lipid and fibre content and unpalatable byproduct components might have resulted in a numeric decrease in DMI and consequent ADG in P1 for HLHFP while the gradual adaptation to new diet and compensatory gain in P2 and P3 resulted in comparable gains to CON. In accordance with greater ADG, CON heifers tended ($P = 0.09$; Table 4.2) to consume more DM than HLHFP heifers. The daily DMI did not differ ($P \geq 0.10$) across periods. The digestible OM intake was higher ($P = 0.01$) for CON heifers, when compared to HLHFP heifers, while no effect ($P \geq 0.27$) of period was observed. The G:F was lower ($P = 0.05$) for heifers fed HLHFP diet than those fed CON diet and it decreased ($P < 0.01$) quadratically with period.

4.3.3 Total tract digestibility

The apparent total tract digestibility of DM, OM, CP, and NDF for HLHFP were less ($P \leq 0.03$; Table 4.2) when compared to the CON; while, ADF and starch digestibility were not different ($P \geq 0.52$) between dietary treatments. There was a treatment × period interaction ($P = 0.03$) for ether extract digestibility with greater digestibility for the HLHFP heifers during P1 and P2 and reduced digestibility relative to CON in P3 and P4 (Fig. 4.2). Total tract digestibility of CP, NDF and starch increased quadratically ($P \leq 0.04$) with advancing periods while that of DM and OM increased linearly ($P \leq 0.02$).

Table 4.2 Performance and apparent digestibility coefficients for beef heifers fed a barley-based diet (CON) or a high-lipid byproduct based diet (HLHFP) during advancing periods of a finishing feedlot phase

Item	Treatment			Period[1]					*P* value			
	CON	HLP	SEM[2]	P1	P2	P3	P4	SEM[2]	Treatment	Period Linear	Period Quadratic	T × Per
BW, kg												
Initial[3]	452.2	455.7	8.0	454.0	480.0	555.8	616.9	8.1				
Final[3]	694.0	618.0	13.8	480.0	555.8	616.9	656.0	8.9				
ADG, kg/d	1.46	0.99	0.08	0.65	1.90	1.53	0.83	0.15	< 0.01	0.79	< 0.01	0.02
DMI, kg/d	10.57	8.51	0.78	10.22	9.84	9.47	8.61	0.68	0.09	0.10	0.73	0.70
Digestible OM intake, kg/d	23.83	17.78	1.16	21.34	21.39	22.48	19.14	1.51	0.01	0.41	0.27	0.38
G:F	0.138	0.119	0.005	0.059	0.200	0.164	0.091	0.016	0.05	0.41	< 0.01	0.26
Apparent digestibility, %												
DM	78.18	72.77	1.07	71.98	75.00	78.26	76.41	1.40	0.01	0.02	0.10	0.53
OM	80.18	74.99	1.04	74.28	77.18	80.07	78.82	1.34	0.01	0.01	0.13	0.23
CP	77.16	74.42	0.62	72.74	75.47	78.57	76.44	1.03	0.01	< 0.01	0.03	0.29
NDF	45.44	36.45	2.35	36.94	41.82	46.37	39.16	2.77	0.03	0.37	0.04	0.51
ADF	27.64	27.65	4.31	25.22	25.28	31.32	25.82	2.67	0.99	0.51	0.31	0.12
Starch	97.27	97.64	0.18	94.57	97.67	98.64	98.93	0.29	0.52	< 0.01	< 0.01	0.72
Ether extract	77.39	76.37	2.91	76.27	79.06	76.27	77.62	1.89	0.69	0.88	0.71	0.03

[1]P1= d 1 to 40; P2 = d 41 to 80; P3 = d 81 to 120; P4 = d 121 to 160.

[2]n = 4/treatment.

[3]T = treatment; Per = period.

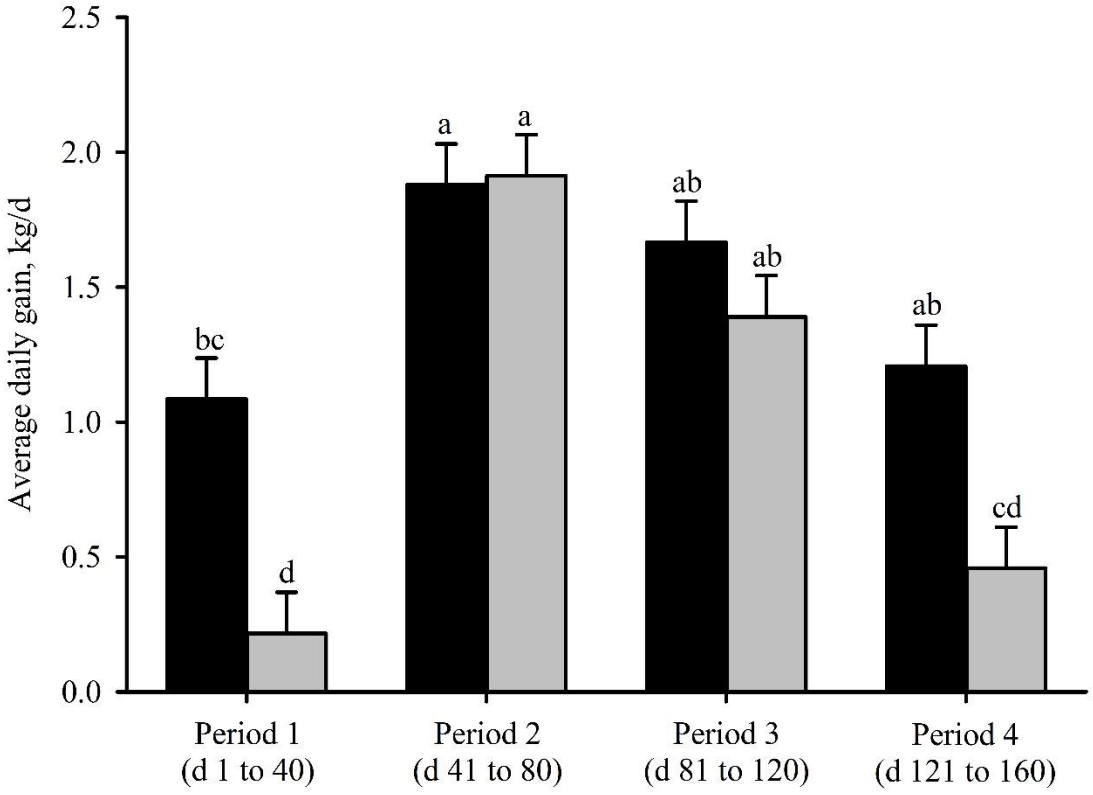

Figure 4.1 Interaction between treatment and days on feed for ADG for heifers fed either barley-based finishing diet (CON) or a diet where high-lipid byproduct pellets replaced 55% of the barley grain and 100% canola meal (HLHFP). Black columns indicate heifers fed the CON and grey columns indicate heifers fed the HLHFP diet. The *P*-values for the treatment, period, and treatment × period interaction are < 0.01, < 0.01, and 0.02 respectively. Columns with uncommon letters differ ($P < 0.05$).

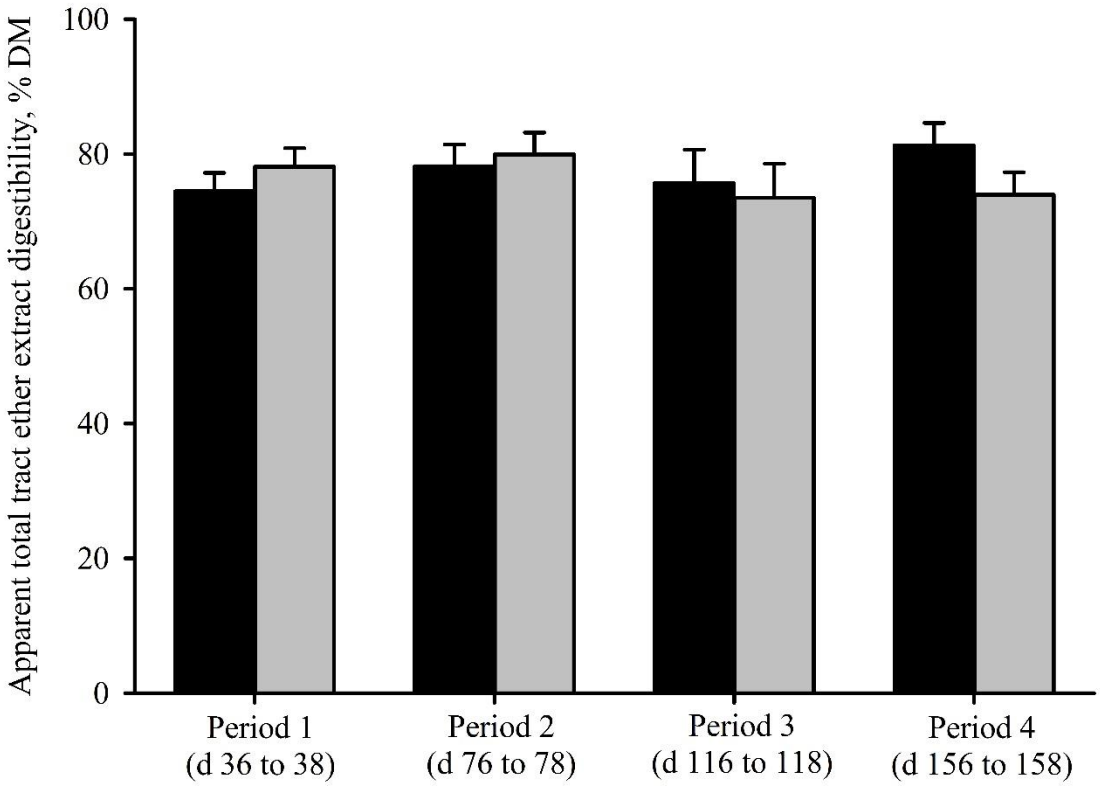

Figure 4.2 Interaction between treatment and days on feed for apparent total tract digestibility of ether extract for heifers fed either a barley-based finishing diet (CON) or a diet where high-lipid byproduct pellets replaced 55% of the barley grain and 100% canola meal (HLHFP). Black columns indicate heifers fed the CON and grey columns indicate heifers fed the HLHFP diet. The *P*-values for the treatment, period, and treatment × period interaction were 0.69, 0.49, and 0.03 respectively. Although the interaction was significant, the Tukey's post-hoc separation did not indicate individual means that differed ($P < 0.05$).

4.3.4 Ruminal fermentation and short-chain fatty acid absorption

Mean ruminal pH tended ($P = 0.07$) to be greater for heifers fed HLHFP than CON diet, but minimum, maximum, DUR and AREA were not affected ($P > 0.11$; Table 4.3) by treatment or period. The total SCFA concentration for heifers fed HLHFP diet was 9.5 % less ($P < 0.01$) than for those fed CON diet. Dietary treatment had no effect ($P > 0.30$) on the molar proportions of individual SCFA except for butyrate for which a treatment × period interaction ($P = 0.05$; Fig. 4.3) was observed. The interaction was a result of CON heifers having a greater molar proportion in P1 than other periods, while for HLHFP, the proportion did not differ among periods. Total SCFA concentration tended to decrease ($P = 0.05$) linearly from P1 to P4. The proportion of acetate tended to increase ($P = 0.09$) quadratically while isobutyrate tended to increase linearly ($P = 0.05$) with advancing period. Molar proportion of valerate decreased ($P = 0.03$) linearly with advancing period.

The ruminal Ka, Kc and Kp did not differ ($P \geq 0.73$; Table 4.3) between treatments. A tendency for linear increase ($P = 0.06$) in Ka and linear decrease ($P = 0.08$) in Kp were observed with advancing periods.

4.3.5 Plasma glucose and acetate clearance

The fasted plasma glucose concentration (Table 4.4) did not differ between treatments ($P = 0.70$) but tended to differ quadratically with periods ($P = 0.05$). Fasting insulin concentration was not affected ($P = 0.40$) by diet but, increased ($P = 0.04$) linearly from P1 to P4. The composite plasma insulin did not differ ($P \geq 0.14$) between treatments or periods. The insulinogenic ratio in fasting and composite plasma, a measure of insulin sensitivity, did not differ ($P \geq 0.25$) between treatments. However, it tended to linearly increase ($P \leq 0.10$) with period for both fasting and composite plasma samples, indicating a decreased insulin sensitivity.

Table 4.3 Ruminal fermentation parameters for beef heifers fed a barley-based diet (CON) or a high-lipid byproduct-based diet (HLHFP) during advancing periods of a finishing feedlot phase

Item	Treatment			Period[1]					*P* value			
	CON	HLP	SEM[2]	P1	P2	P3	P4	SEM[2]	Treatment	Period Linear	Period Quadratic	T × Per[2]
Ruminal pH												
Mean	5.96	6.1	0.05	6.02	5.94	6.03	6.12	0.08	0.07	0.28	0.28	0.37
Minimum	5.24	5.32	0.08	5.34	5.20	5.24	5.33	0.08	0.50	0.99	0.19	0.56
Maximum	6.83	6.93	0.05	6.86	6.82	6.89	6.95	0.06	0.18	0.19	0.34	0.11
Duration pH<5.5, min/d	306	235	82	230	336	289	193	85	0.56	0.67	0.25	0.27
Area pH<5.5, pH × min/d	44.7	49.7	29.2	38.0	81.65	61.9	32.0	24.5	0.91	0.73	0.15	0.20
Total ruminal SCFA[3], m*M*	141.6	128.1	3.1	139.9	137.6	136.8	124.9	4.9	< 0.01	0.05	0.34	0.62
Acetate, mol/100mol	47.94	46.62	2.08	41.01	50.41	47.59	50.12	1.93	0.67	< 0.01	0.09	0.74
Propionate, mol/100mol	32.07	29.91	3.15	33.00	28.58	32.95	29.41	2.87	0.64	0.62	0.88	0.72
Butyrate, mol/100mol	12.72	13.18	2.27	17.15	12.32	10.80	11.53	1.86	0.89	0.04	0.15	0.05
Isobutyrate, mol/100mol	0.89	0.91	0.12	0.8	0.83	0.92	1.06	0.10	0.92	0.05	0.59	0.27
Isovalerate, mol/100mol	1.48	1.70	0.31	1.55	1.45	1.55	1.81	0.26	0.63	0.45	0.49	0.11
Valerate, mol/100mol	2.15	1.85	0.22	2.38	2.18	1.97	1.46	0.28	0.37	0.03	0.59	0.76
Ruminal clearance rates, %/h												
Valerate absorption, Ka	36.71	38.00	6.52	29.28	33.67	40.74	45.81	6.39	0.89	0.06	0.96	0.98
Valerate clearance, Kc	53.18	48.81	8.40	44.65	52.55	51.54	55.25	6.82	0.73	0.32	0.76	0.72
Chromium passage, Kp	11.93	10.82	2.92	15.46	14.89	10.8	9.45	2.72	0.80	0.08	0.89	0.20

[1]P1 = d 1 to 40; P2 = d 41 to 80; P3 = d 81 to 120; P4 = d 121 to 160.
[2]T = treatment; Per = period; SEM = Standard error of mean, n=4/treatment
[3]SCFA = short chain fatty acid.

Table 4.4 Plasma metabolite clearance and insulin parameters for beef heifers fed a barley-based diet (CON) or a high-lipid byproduct based diet (HLHFP) during advancing periods of a finishing feedlot phase

Item	Treatment			Period[1]					*P* value			
	CON	HLP	SEM[3]	P1	P2	P3	P4	SEM[3]	Treatment	Period Linear	Period Quadratic	T × Per[2]
Infused plasma metabolites												
Basal acetate, µ*M*	390.1	295.8	34.4	347	342.6	364.5	317.6	36.8	0.10	0.69	0.57	0.14
Acetate clearance, µmol/min	308.8	328.9	43.8	276	357.5	323.1	318.5	32.8	0.83	0.71	0.06	0.95
Basal glucose, m*M*	4.19	4.15	0.08	4.10	4.23	4.30	4.05	0.10	0.70	0.89	0.05	0.36
Glucose clearance, mmol/min	0.67	0.67	0.001	0.67	0.67	0.67	0.67	0.002	0.60	0.21	0.55	0.52
Fasting plasma insulin, µg/L	1.65	1.37	0.21	1.17	1.39	1.81	1.58	0.17	0.40	0.04	0.21	0.12
Composite plasma insulin, µg/L	4.57	2.78	0.86	2.72	3.28	4.82	3.88	0.74	0.19	0.14	0.32	0.14
Insulinogenic ratio,												
Fasting insulin:glucose	0.39	0.33	0.05	0.28	0.35	0.42	0.39	0.04	0.39	0.05	0.25	0.10
Composite insulin:glucose	1.19	0.8	0.22	0.75	0.89	1.09	1.13	0.17	0.25	0.10	0.78	0.19
Insulin response after glucose infusion,												
Area of insulin curve, µg × min	220.1	236.5	27.6	188	214.8	262.8	247.7	23.3	0.69	0.04	0.40	0.30
Peak concentration, µg/L	8.5	9.8	0.9	8.4	7.6	11.3	9.0	0.9	0.37	0.17	0.43	0.48
Time to peak, min	11.9	11.3	0.8	10.6	11.9	10.0	13.8	1.1	0.60	0.13	0.25	0.27

[1]P1= d 1 to 40; P2 = d 41 to 80; P3 = d 81 to 120; P4 = d 121 to 160.
[2]T = treatment, Per = period.
[3] n = 4/treatment.

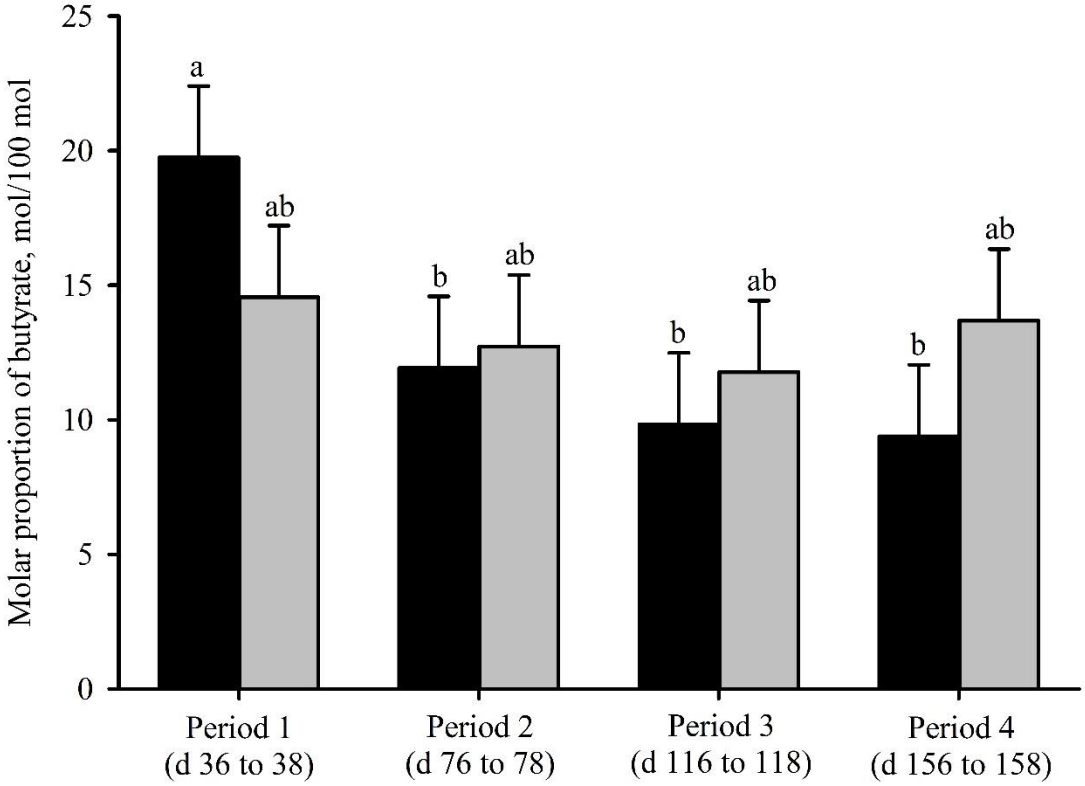

Figure 4.3 Interaction between treatment and days on feed for the molar proportion of butyrate in ruminal fluid for heifers fed either a barley-based finishing diet (CON) or a diet where high-lipid byproduct pellets replaced 55% of the barley grain and 100% canola meal (HLHFP). The *P*-values for the treatment, period, and treatment × period interaction was 0.89, < 0.01 and 0.05 respectively. Black columns indicate heifers fed the CON and grey columns indicate heifers fed the HLHFP diet.

The area under the insulin curve in response to glucose infusion did not differ ($P = 0.69$) between treatments, but increased linearly ($P = 0.04$) with advancing periods. Peak insulin concentration in plasma following glucose infusion and time required for plasma insulin concentration to peak following the glucose challenge did not differ ($P \geq 0.13$) between CON and HLHFP treatments and nor with period.

The plasma clearance rate of glucose was not affected by treatment or period ($P \geq 0.21$; Table 4.4) with a mean clearance rate of 0.67 mmol/min. The urinary excretion of glucose following a mean pulse dose of 78 ± 8.9 g of glucose averaged 1.4 ± 1.02 g and was not different ($P > 0.10$) between treatments or periods (data not shown). Thus, renal excretion of glucose accounted for less than 2% of the total glucose dose. There was a tendency for greater basal plasma acetate concentration in CON compared to HLHFP heifers (390.1 vs 295.8 μ*M*; $P = 0.10$) while no differences ($P \geq 0.57$; Table 4.4) were observed among periods. The arterial clearance rate of acetate did not differ with treatment ($P \geq 0.83$) but tended to increase ($P = 0.06$) quadratically with period.

4.4 Discussion

In this study, the effects of diet (treatment), period, and their interaction were evaluated. Because no major interactions were observed, the effects of treatment and period are discussed separately.

4.4.1 Effect of dietary treatment

One of the reason for observed decrease in G:F in late finishing stages of feedlot cattle (Joy et al., 2016; NASEM, 2016) might be ruminal acidosis (Castillo-Lopez et al., 2014). Despite the tendency for improved ruminal pH observed in the current study and that of Górka et al. (2015) when using HLHFP as a partial substitute for barley grain, we observed that HLHFP reduced G:F. Thus, reducing fermentable carbohydrate by increasing lipid as a strategy to reduce risk for ruminal acidosis is not likely to improve G:F. Diet digestibility contributes toward efficient feed conversion and the current study supports past research demonstrating that the use of HLHFP results in a marked decrease in apparent total tract OM digestibility compared to barley fed cattle (Górka et al., 2015). The reasons for decreased digestibility with HLHFP diet are not known, but it is likely

that the use of oat hulls within the pellet (Thompson et al., 2000), greater ether-extract content (Jenkins, 1993; Hess et al., 2008), and small particle size of ingredients (Abouheif et al., 2012) in HLHFP, or a combination of any of these factors (Joy et al., 2016) can be implicated.

Increased particle passage rate may be beneficial for HLHFP when considering the high ether extract content and the potential negative effect of lipids on ruminal fermentation. That said, there is debate whether lipid sources positively or negatively affect performance of cattle when fed finishing diets (Górka et al., 2013; Lima et al., 2016). Some studies have indicated a negative consequence of lipid on fibre digestion (Jenkins, 1993; Hess et al., 2008) while others have shown no effect (Kucuk et al., 2004), when dietary lipid concentration goes beyond 6% DM. The potential negative effect of lipid on fibre digestion may be an important factor for HLHFP as byproduct pellets have a greater concentration of NDF relative to barley grain. On the other hand, given the low level of forage inclusion in finishing diets for feedlot cattle and reduced NDF digestibility for HLHFP diet, it is unlikely that fermentation of NDF contributes substantially towards the net energy supply.

In the current study, the ruminal SCFA concentration decreased with HLHFP feeding compared to the CON diet. However, the rate of SCFA absorption from the rumen did not differ between treatments. The response for less ruminal SCFA concentration with HLHFP compared to CON was expected as the diet contained less starch, but greater NDF and ether extract concentrations alongside a numerically lower DMI. These dietary shifts were designed to reduce the quantity of substrate available for rapid fermentation (Aschenbach et al., 2011) as an approach to help stabilize ruminal pH. Given that liquid passage rate and SCFA absorption were not affected, the primary cause for the tendency for stabilization of ruminal pH was likely due to reduced ruminal digestibility. Supporting the previous suggestion, Górka et al. (2015) observed increased OM flow from the reticulo-rumen with increasing inclusion rates of HLHFP in the diet. Collectively, this suggests that the cause for improved ruminal pH and reduced SCFA concentration are likely due to reduced ruminal digestibility, and particularly fibre digestibility.

4.4.2 Effect of days on feed

While it is accepted that a general decline in G:F with advancing DOF for finishing cattle is due to increased BW and a shift in composition of accreted tissue (NASEM, 2016), the effect of the latter is confounded with DOF. Thus, current models may underemphasize the importance of

changes in energetic losses before the contribution of feed toward retained energy. A partial objective of the present study was to evaluate whether factors related to digestion, absorption, and post-absorptive utilization of nutrients may also change with DOF. In the current study, we observed an increase in OM digestibility with advancing periods, and this is in agreement with the findings of Krehbiel et al. (2000) and Hersom (2005) where older and heavier beef cattle had greater OM digestibility compared to their younger and lighter counterparts. The improved apparent total tract digestibility for NDF and OM corresponded to a tendency for decreased fluid passage rate from the rumen, apparently from increased rumen volume and thereby increased rumen retention time. Though not significant, DMI decreased with period which might also have reduced Kp and consequently enhanced feed digestibility.

On the other hand, others have found that the proportion of starch digested in the rumen was less for heavy-weight steers compared to light-weight steers when they were fed a fat supplemented diet (Plascencia et al., 2003). A shift in site of digestion could be beneficial from an efficiency standpoint, as starch digestion in intestine has been observed to be 42% more efficient than ruminal starch fermentation (Owens et al., 1986). The increase in apparent total tract starch digestibility and tendency for decreased ruminal SCFA concentration with period observed in our study also support the suggestion of a shift in site of starch digestion. However, probably due to reductions in energetic efficiency associated with post absorptive metabolic processes, in the present study the G:F declined with advancing periods.

In ruminants, acetate and glucose are major energy substrates for muscle and adipose tissue (Rhoades et al., 2007). We observed that while basal arterial acetate concentration did not differ with periods, the clearance rate of acetate post infusion tended to be greater with advancing DOF compared to P1. Depending on the growth phase, beef cattle on finishing diets should accrue a greater proportion of lean tissue during the initial portion of the finishing period with increasing proportions of fat deposition with advancing periods. The increased subcutaneous fat accretion relies increasingly on acetate as an energy source rather than glucose (Rhoades et al., 2007).

While past studies have shown that different dietary energy substrates affect glucose supply and tissue utilization of glucose in response to insulin (Rhoades et al., 2007), different energy contents of similar diets do not change insulin sensitivity (Vasconcelos et al., 2009). While insulin has an important role in maintaining glucose homeostasis, tissue responsiveness to insulin stimulation is lower in ruminants compared to other species (Hocquette et al., 1995; Sasaki, 2002).

In dairy cattle, insulin resistance has been reported during early lactation to facilitate increased arterial glucose flow to mammary tissue to cope with increased demand (Bell and Bauman, 1997). In the current study, beef heifers displayed insulin resistance with advancing periods. Insulin resistance can be due to decreased insulin sensitivity or decreased insulin responsiveness (in response to a glucose challenge) or a combination of the 2 factors (Kahn, 1978; Muniyappa et al., 2008). The decreased sensitivity of insulin with advancing periods in the current study, evident from the fasting and composite plasma insulin levels, is often linked to increased deposition of adipose tissue. Hocquette et al. (1999) reported a positive relationship between plasma insulin concentration and carcass fat weight. Later, Lawrence et al. (2012) and Fitzsimons et al. (2014) reported that cattle differing in their residual feed intake (RFI) rank, despite having similar back fat thickness, have similar insulin concentrations, suggesting that decreased insulin sensitivity with advancing periods in the current study might be associated with changing tissue composition as more adipose tissue is deposited. However, a cause-effect relationship between insulin concentration and tissue adiposity is difficult to establish, as the underlying molecular mechanisms in ruminants are still to be elucidated. The increasing area under the insulin curve following the glucose infusion with advancing periods suggests decreasing insulin responsiveness. Hence, the insulin resistance observed in finishing beef cattle towards late finishing stages could be a sequela of a combination of decreasing insulin sensitivity and insulin responsiveness. Future research is needed to evaluate whether the onset of reduced insulin sensitivity and responsiveness can be mitigated and whether such a strategy may alter adipose tissue deposition.

Development of insulin resistance in the current study interpolate with the decrease in feed efficiency. Multiple factors contributing to insulin resistance might collectively have a negative effect on energetic efficiency. Leptin, synthesized from the adipose tissue is stimulated by increased plasma insulin concentration (Saladin et al., 1995) and it has been shown to decrease insulin-stimulated glucose uptake by adipocytes (Muller et al., 1997). Studies evaluating molecular mechanisms of hyperinsulinemia in humans have shown that insulin induced GLUT4 translocation to the plasma membrane is reduced in large adipocytes when compared to small adipocytes (Franck et al., 2007). Meanwhile Fitzsimons et al. (2014) has observed an increased expression of GLUT4 in longissimus muscle of steers at d 92 compared to d 50 of finishing phase, indicating different regulatory actions of insulin in different tissues at different growth stages. In muscle tissue, insulin normally increases the energy consumption by increasing amino acid uptake and

protein synthesis and reduced proteolysis (Hocquette et al., 1998; Richardson et al., 2004). Keomanivong et al. (2017) has reported increased serum insulin in overfed ewes compared to underfed and control ewes while no difference was observed in pancreatic insulin-containing cell clusters. Because of the pancreatic exhaustion due to continuous stimulation to produce excess insulin and its effects on target tissues for anabolic responses, insulin resistance may be considered one of the major contributing factors to the decreased feed efficiency associated with late finishing stages. Briefly, the reduction in G:F observed with advancing periods and its association with changes in the composition of tissue accretion, might be through the molecular mechanisms involved in insulin homeostasis.

4.5 Conclusion

In conclusion, the decrease in the feed efficiency with advancing DOF for finishing beef cattle was not influenced by the dietary energy source. However, use of HLHFP can be expected to decrease the G:F compared to barley grain, due to lower nutrient digestibility. Considering plausible reasons for increased apparent total tract digestibility and no change in plasma acetate and glucose clearance with period, increasing insulin resistance with advancing DOF may be an important factor contributing to decreased feed efficiency in finishing cattle.

5.0 EFFECT OF FORAGE LEVEL IN FINISHING DIET OF BEEF HEIFERS CONTAINING HIGH-FIBRE, HIGH-LIPID BYPRODUCT PELLET

Lessons learned so far:

The strategy of using HLP as an alternative to barley grain has been successful with manipulation of timing and duration of provision. High lipid pellet diet has been observed to have lower digestibility and concentrations of total SCFA in the rumen compared to CON, even though the SCFA absorption rate and post absorptive utilization of glucose and acetate did not differ. Increasing digestibility with advancing DOF may be due to the decrease in the passage rate. Basal insulin secretion and insulin response to a glucose challenge increased with advancing DOF independent of dietary energy source. Insulin resistance may be a factor contributing to reduced energetic efficiency with advancing DOF.

The negative effects associated with feeding HLP throughout the finishing period seems not to be related to the digestion kinetics, but rather due the inherent nature of the diet. Future studies should focus on identifying the intrinsic factors in the formulated HLP. It was speculated that ruminal retention time of HLP was low, leading to low ruminal degradation. The current study discussed in chapter 5 evaluated whether a modest increase in forage inclusion rate would improve digestibility, presumably through increased ruminal retention.

ABSTRACT: A study was conducted to evaluate the effect of marginal increase in forage concentration in a beef finishing diet utilizing a high-lipid high-fibre byproduct pellet (**HLP**). High forage (**HF**) fed animals exhibited higher ADG compared to low forage (**LF**) fed animals ($P \leq 0.05$). Nutrient digestibility was not different among the treatments. Marginal increases in forage concentration in a HLP diet will improve animal performance probably by alleviating rumen acidosis.

5.1 Introduction

Volatile feed grain prices in western Canada have prompted feedlot operators to search for viable energy-rich alternatives to cereal grains. Several studies evaluating the use of byproducts from the grain, oilseed, and bioethanol industries have produced promising results for feedlot cattle (Pylot et al., 2000; Amat et al., 2012). Most of these studies have evaluated these byproducts in isolation resulting in over or underfeeding of nutrients. To address the issue of nutrient imbalance, several studies have strategically combined several byproducts in the form of a pellet to attain a desired nutrient composition (Górka et al., 2013, Zenobi et al., 2014, Joy et al., 2016). The high fibre content and reduced energy density of many of byproducts, when compared to barley grain, has been offset with the inclusion of lipid sources, such as heated canola, to attain a predicted energy content similar to barley grain. However, studies utilizing high-lipid high-fibre byproduct pellets (**HLP**) as a partial replacement for barley grain in finishing diets has shown that even though the HLP could be an economically viable alternative to barley grain, use of HLP might adversely impact the G:F ratio (Górka et al., 2013; Joy et al., 2016).

Factors that result in a less favorable G:F may be diverse. Because both the HLP and CON diets in previous studies were formulated to be similar in energy and protein content (Górka et al., 2013; Joy et al., 2016), it is expected that there might be other intrinsic factors decreasing the availability or utilization of energy for cattle fed HLP. It was speculated that ruminal retention time of HLP was low, thereby reducing the potential for degradation in the rumen (Górka et al., 2013; Górka et al., 2015; Joy et al., 2016). This speculation is supported by the notion that the byproduct feeds comprising the HLP were ground before to pelleting and contained a small particle size. Thus, strategies to increase ruminal retention time may yield positive associative effects and increase energy availability. This may be particularly important as most finishing feedlot diets only contain 4.5 to 13.5% forage on a DM basis (Galyean and Gleghorn, 2001) and past studies with HLP utilized a low forage inclusion level of 6% (Górka et al., 2013; Górka et al., 2015; Joy et al., 2016).

We hypothesized that a modest increase in the forage inclusion (from 6 to 12% of dietary DM), in a finishing diet utilizing a high-lipid, high-fibre byproduct pellet will increase apparent total tract digestibility.

5.2 Materials and methods

Eight growing cross bred beef heifers from the University of Saskatchewan Goodale Farm were used for this study. Upon arrival, all heifers were treated with Ivermectin pour-on endecto-paraciticide (5 mg/mL; Alberta Veterinary Laboratories, Calgary, AB) by topical application. Throughout the study, heifers were housed at the Livestock Research Building at the University of Saskatchewan in individual pens (9 m^2) fitted with rubber mats on the floor and fed twice daily at 0800 and 1600 h. Pens were cleaned daily and heifers had ad libitum access to water. All procedures involving animals had been pre-approved by the University of Saskatchewan Animal Research Ethics Board (Protocol number 20100021) and followed the guidelines presented by the Canadian Council on Animal Care (2009).

Heifers were housed in individual pens on arrival and were fed ad libitum hay forage along with a mineral supplement for 7 d of initial adaptation. At the end of the adaptation period heifers were weighed on two consecutive days and were randomly assigned to 1 of 2 treatments based on average BW. Dietary treatments consisted of either a high forage diet (HF; barley silage 12%, barley grain 28.1%, HLP 51.2%, mineral and vitamin pellet 8.7% on a DM basis) or the low forage diet (LF: barley silage 6%, barley grain 34.1%, HLP 51.2%, mineral and vitamin pellet 8.7% on a DM basis; Table 5.1). The HLP pellet was formulated from various byproducts from the oil and grain industries and was similar to that used in previous studies (Górka et al., 2015; Joy et al., 2016).The current study was conducted over a 22-d duration following a 21-d dietary transition from a high forage to a high concentrate diet. The 21-d dietary transition from 41.3% concentrate to 79.3 and 85.3% concentrate levels for HF and LF respectively, consisted of 7 steps with each diet fed for 3 d. Heifers were weighed on 2 consecutive d at the end of dietary transition and again at the end of the study. The change in weight between the start and end of the study was used to determine ADG. Feed intake and feed refusals were measured and recorded daily.

Table 5.1 Dietary ingredient and chemical composition of high forage (HF) diet and low forage (LF) diet.

	Diets[1]	
	HF	LF
Ingredient (% of DM)		
Barley silage	12.0	6.0
Rolled barley grain	28.1	34.1
High-lipid byproduct pellet[2]	51.2	51.2
Vitamin-mineral pellet[3]	8.0	8.0
Limestone	0.7	0.7
Chemical composition		
DM, %	83.3	86.8
OM, % DM	91.2	91.5
CP, % DM	13.3	13.3
Starch % DM	37.7	40.2
Ether extract, % of DM	5.8	5.7
NDF, % of DM	27.9	26.3
ADF, % of DM	16.2	14.9
Lignin, % of DM	3.7	3.6
Ca, % of DM	0.92	0.90
P, % of DM	0.39	0.39
NEm[4], Mcal kg of DM^{-1}	1.75	1.77
NEg[4], Mcal kg of DM^{-1}	1.13	1.16

[1]Diets: HF diet: Finishing feedlot diet consisting mainly of 12% barley silage; LF diet: Finishing feedlot diet consisting of 6% barley silage.
[2]Ingredient composition of HLP: 29.7% wheat, 14.9% off-grade canola, 26.4% wheat screenings, 11.2% oat hulls and 17.8% pea screenings.
[3]On DM basis: 2.5% of NaCl, 5% of Ca, 0.46% of P, 2.0% of Mg, 1.96% of K, 2.0% of S, 5.06 mg/kg of Co, 161.0 mg/kg of Cu, 8.8 mg/kg of I, 494.8 mg /kg of Fe, 370.6 mg/kg of Mn, 2.5 mg/kg of Se, 345.2 mg/kg of Zn, 44052.8 IU/kg of vit A, 16519.8 IU of vit D, 330.4 IU of vit E, 901.4 mg/kg of choline, 442.7 mg/kg of monensin and 0.68 mg/kg of MGA.

[4]Net energy calculated based on a summation equation (Weiss, 1998).

The 22-d study period consisted of 19 d for dietary adaptation and 3 d for sample collection. The 3-d sample collection period was used for measurement of DMI and total tract digestibility. Throughout the study, feed was offered ad libitum to allow for refusals equating to 5% of weight offered on an as fed basis. Total fecal collection was used to determine the apparent total tract digestibility during the last 3-d of the study. Before the start of total collections, heifers were restrained with halters for 2 d before the start of fecal collection to allow for adaptation. Twenty-four hours before the start of total collections, urinary catheters (Bardex Foley Catheter, C.R. Bard Inc. Covington, GA) were inserted and urine was collected to avoid urinary contamination of feces. Subsequently, feces were collected every 4 h, weighed and recorded, thoroughly mixed, and a representative sample equating to 5% of the wet weight was collected and composited within the subsequent sampling times. The composite fecal samples arising from 3 d of total collection were stored at -20^{0}C until being used to determine DM content and for chemical analysis.

During the fecal collection period, representative samples of each feed ingredient and feed refusals were collected daily and composited for each heifer. The DM offered and refused was used to calculate DMI. The composite feed and refusal samples were dried in a forced air over at 55^{o}C for 72 h and feces were dried for 7 d. Dried samples were ground using a hammer mill with a 1-mm screen (Christy and Norris Ltd., Chelmsford, UK). Ground samples were submitted to Cumberland Valley Analytical Services (Hagerstown, MD) and analyzed for CP, NDF, ADF, lignin, ash, starch, ether extract (acid hydrolysis), Ca, and P as described by Rosser et al. (2013).

The experiment was conducted as a completely randomized design with fixed effects of the treatment. Each heifer was considered as an experimental unit. The mixed model of SAS (SAS version 9.2; SAS Inc., Cary, NC) was used for statistical analysis.

5.3 Results and discussion

The two experimental diets were formulated to be iso-nitrogenous. While dietary data were not statistically analyzed, the HF diet consisted of 6.2% less starch content than the LF diet (37.7 vs 40.2 % DM; Table 5.1). The NDF and ADF were numerically greater in HF compared to LF diet, due to higher fibre content from barley silage (27.9 and 16.2 % vs 26.3 and 14.9 % respectively). The DMI between the HF and LF diet did not differ (7.32 vs 6.90 kg/d respectively; $P = 0.36$; Table 5.2). The ADG calculated over the 22-d study period was greater for the HF heifers compared to the LF heifers (1.61 vs 1.35 kg/d; $P = 0.04$).

Table 5.2 Performance and digestibility of beef heifers on feeding HLP diets with 6 (LF) and 12% (HF) forage incorporation

Variable	Treatment[1]			
	HF	LF	SEM[2]	*P*-Value
Start BW, kg	243.4	243.6	9.76	0.99
End BW, kg	278.7	273.2	10.23	0.71
DMI, kg d^{-1}	7.3	6.9	0.294	0.36
ADG, kg d^{-1}	1.61	1.35	0.07	0.04
Digestibility,				
DM, %	65.74	67.62	0.938	0.21
OM, %	67.82	69.78	0.995	0.21
CP, %	70.88	69.67	1.265	0.53
NDF, %	22.86	27.19	4.491	0.52
ADF, %	15.37	19.77	3.761	0.44
Starch, %	97.35	97.58	0.263	0.56
Gross Energy, %	65.15	66.74	1.137	0.36
Ether extract[3], %	56.89	51.81	4.32	0.44

[1]Treatment: HF = high fibre is a high lipid pellet based diet with 12% forage on DM basis. LF = low fibre is a high lipid pellet based diet with 6% forage on DM basis.

[2]Standard error of mean

[3]Acid hydrolyzed ether extract

The apparent total tract digestibility of DM, OM, CP, NDF, ADF, starch, and ether extract did not differ between the dietary treatments ($P \geq 0.10$; Table 5.2). A past study (Zinn and Plascencia, 1996) has shown that increasing the forage level from 10 to 30% in feedlot steers fed with 6% supplemental fat resulted in a 13% increase in ADG, while the total tract digestibility of OM, starch and lipid did not differ.

As part of the pelleting process, byproducts and other ingredients are ground before pelleting. Thus, pellets are expected to lose their physical structure resulting in smaller particles as a consequence of chewing and hydration in the rumen. Small dense particles may escape the reticulo-rumen rapidly resulting in inadequate retention time for fermentative digestion (Abouheif et al., 2012). The mean rumen retention time for forage fibre was reported to be greater than concentrate fibre (Kramer et al., 2013) and longer retention of forage compared to concentrate particles were related to larger particle size and lower specific gravity of the former (Huhtanen et al., 2006). Other studies have reported that rumen stratification and particulate retention were not affected by the NDF content (Schulze et al., 2014), but they were related to the properties of NDF such as, maturity, forage species and plant tissue of origin (Jung and Allen, 1995). As a strategy to increase particle retention, the proportion of forage in the diet was increased from 6 to 12%. While particle retention in the rumen and particulate flow rate were not assessed, inclusion of a greater proportion of forage did not reduce apparent total tract digestibility, despite a numerical reduction in dietary energy density and numerical increase in DMI. This differs from a past study where increasing the forage inclusion rate from 6% to 12% reduced the total tract DM, OM, and NDF digestibility (Benton et al., 2015). Roughage sources used in that study were alfalfa hay and corn stalk and the byproduct included in the diet was wet distiller's grain with solubles, while in the current study it was pelleted byproducts which would have benefitted more from extended rumen retention. While we cannot confirm greater ruminal digestibility, increasing the forage inclusion rate may help to reduce the risk for ruminal acidosis (Felix and Loerch, 2011) and stimulate rumination (Owens et al., 1998; Shain et al., 1999). It has also been shown that potentially digestible NDF (pdNDF) was selectively retained in the rumen (Tamminga et al., 1989; Lund et al., 2007), compared to iNDF. Thus, increasing the content of pdNDF in the diet by moderately increasing the proportion of barley silage along with byproduct pellet containing a higher iNDF from oat hulls, might have marginally improved rumen retention time and digestibility.

In the current study, the use of a greater forage inclusion rate resulted in improved ADG. However, this improved performance was not supported by a concurrent increase in nutrient digestibility. Past studies have demonstrated a similar increase in ADG associated with moderately greater inclusion rates of forage in finishing diets (Turgeon et al., 2010; Benton et al., 2015) irrespective of the roughage sources. Other studies have noted decreased DMI and ADG and a variable response for G:F in association with decreased forage inclusion rates in finishing diets (Shain et al., 1999; Farran et al., 2006). Overall, the beneficial effects on gain by moderate inclusion of forage in finishing diets were documented in literature, the feed intake and G:F responses were inconsistent. Crawford et al. (2008) suggested that for cattle fed high concentrate diets, dietary roughage concentration has minimal effects on ruminal nutrient digestion. This might be an over-simplification considering past studies which reported increased total tract NDF digestibility (Salinas-chavira et al., 2013) and improved microbial efficiency (Zinn, 1986) associated with a moderately high forage inclusion in finishing diets. While we cannot conclude the factors leading to improved ADG with HF relative to LF, the improvement may be related to a cumulative effect of increased forage that may include a numerical increase for DMI and a reduced severity of ruminal acidosis. In addition to improved weight gain, past studies on meat characteristics have shown that Jersey steers fed a 12% forage had superior marbling and higher quality grades than conventionally fed finishing cattle (Arnett et al., 2012). Attaining the mature body weight in a shorter time with greater ADG, as seen in the current study, could be a contributing factor to earlier and better marbling fat deposition resulting in superior carcass grades.

5.4 Conclusion

In conclusion, marginally increasing the forage concentration in a finishing feedlot diet consisting of high lipid byproduct pellets does not reduce apparent total tract digestibility and may improve heifer growth performance.

Funding for this study was provided by the Alberta Crop Industry Development Fund Ltd. (Lacombe, AB, Canada), and the Beef Cattle Research Council of Canada (Calgary, AB, Canada).

6.0 EFFECT OF DIETARY LIPID INCLUSION FROM BYPRODUCT PELLETS ON DRY MATTER INTAKE, RUMINAL FERMENTATION, AND NUTRIENT DIGESTION IN FINISHING BEEF HEIFERS

Lessons Learned so far:

A marginal increase in forage concentration in finishing feedlot diet with HLP may improve animal performance without reductions in total tract digestibility. This is presumably due to the combined effect of reduced rumen acidosis as indicated by higher rumen pH and improved rumen stratification, leading to slower digesta passage rate. The current study discussed in chapter 6 was designed to further investigate the intrinsic factors reducing G:F in the HLP pellet, by demarcating the effects of lipid and fibre.

ABSTRACT: The objective of this study was to evaluate dry matter intake (DMI), ruminal fermentation, ruminal digesta outflow, and the ruminal and total tract digestibility in response to increasing concentrations of dietary lipid in finishing beef cattle. Five ruminally cannulated, cross-bred growing heifers were used in a 5 × 5 Latin square design, with heifers receiving one of the five dietary treatments for 28 d periods. The first 19 d were used for dietary adaptation, d 17 to 26 were used for digesta and microbial marker infusion, and the last 9 d of each period were used for sample and data collection. Dietary treatments were isonitrogenous with increasing ether extract concentrations of 3.5, 4.2, 4.7, 5.1 and 5.9% of DM. The NDF and starch content of the final diet were kept constant to elucidate the effect of increasing lipid content of the diet. Dry matter intake, ruminal pH, short chain fatty acid (SCFA) concentrations, and ruminal in situ NDF and ADF digestibility did not differ with dietary treatments ($P \geq 0.05$). With increasing dietary ether extract, ruminal ether extract outflow increased ($P < 0.001$), while no changes in outflow were observed for any other constituents. The apparent total tract digestibility of ether extract increased ($P = 0.03$), but no changes were observed for the digestibility of other chemical constituents. Ruminal ether extract digestibility was negative, and digestibility increased with increasing dietary fat levels. No differences were observed for omasal flow of nitrogen, ammonia nitrogen, non-ammonia nitrogen, non-ammonia non-bacterial nitrogen and total bacterial non-ammonia nitrogen. In conclusion, increasing dietary lipid up to 5.9% of DM with canola seed did not affect ruminal digesta flow and rumen fermentation parameters, and hence is not responsible for the reduced feed efficiency associated with high fibre high lipid byproduct pellets in finishing beef cattle.

6.1 Introduction

Previous studies have demonstrated that feeding byproduct based high-lipid pellets (HLP) in diets for finishing feedlot cattle can be an effective alternative to diets based on cereal grain (Górka et al., 2013; Joy et al., 2016). In fact, use of HLP did not affect ADG (Górka et al., 2013), increased mean ruminal pH (Górka et al., 2015; Joy et al., 2017), and despite reducing feed efficiency (Górka et al., 2013; Joy et al., 2016), has the opportunity to reduce the cost of gain. While HLP have been formulated to contain a similar energy density as the cereal grain being replaced, the energy density based on DMI, BW, and ADG has been less than predicted (Górka et al., 2013; Zenobi et al., 2014; Joy et al., 2016). The reasons for the decreased energy density of the HLP can be explained by many factors including particle size of ingredients comprising the pellet, digestibility of the byproducts within the pellet, and the lipid concentration of the pellet (Górka et al., 2015; Joy et al., 2017).

Use of lipids in diets for finishing cattle has received considerable attention as a strategy to increase energy density. While lipids have a greater caloric value than carbohydrates, lipids may interact with fibre digestion (Jenkins, 1993; Pantoja et al., 1994), alter the site of starch digestion (Montgomery et al., 2008), and may increase insulin resistance in finishing cattle (Rico et al., 2016). Thus, it is possible that the compromised feed efficiency observed in previous studies where HLP replaced barley grain (Górka et al., 2015; Joy et al., 2016) may be in part due to negative effects of increased dietary ether extract concentration. We hypothesised that increasing the dietary ether extract concentration for finishing cattle will increase the rate of rumen passage and will shift the site of digestion to post ruminal digestion. The objectives of this study were to evaluate DMI, ruminal fermentation, and ruminal and total tract digestibility in response to increasing concentrations of dietary lipids.

6.2 Materials and methods

All procedures involving heifers were pre-approved by the University of Saskatchewan Animal Research Ethics Board (protocol number 20100021) and followed the guidelines of the Canadian Council on Animal Care (Tenessen et al., 2009).

6.2.1 Heifer management

Five Hereford-cross yearling beef heifers from the University of Saskatchewan Goodale Research Farm (Saskatoon, SK, Canada) were purchased and fit with a 7.6-cm ruminal cannula (model 3C; Bar Diamond Inc., Parma, ID) before the start of the study. Three weeks following

surgery, the 7.6-cm cannula was replaced with a 9-cm ruminal cannula (model 9C; Bar Diamond Inc., Parma, ID, USA). Heifers were treated with Ivermectin pour-on endecto-paraciticide (500 mcg/kg; Alberta Veterinary Laboratories, Calgary, AB) by topical application before the start of the study. Heifers was housed in individual pens (9 m^2) with rubber mats on the floor and had ad libitum access to fresh water. All heifers were fed once daily at 0830 h. Pens were cleaned and washed daily. Before starting the study, all heifers were maintained on a grass hay-based diet with a vitamin and mineral supplementation to meet predicted requirements (NRC, 2000). Heifers were gradually transitioned to a diet containing 85% rolled barley grain using 5 intermediary diets with each one fed for 4 d.

6.2.2 Dietary treatments and experimental design

This study was conducted as a 5 × 5 Latin square design with treatment sequences balanced for carry-over effects. The dietary treatments (Table 6.1) had the same inclusion rates (DM basis) of barley silage (6%), barley grain (34.1%), HLP (51.2%), and minerals and vitamins (8.7%). However, the formulation of the HLP was designed to increase the dietary lipid concentration by increasing off-grade whole canola at the expense of canola meal and wheat screenings (Table 6.2). Diets were formulated to be iso-nitrogenous without controlling for caloric density. The NDF and starch content of the final diet were also kept constant to elucidate the effect of increasing lipid content of the diet. Melengesterol acetate (Elanco Animal Health, IN, USA) was incorporated into the mineral pellet and supplied at 0.4 mg/d to prevent oestrus and all diets contained monensin (33 mg/kg DM; Elanco Animal Health, IN, USA). The ether extract content of the final diets were 3.5, 4.2, 4.7, 5.1 and 5.9% on a DM basis for diets F3.5, F4.2, F4.7, F5.1, and F5.9, respectively.

The total duration of the study was 140 d consisting of 5 periods with 28 d/ period. The first 5 d of each period was used to gradually transition heifers to their respective treatment followed by 14 days for adaptation. The last 9 d of each period was used for data and sample collection.

Table 6.1 Dietary ingredient and chemical composition of the five high-lipid byproduct pellet (HLP) based diets differing in ether extract content

	Diet				
Item	F3.5	F4.2	F4.7	F5.1	F5.9
Ingredient, % DM					
Barley silage	6	6	6	6	6
Rolled barley grain	34.1	34.1	34.1	34.1	34.1
High-lipid byproduct pellet[1]					
HLP 1	51.2	0	0	0	0
HLP 2	0	51.2	0	0	0
HLP 3	0	0	51.2	0	0
HLP 4	0	0	0	51.2	0
HLP 5	0	0	0	0	51.2
Vitamin and mineral pellet[2]	8	8	8	8	8
Limestone	0.7	0.7	0.7	0.7	0.7
Chemical composition, % DM basis[3]					
CP, % DM	15.0 ± 0.14	14.9 ± 0.46	14.6 ± 0.30	14.5 ± 0.38	14.4 ± 0.28
NDF, % DM	21.6 ± .79	20.8 ± .16	21.7 ± 0.39	21.0 ± 0.48	21.4 ± 0.94
ADF, % DM	11.0 ± 0.41	11.1 ± 0.38	11.6 ± 0.21	11.1 ± 0.41	11.6 ± 0.69
Starch, % DM	42.9 ± 0.53	44.0 ± 0.80	42.9 ± 0.20	43.0 ± 0.50	42.3 ± 0.65
Ether extract, % DM	3.5 ± 0.17	4.2 ± 0.38	4.7 ± 0.31	5.1 ± 0.20	5.9 ± 0.17
Ash	5.6 ± 0.06	5.4 ± 0.10	5.6 ± 0.19	5.4 ± 0.11	5.4 ± 0.16
Lignin, % DM	2.9 ± 0.14	2.9 ± 0.05	2.8 ± 0.11	2.9 ± 0.19	2.7 ± 0.03
NE_m, Mcal kg of DM^{-1}	1.81 ± 0.022	1.86 ± 0.021	1.87 ± 0.009	1.90 ± 0.014	1.94 ± 0.015
NE_g, Mcal kg of DM^{-1}	1.19 ± 0.017	1.23 ± 0.013	1.24 ± 0.011	1.26 ± 0.019	1.29 ± 0.015
Ca	0.84 ± 0.062	0.77 ± 0.046	0.81 ± 0.119	0.76 ± 0.045	0.76 ± 0.044
P	0.47 ± 0.019	0.41 ± 0.008	0.39 ± 0.011	0.40 ± 0.008	0.39 ± 0.010

[1]Ingredient composition of HLP represented in Table 2.

[2]On DM basis contained 2.5% of NaCl, 5% of Ca, 0.46% of P, 2.0% of Mg, 1.96% of K, 2.0% of S, 5.06 mg/kg of Co, 161.0 mg/kg of Cu, 8.8 mg/kg of I, 494.8 mg/kg of Fe, 370.6 mg/kg of Mn, 2.5 mg/kg of Se, 345.2 mg/kg of Zn, 44052.8 IU/kg of vitamin A, 16519.8 IU of vitamin D, 330.4 IU of vitamin E, 901.4 mg/kg of choline, 417.6 mg/kg of monensin and 0.68 mg/kg of MGA.

[3]Mean ± Standard deviation.

Table 6.2 Ingredient and chemical composition of the five high-lipid byproduct pellets (HLP) used in the five dietary treatments differing in ether extract content

	High-lipid byproduct pellet				
Variable	HLP 1	HLP 2	HLP 3	HLP 4	HLP 5
Ingredient, % DM					
Pea screenings	17.8	17.8	17.8	17.8	17.8
Wheat screenings	33.8	30.4	27.1	23.7	20.2
Wheat	29.7	29.7	29.7	29.7	29.7
Oat hulls	11.2	11.2	11.2	11.2	11.2
Off-grade canola	0	5.3	10.5	15.8	21.1
Canola meal	7.5	5.6	3.7	1.8	0
Chemical composition, % DM basis					
CP, % DM	18.2	18.0	17.4	17.3	17.0
NDF, % DM	23.3	21.8	23.6	22.1	22.8
ADF, % DM	11.4	11.6	12.5	11.6	12.6
Starch, % DM	39.9	42.1	39.8	40.1	38.8
Crude Fat, % DM	3.6	4.9	5.8	6.6	8.3
Ash	4.2	3.8	4.1	3.9	3.9
Lignin, % DM	3.2	3.1	3.0	3.1	2.8
TDN, % DM	76.9	79.9	80.7	82.4	85.3
NE_m, Mcal kg of DM^{-1}	1.85	1.94	1.97	2.02	2.10
NE_g, Mcal kg of DM^{-1}	1.21	1.29	1.31	1.36	1.42
NFC	50.7	51.6	49.0	50.2	48.0
NSC	39.9	42.1	39.8	40.1	38.8
Ca	0.30	0.18	0.25	0.15	0.14
P	0.56	0.46	0.41	0.43	0.40

6.2.3 Dry matter intake and ruminal and apparent total tract digestibility

Feed intake and refusals were measured daily with samples of feed and refusals collected to ensure ad libitum feed intake. Feed ingredient samples were collected twice weekly throughout the study. The feed ingredients were used to determine DM concentration by oven drying at 55°C in a forced-air oven to ensure that the desired ingredient inclusion rates fed matched the DM formulation. From d 24 through 26, the amount of feed offered and refused was recorded and daily samples of feed and orts were composited proportionally by heifer for each period to determine DMI.

Feed ingredient samples and diet refusals were dried in a forced-air oven at 55°C for 72 h. Samples were composited by period and heifer and were ground using a hammer mill to pass through a 1-mm screen (Christy and Norris Ltd., Chelmsford, UK). Concentrate samples (barley grain and HLP) were ground using a Retch ZM 200 grinder (Haan, Germany) to pass through a 1-mm screen. Subsequently ground samples were submitted to Cumberland Valley Analytical Services (Hagerstown, MD) and analysed for CP, NDF, ADF, lignin, ash, starch, Ca, and P as described by Rosser et al. (2013). Ether extract was analysed using acid hydrolysis as described in AOAC (2000) using the official method 954.02.

To measure ruminal outflow and digestibility, digesta and microbial markers were infused into the rumen from d 17 through 26 using a peristaltic pump (Model 205U, Watson and Marlow, Cornwall, UK). Double distilled water was used to prepare marker solutions of $YbCl_3$ (Siddons et al., 1985) and Cr-EDTA (Uden et al., 1980) which were used as digesta markers for the particulate phase and fluid phases, respectively. In addition, $^{15}NH_4SO_4$ was used to quantify the microbial flow from the rumen (Reynal et al., 2003). The markers were infused and analyzed as described by Chibisa et al. (2012) and Górka et al. (2015). A daily dose rate of 2.77 g of Cr, 3.35 g of Yb, and 0.22 g of ^{15}N (Brito et al., 2006) was targeted by infusing 1 L of the solution. The actual quantity infused was assessed by daily quantifying the weight of the marker container. Before the start of infusions, a 500-mL sample of ruminal digesta was collected and stored at -20°C to analyze the background concentration of ^{15}N. A priming dose of half the daily dose of all marker solutions was infused before the start of the infusions and a sample of each marker solution was subsampled to measure the marker concentration and kept at room temperature.

The omasal sampling technique described by Huhtanen et al. (1997) and Chibisa et al. (2012) was used for collection of samples. Omasal digesta (550 mL) was collected at 0900,

1500, and 2100 h on d 24, 0300, 1200, and 1800 h on d 25, and 0000 and 0600 h on d 26. The sampling protocol allowed for the collection of 8 samples representing every 3 h of a 24-h period when compressed. The 550-mL sample from each time point was subdivided into 300 mL, 125 mL, and 125 mL of subsamples. The 300-mL subsamples was composited by heifer and period resulting in a 2.4-L sample that was stored at -20°C and later was used to derive the particulate- (PP) and fluid-phase (FP) digesta fractions (Ahvenjärvi et al., 2002). The PP and FP were utilized to calculate the DM outflow from the rumen using the double marker technique (Faichney, 1975).

The second 125-mL omasal sample was kept on ice and used to analyze the particle associated bacteria (PAB) and fluid associated bacteria (FAB) (Brito et al., 2009; Chibisa et al., 2012). Samples from two consecutive collections were composited to form a 250-mL sample that was filtered through two layers of cheese cloth. The filtrand was again washed in 250 mL of 0.85% saline solution and squeezed through two 2 layers of cheese cloth. The resulting filtrand was transferred to a PAB container with 175 mL of cold 0.85% saline solution containing 0.1% (w/v) of Tween-80, and mixed thoroughly. The filtrate from these two filtrations was then centrifuged at 1,000 × *g* for 5 min at 5°C and the resulting pellet was transferred to the PAB container and supernatant was kept in a FAB container. The contents of PAB were blended at low speed for 30 s. The resulting PAB solution was kept at 5°C for 24 h before being used for further processing. After 24 h, the solution for PAB was again filtered through 2 layers of cheese cloth. The filtrand was discarded and the filtrate was centrifuged at 1,000 × *g* for 5 min at 5°C. The pellet was discarded and the supernatant was centrifuged at 11,300 × *g* for 30 min at 5°C. The supernatant was discarded and the resulting pellet was reconstituted in 50 mL of McDougall's buffer (McDougall, 1948). It was centrifuged again at 11,300 × *g* for 30 min at 5°C and the resulting PAB pellet was stored at -20°C until further analysis.

The supernatant arising from the first centrifugation and kept in the FAB container was then used for FAB isolation and was centrifuged at 11,300 × *g* for 30 min at 5°C. The supernatant was discarded and the resulting pellet was reconstituted in 50 mL of McDougall's buffer (McDougall, 1948). The samples were then centrifuged at 11,300 × *g* for 30 min at 5°C and the resulting FAB pellet was stored at -20°C.

Omasal digesta were analyzed for Cr, Yb, and ^{15}N as described by Chibisa et al. (2012) and Górka et al. (2015). The omasal digesta fractions were freeze dried and ground and the reconstituted digesta samples were also analyzed for DM, OM, CP, NDF, ADF, ether extract,

starch, ash, Ca, and P, at Cumberland Valley Analytical Services (Hagerstown, MD) as described by Rosser et al. (2013) with the exception that acid hydrolysis was used for ether extract. The remaining 125-mL sample was composited by heifer and period and was stored at -20˚C as a spare sample.

Corresponding to the time of omasal digesta sampling, a fecal grab sample (100 g) was collected directly from the rectum of each heifer and stored at -20˚C. Consecutive samples from each heifer were composited, used to determine DM concentration, and ground using a hammer mill (Christy and Norris Ltd., Chelmsford, UK) to pass through 1-mm screen. The ground fecal samples were sent to Cumberland Valley Analytical Services (Hagerstown, MD) for nutrient analysis. The fecal samples were also analyzed for Yb and Cr marker concentrations using atomic absorption spectrophotometry and atomic emission spectroscopy (iCE 3000 series; Thermo Fisher Scientific Inc., Waltham, MA) respectively. Chromium concentration in feces was used to predict the total fecal output, which was then used to calculate the apparent total tract digestibility.

6.2.4 Ruminal pH and short-chain fatty acid concentrations

Ruminal pH was measured in the ventral sac of the rumen every 5 min for 4 d from d 20 through d 23 of each period using the Lethbridge Research Centre Ruminal pH Measurement System (LRCpH; Model Dascor, Escondido, CA) as described in detail by Penner et al. (2006). The pH probes were standardized in pH buffer solutions 7 and 4 at 39°C before being inserted into the rumen of each heifer and after retrieval. Data were transformed from mV recordings to pH using beginning and end linear regressions and assuming linear drift. Ruminal pH thresholds of 5.5 and 5.2 were used to evaluate the duration and area below these thresholds (Penner et al., 2007).

Ruminal digesta was collected at the same time points as omasal digesta (day 24 to 26). Ruminal digesta was collected from the anterior, ventral, and posterior regions of the rumen (250 mL/region) and placed in a common container. Digesta samples were strained through two layers of cheesecloth and a 10-mL aliquot of filtrate were transferred into a 15-mL tube containing 2 mL of 25% (wt/vol) metaphosphoric acid. The sample was sealed and stored at -20°C until being used for determination of SCFA concentration using gas chromatography (Agilent 6890, Mississauga, ON, Canada) as described by Khorasani et al. (1996).

6.2.5 In-situ NDF digestion

To evaluate the effect of dietary lipid on NDF digestibility, a 10 kg barley silage sample was dried in a forced-air oven at 55°C for 48 h and ground to pass through a 2-mm screen using a hammer mill (Christy & Norris, Christy Turner Ltd., Chelmsford, UK). Representative sub-samples from the barley silage sample were used as the standard fibre source for the in situ incubations. Seven grams of the ground barley silage were weighed into 5 × 10 cm nylon bags (model #R510,Ankom Technology, Macedon, NY) with a pore size of 50 μm. Bags were heat-sealed and incubated in the ventral sac of the rumen of each heifer in each period for 0, 6, 12, and 24 h using 2, 3, 4, and 5 bags, respectively. A sequential-in all-out approach was used with incubations starting at 0800 h on day 27.

Following incubation, bags were immediately washed 5 times in cold water and placed in a forced-air oven at 55°C for 48 h. Residue in bags were then composited for each treatment and time duration. The composited samples were analyzed for NDF at Cumberland Valley Analytical Services (Hagerstown, MD). Data obtained were used to calculate the rate of disappearance NDF after 6, 12, and 24 h ruminal incubation.

6.2.6 Calculations and statistics

Calculations for the omasal flow of nutrients were conducted as described by Brito et al. (2009) with modifications described by Chibisa et al. (2012). Briefly, ^{15}N enrichment in bacterial and omasal fractions were used to calculate atom percent excess (APE): ^{15}N APE = ^{15}N atom % – ^{15}NB. Based on the assumption that FAB represented bacteria flowing with the fluid phase and PAB represented bacteria flowing with the particulate phase, omasal flow of FAB N, PP N, total microbial N, and OM flow were calculated as follows:

FAB N flow = FP N flow × (FP ^{15}N APE ÷ FAB ^{15}N APE);

PAB N flow = PP N flow × (PP ^{15}N APE ÷ PAB ^{15}N APE);

Total microbial N flow = FAB N flow + PAB N flow;

FAB OM flow = (FAB DM flow × % FAB OM) ÷ 100;

PAB OM flow = (PAB DM flow × % PAB OM) ÷ 100;

Total bacteria OM flow = FAB OM flow + PAB OM flow.

Data were analyzed as 5 × 5 Latin square design using the MIXED procedure of SAS version 9.2 (SAS Institute, Cary, NC) according to the following model statement:

$Y_{ijk} = \mu + P_i + H_j + T_k + E_{ijk}$,

Where, Y_{ijk} was the dependent variable, μ was the overall mean, P_i was the fixed effect of period i, H_j was the random effect of heifer j, T_k was the fixed effect of dietary treatment k, and E_{ijk} was the residual error. Data are presented as least square means with their corresponding standard errors. Because the increases in dietary ether extract content were unequally spaced, the IML procedure of SAS was used to calculate the unequally spaced coefficients for linear, quadratic, and cubic contrasts. Significance was declared at $P \leq 0.05$.

6.3 Results

DMI did not differ among treatments averaging at 13.4 ± 0.58 kg/d (Table 6.3). Likewise, mean, minimum, and maximum ruminal pH did not differ ($P \geq 0.17$) among dietary treatments. The duration and area that ruminal pH was below 5.8, 5.5, and 5.2 did not differ among treatments ($P \geq 0.05$). Increasing dietary ether extract had no effect on the total SCFA concentration and did not affect the molar proportion of individual SCFA ($P \geq 0.45$).

Treatment did not affect the 6, 12, or 24-h in situ NDF digestibility (Table 6.4). Additionally, ruminal digestibility was quite low with average values for NDF of 27.75, 26.82 and 27.55% for 6, 12, and 24-h, respectively.

With increasing dietary lipid, the ruminal outflow of ether extract linearly increased ($P < 0.001$; Table 6.5); while, the outflow of OM, CP, NDF, ADF, and starch did not differ ($P \geq 0.32$). The apparent ruminal digestibility of ether extract was negative for all dietary treatments indicating greater ruminal outflow of ether extract when compared to intake, but ruminal digestibility of ether extract linearly increased with increasing dietary lipid concentration ($P < 0.01$). Apparent ruminal digestibility of other chemical constituents were not affected ($P > 0.47$) by dietary lipid supply.

N intake, apparent ruminal N digestion, and N truly digested in the rumen did not differ among treatments (Table 6.6). Likewise, the flow of total N, NH_3-N, NAN, NANBN, and bacterial NAN at the omasal canal did not differ among treatments ($P \geq 0.19$).

Table 6.3 Effect of increasing levels of dietary ether extract in high-lipid byproduct pellet based diet in finishing beef cattle on DMI and rumen pH parameters.

	Treatment[1]						Contrast		
	F3.5	F4.2	F4.7	F5.1	F5.9	SEM[2]	Linear	Quadratic	Cubic
DMI, kg/d	14.0	13.2	13.5	13.2	13.4	0.58	0.56	0.47	0.79
Ruminal pH									
Mean	6.02	5.96	6.05	5.92	6.11	0.085	0.53	0.33	0.65
Minimum	5.34	5.24	5.42	5.29	5.43	0.088	0.42	0.50	0.87
Maximum	6.79	6.83	6.79	6.73	6.84	0.053	0.92	0.55	0.17
Duration pH <5.8, min/d	474	555	460	606	350	116.1	0.53	0.28	0.64
Area pH <5.8, pH × min/d	121	215	106	159	88	56.3	0.50	0.38	0.55
Duration pH <5.5, min/d	175	333	134	228	121	97.0	0.50	0.46	0.52
Area pH <5.5, pH × min/d	27	86	19	35	21	24.3	0.47	0.43	0.17
Duration pH <5.2, min/d	22	128	18	30	23	36.8	0.50	0.43	0.08
Area pH <5.2, pH × min/d	1	15	1	3	2	4.2	0.50	0.34	0.05
Total SCFA, m*M*	130.8	132.6	127.6	136.3	128.8	6.53	0.93	0.76	0.69
Acetate, mol/100 mol	51.4	51.0	51.5	51.8	50.9	5.31	0.95	0.83	0.72
Propionate, mol/100 mol	31.2	30.5	31.1	31.4	28.0	11.19	0.50	0.59	0.62
Butyrate, mol/100 mol	15.0	15.6	14.8	13.4	16.9	1.99	0.71	0.45	0.36
Isobutyrate, mol/100 mol	0.7	0.7	0.8	0.6	0.7	0.43	0.85	0.90	0.65
Isovalerate, mol/100 mol	1.0	1.2	1.3	1.0	1.3	0.30	0.61	0.97	0.53
Valerate, mol/100 mol	2.7	2.6	2.0	2.8	3.0	0.74	0.75	0.55	0.93

[1]Treatment: The different diets consisted of 3.5, 4.2, 4.7, 5.1 and 5.9 % of fat on a dry matter basis.

[2] Standard error of mean.

Table 6.4 Effect of increasing dietary ether extract level on NDF digestibility after rumen incubation with increasing time points measured by in-situ nylon bag technique in finishing beef cattle fed a high-lipid byproduct pellet.

	Treatment[1]						Contrast		
	F3.5	F4.2	F4.7	F5.1	F5.9	SEM[2]	Linear	Quadratic	Cubic
NDF digestibility, % DM									
6 h	28.20	27.96	27.23	27.87	27.51	0.678	0.48	0.72	0.88
12 h	27.45	27.78	26.63	26.76	25.46	0.925	0.10	0.55	0.81
24 h	28.08	28.78	26.92	27.80	26.18	1.263	0.24	0.64	0.84

[1]Treatment: The different diets consisted of 3.5, 4.2, 4.7, 5.1 and 5.9 % of fat on a dry matter basis.

[2]Standard error of mean.

Table 6.5 Nutrient flow out of rumen in finishing beef cattle fed HLP diet with increasing levels of ether extract.

	Treatment[1]					SEM[2]	Contrasts		
	F3.5	F4.2	F4.7	F5.1	F5.9		Linear	Quadratic	Cubic
Ruminal outflow, kg/d[3]									
OM	7.2	6.8	7.3	6.6	6.8	0.37	0.47	0.88	0.96
CP	2.5	2.4	2.3	2.3	2.3	0.11	0.32	0.76	0.90
Ether extract[4]	0.60	0.65	0.73	0.73	0.87	0.033	< 0.001	0.39	0.81
NDF	2.8	2.6	2.9	2.4	2.8	0.19	0.62	0.37	0.45
Starch	0.9	0.9	1.0	0.9	0.9	0.14	0.84	0.84	0.90
Apparent ruminal digestibility, % DM									
OM	46.0	46.2	42.8	47.1	46.1	2.98	0.92	0.71	0.86
CP	-17.1	-21.2	-19.0	-22.8	-18.8	4.15	0.74	0.47	0.93
Ether extract[4]	-21.6	-15.4	-14.4	-8.0	-9.4	3.23	0.008	0.35	0.63
NDF	7.4	5.6	2.5	16.4	3.1	7.37	0.96	0.72	0.31
Starch	85.2	84.4	82.0	84.2	82.6	2.69	0.51	0.82	0.86
Apparent total tract digestibility, % DM									
DM	61.4	61.1	60.8	60.3	61.5	5.09	0.94	0.65	0.79
OM	64.0	63.4	63.1	62.7	63.5	5.11	0.78	0.65	0.85
CP	61.1	59.4	60.1	58.8	60.0	3.82	0.57	0.43	0.95
Ether extract[4]	45.8	45.5	52.0	50.8	54.4	8.33	0.03	0.95	0.60
NDF	18.0	15.3	16.7	15.0	18.3	13.80	0.96	0.48	0.98
Starch	90.0	90.6	89.6	89.2	89.0	5.33	0.54	0.88	0.65

[1]Treatment: The different diets consisted of 3.5, 4.2, 4.7, 5.1 and 5.9 % of fat on a dry matter basis.

[2]Standard error of mean.

[3]Flow rate calculated using single marker system utilizing Cr as the whole digesta marker.

[4]Ether extract using acid hydrolysis.

Table 6.6 Omasal flow of N constituents from rumen in finishing beef cattle fed high-lipid byproduct pellet diets with increasing ether extract levels.

	Dietary Treatments[1]					SEM[2]	Contrasts		
	F3.5	F4.2	F4.7	F5.1	F5.9		Linear	Quadratic	Cubic
N intake, g/d	335.23	314.3	315.01	305.54	309.44	13.705	0.19	0.41	0.92
N apparent digested in the rumen									
g/d	-59.1	-67.3	-58.6	-69.8	-59.1	12.20	0.98	0.64	0.93
% of N intake	-17.08	-21.16	-18.98	-22.76	-18.82	4.149	0.74	0.47	0.93
N truly digested in the rumen									
g/d	211.6	190.7	212.0	190.2	190.5	79.17	0.46	0.92	0.75
% of N intake	67.0	64.5	70.6	65.8	65.7	17.28	0.92	0.78	0.77
Flow at omasal canal[3]									
N									
g/d	394.3	381.6	373.6	375.3	368.5	18.04	0.32	0.76	0.90
% of N intake	117.1	121.2	119.0	122.8	118.8	4.15	0.74	0.47	0.93
NH3-N, g/d	9.4	7.5	8.2	7.2	7.5	3.93	0.21	0.44	0.72
NAN									
g/d	386.0	375.2	366.5	369.2	362.2	17.64	0.34	0.78	0.91
% of N intake	114.6	119.1	116.7	120.8	116.8	4.14	0.69	0.45	0.94
NANBN									
g/d	101.3	103.2	81.8	95.1	98.4	51.42	0.77	0.52	0.73
% of NAN flow	25.3	26.6	20.9	25.2	25.8	11.99	0.99	0.56	0.73
% of N intake	29.4	32.3	26.0	31.1	31.1	16.96	0.87	0.81	0.76
% of DM intake	0.7	0.8	0.6	0.7	0.7	0.40	0.91	0.79	0.70
Total bacterial NAN									
g/d	294.8	282.1	294.8	284.1	273.8	51.62	0.38	0.79	0.65
% of NAN	74.7	73.4	79.1	74.8	74.2	11.99	0.99	0.56	0.73

[1]Treatments: The different HLP diets has linearly increasing fat percentage 3.5, 4.2, 4.7, 5.1 and 5.9 % of dietary DM.

[2]Standard error of mean.

[3]Flow rate calculated using single marker system utilizing Cr as the whole digesta marker; N = Nitrogen; NH3-N = Ammonia nitrogen; NAN = Non-ammonia nitrogen; NANBN = Non-ammonia non-bacterial nitrogen.

6.4 Discussion

The objective of the study was to evaluate the effect of dietary lipid on DMI, ruminal fermentation, ruminal digesta outflow, and ruminal and total tract digestibility. The experimental approach relied on maintaining similar NDF and starch concentrations among dietary treatments. This approach was used to elucidate whether dietary lipid supply partially explained reduced feed conversion efficiency with the use of HLP as reported by Górka et al. (2013) and Joy et al. (2017; Chapter 4). While all treatments had similar NDF, ADF, and starch concentrations (21.3, 11.4, and 43% respectively), the ether extract concentration of the diets increased from 3.5% to 5.9%. Corresponding to the increased lipid content, the total energy content of the diets increased linearly from 1.19 Mcal/kg NEg in diet F3.5 (fat 3.5%) to 1.29 in diet F5.9.

Increasing the supply of dietary lipid has been shown to improve palatability, reproductive efficiency, feed efficiency, alleviate heat stress (Zinn and Jorquera, 2007), increase energy density of diet (NRC, 2000), reduce feed dustiness (Chiba et al., 1985), alter rumen fermentation, and reduce incidence of ruminal acidosis (Górka et al., 2015). However, source of lipid may also influence the response. For example, yellow grease supplementation resulted in greater ruminal fibre digestion and greater ruminal molar proportion of propionate when compared to blended animal-vegetable fat (Zinn, 1989); likely due to the differing degree of saturation between the two fat sources. Børsting et al. (1992) observed that intestinal C18:0 digestion of formaldehyde protected vegetable fats were 92% whereas, C18:0 digestion from tallow and yellow grease was generally less than 75%. The lipid in our experimental diets originated from off-grade canola seeds that are rich in mono and poly unsaturated fatty acids (Assadi et al., 2011). However, lipids associated with forage or plants are known to be less degraded in the rumen compared to free oils (Perrier et al., 1992), probably due to plant secondary metabolites (Vasta et al., 2009b) or due to protection of lipids from lipolysis and biohydrogenation by cellular structures (Doreau and Ferlay, 1994). Thus, increased dietary lipid, when provided as part of the original seed matrix, results in alleviation of negative effect on ruminal digestion (Maczulak et al., 1981; Zinn and Jorquera, 2007) and may partially explain the lack of effect on ruminal fermentation and ruminal nutrient digestibility in the present study. Nevertheless, it is important to consider that while we increased dietary lipid concentration, the lipid provided was not a free oil as it was still contained within the seed matrix.

The lack of difference in the DMI between dietary treatments is interpreted to indicate that a moderate increase in dietary lipid concentration and hence dietary energy density may not reduce DMI for finishing beef cattle. The results support previous findings as increasing dietary lipid did not affect DMI in finishing beef cattle fed with a variety of lipid sources such as sunflower oil (Sackmann et al., 2003), yellow grease (Zinn et al., 2000), or corn oil (Duckett et al., 2002). Moreover, past studies using byproduct based pellets have resulted in either increased or similar DMI when compared to barley based diets (Górka et al., 2015; Joy et al., 2017). These results collectively suggest that increasing dietary lipid can be an effective strategy to increase energy intake by finishing beef cattle.

The apparent ruminal digestibility of lipid was negative in the current study and supports that observed by Montgomery et al. (2008) and Duckett and Gillis (2010). In fact, increasing the supply of dietary lipid has been reported to increase the free fatty acid concentration of rumen bacteria by 150% via increases in intracellular lipid droplets (Bauchart et al., 1990). According to Ferlay et al. (1993), the microbial contribution to the total duodenal fatty acid flow could range from 40 to 50% depending on the the lipid content of the diet. With increasing dietary lipid, the microbial contribution may be increased and potentially overestimated due to incorporation into microbial cells and adsorption of lipid on microbial cells (Bauchart et al., 1990; Doreau and Ferlay, 1994). Eventhough microbial de novo lipid biosythesis was not quantitatively estimated in the present study, it is clear that the microbial flow results in negative ether extract digestibility and that increasing dietary lipid decreases the relative contribution of the microbial ether extract flow relative to the total omasal ether extract flow. De novo lipid synthesis by rumen bacteria and protozoa from substrates like SCFA (Harfoot, 1978), amino acids (Kaneda, 1991), and glucose (Patton et al., 1970) have been described in the past and would contribute to the increased ether extract flow relative to dietary supply. Futhermore, our treatment diets included monensin and in vitro studies have shown increased microbial lipid synthesis in the presence of ionophores (O'Kelly and Spiers, 1990). In conclusion, rumen microbial lipid content may increase in response to diets with greater lipid concentration, by way of denovo biosynthesis from other energy substrates, adsorption of fat on the microbial surfaces, or incorporation of free FA into the intracytoplasmic structures thereby decreasing ruminal ether digestibility.

Apparent ruminal ether extract digestiblilty increased with increasing level of dietary lipid, similar to the results reported by others (Sackmann et al., 2003; Messana et al., 2013), where they

fed increasing concentrations of lipid sourced from sunflower and soybean respectively to beef steers. As lipids are not extensively digested in the rumen, increasing dietary lipid supply dilutes the contribution of the microbial lipid relative to total omasal lipid flow. As microbial ether extract flow is the major driver for negative ruminal ether extract digestibility, the dilution of microbial ether extract flow relative to the total ether extract flow explains why increasing dietary lipid intake increased ruminal ether extract digestibility in the present study. Supporting this arguement, there were no changes in ruminal microbial outflow with increasing dietary lipid concentration, thus eliminating the possibility of a negative effect of lipid content on microbial flow and attributing the increased ruminal ether extract digestibility to the dilution effect discussed.

There were no changes in ruminal digestiblity of NDF, CP, or starch with increasing dietary lipid concentration. Similarly, ruminal pH and SCFA were not altered. In a study conducted using growing beef cattle fed a dietary ether extract ranging from 3 to 9% and sourced from corn distillers solubles, it was found that NDF or ADF digestiblity were not affected while the ether extract digestibility increased with increasing dietary lipid content (Segers et al., 2015). Also, as observed in the present study, increasing lipid content had no effect on ruminal pH, SCFA concentrations, or apparent ruminal nutrient digestibility other than for ether extract. Briefly, increasing dietary lipid content up to 6% dietary DM does not appear to influence ruminal fermentation in finishing beef cattle.

Ruminal NDF digestibility was not affected by the increasing dietary fat concentration, as mentioned above. Several theories have been postulated to explain decreased NDF digestiblity in association with high lipid diets. Theories include: 1) lipid coating the feed and microbial cells thus interfering with the attachment of bacterial cellulase with cellulose; 2) long chain fatty acids attaching and altering the biological membrane of rumen micobes and having a cytotoxic effect; and 3) lipids reducing the availability of Ca needed for microbial cells (Jenkins, 1993). However, the lack of a dietary lipid effect on NDF digestiblity in the current study may be due to the use of whole canola seeds as our lipid source, as canola-seed associated oil may supply a source of ruminal bypass fat (described above) and hence having a lesser deleterious effect on cellulolytic microbes in the rumen. In addition, the greatest dietary lipid concentration was 5.9% of DM: a dietary concentration suggested to be within levels sufficient to avoid negative effects on ruminal fermentation (Zinn and Jorquera, 2007).

On the other hand, the NDF in the diet was largely sourced from non-forage fibre sources like oat hulls, that inherently have a low digestibility (Thompson et al., 2000). Low apparent ruminal NDF digestibility has previously been reported for beef heifers when fed byproduct-pellets based diets (Górka et al., 2015). However, the low fibre digestiblity observed with in situ incubation data in the current study suggests that low NDF digestibility may be due to factors other than increasing lipid and inherent digestibility of the non-forage fibre sources used. Low ruminal pH observed in the current study could be another reason for reduced ruminal fibre digestiblity. Despite replacing a considerable amount of barley with byproduct pellet, in the current study we still observed low rumen pH, probably because of the wheat used as a binder in the HLP pellet. Low ruminal pH creates a greater pH gradient across the cell membranes of cellulolytic bacteria which could be detrimental to them and reduce ruminal NDF digestibilty (Russell and Wilson, 1996).

In the current study with increasing levels of dietary fat, there was no effect on the digesta flow or site of digestion for DM, OM, CP, NDF, or starch. Past studies with finishing diets in steers have shown that supplemental fat has no effect on the digesta kinetic parameters like flow rate, fluid dilution rate, turnover rate and rate of passage (Clary et al., 1993); however, Montgomery et al. (2008) reported that increasing dietary lipid shifted the site of starch digestion from the rumen to the intestine. Moreover, previous research has shown that total SCFA concentration and the molar proportions of SCFA were not affected by supplemental lipid in finishing diets (Zinn, 1988; Clary et al., 1993) or in the present study, likely due to dietary starch being held constant among all diets.

In conclusion, increasing dietary lipid up to 6% of dietary DM for finishing beef cattle did not negatively affect nutrient intake, ruminal fermentation, or apparent ruminal and total tract digestilbity. But, increasing dietary lipid increased apparent ruminal and total tract ether extract digestilbity. The hypothesis for a potential shift in the site of digestion in association with increased dietary lipid content was not supported due to the lack of differences in ruminal digestiblities and rumen fermentation parameters.

7.0 GENERAL DISCUSSION AND CONCLUSION

7.1 Economics of using HLP

Profitability in the feedlot sector depends heavily on feed cost, gain to feed ratio and cattle purchasing and marketing decisions. Previous studies have evaluated the use of low-cost byproduct feeds (Górka et al., 2013; Zenobi et al., 2014) with the objective of impoving the profitability of the backgrounding and finishing beef sectors. While feeding HLP decreased G:F (Górka et al., 2013), the lower cost of the HLP resulted in a $10/steer savings over a conventional barley-grain based finishing program. In the studies within this thesis I evaluated and employed several strategies to improve profitability and minimize the negative impact on G:F. For example, the research within this thesis was the first known to employ a phase feeding strategy where diets were modulated at different stages of finishing. This approach of partially replacing barley grain and canola meal with a high-fibre high-lipid byproduct pellets in the latter part of the finishing period has improved carcass yield grade without affecting ADG and G:F ratio.

Understanding the reasons for decreasing feed efficiency with advancing days on feed (DOF) and overcoming the challenges associated with feeding cheap alternative feed resources are both integral parts of making the beef industry successful. In my studies, using feed costs at the time, the cost of the HLP diet, replacing 60% of barley, was $25/tonne cheaper than a conventional barley based finishing diet.

7.2 Effects of DOF on G:F

It is widely accepted that G:F declines with advancing DOF and the NASEM (2016) indicates that the reduced G:F can be attributed to increased maintenance cost for BW and increased energy required for each unit of tissue deposited as fat deposition increases over protein deposition. However, it is clear that there is substantial individual variability in G:F among cattle and such variability suggests that individual aspects related to the capture of nutrients from the diet or utilization of absorbed nutrients may differ and further explain causes for reduced G:F with advancing DOF. The reasons for decreasing feed efficiency with advancing DOF were investigated at different points within the digestive and metabolic process including digestion,

indicators for absorption, and post absorptive nutrient utilization. Despite having increased OM digestibility and no significant changes with SCFA absorption across the reticulorumen (Joy et al., 2017; Chapter 4), G:F decreased with advancing DOF. However, an important outcome in my studies was the observation that insulin resistance developed in beef cattle with advancing DOF. The pancreatic exhaution from continous stimulation to produce excess insulin and its anabolic responses on target organs could result in reduced feed efficency. There could be multiple factors that lead to the development of insulin resistance, which need further research. Neverthless the understanding that cellular metabolism and endocrine sesnsitivites are altered with DOF was an important finding that could guide future research on developing startegies to counter the decreasing feed efficiency with advancing DOF.

7.3 Use of HLP and reduced G:F

An opportunity to use low-cost byproduct feeds were addressed with the introduction of a high-lipid high-fibre byproduct pellet (HLP). Similar HLP were used previously in other studies (Górka et al., 2013; Górka et al., 2015) and HLP were found to be an effective alternative to barley grain. The concept of this dietary approach relied on the replacement of starch in cereal grain as an energy source with lipid in byproducts from oilseed industries as an alternative concentrated source of energy. However, partially replacing barley grain with an HLP pellet further aggravated the problem of decreasing feed efficiency (Chapter 3; Joy et al., 2016). The causes for decreased feed efficiency associated with the HLP diet when compared to a barley based diet could be multifactorial and diffcult to delineate. The major nutritional components, lipids and non-forage fibre sources included in the HLP both have the ability to negatively influence total tract nutrient digestibility as well as digesta kinetics in ruminants as they may shift the site of fibre and starch digestion post-ruminally and thereby influence apparent total tract nutrient digestiblity. To identify the factors leading to decreased feed efficiency, it was important to address each factor separately.

The first approach was to alleviate the impact of feed efficiency assoicated with the HLP diet with a phase-feeding strategy. Under this approach, HLP feeding was postponed to the middle or last third of finishing phase. Past studies focusing on ruminal pH have indicated that repeated exposure to ruminal acidosis may increase the risk and severity of subsequent ruminal acidosis bouts (Dohme et al., 2008) and that bouts of ruminal acidosis can result in reduced feed efficiency (Castillo-Lopez et al., 2014). Moreover, the risk for digestive disorder related morbidity increases

during the later stages of the finishing period (Castillo-Lopez et al., 2014; Xu and Ding, 2011). Hence the approach of phase-feeding was aimed at limiting digestive associated morbidity linked to ruminal acidosis by partially replacing barley grain with HLP in the latter stages of finishing. This strategy was beneficial in terms of feed efficiency and animal performance with increased G:F ratio and ADG, when compared to a full HLP feeding regimen; however, that strategy was not fully beneficial from an economic stand point due reduced days of allocation of HLP diet. Profitability of feeding an HLP diet depends heavily on the prevailing market price of cereal grains, and HLP feeding was profitable in situations where the grain prizes were high and volatile. To increase the profitability of HLP feeding, it needed to be fed throughout the finishing period, without affecting feed efficiency. So it becomes imperative to address the issue of decreased feed efficiency within the HLP pellet.

As alluded above, increasing dietary lipid supply may have negative effects on ruminal fermentation by cellulolytic bacteria (Jenkins, 1993). The effects of a gradual increase in dietary lipid up to 5.9 % of dietary DM through the use of HLP were evaluated in finishing beef heifers (Chapter 6). Increasing the supply of lipid did not influence the ruminal or total tract digestiblity of any other nutrients. There was also no evidence of altered ruminal fermentation with increasing concentration of dietary lipid. The only difference observed was that total tract digestibility of lipid increased with increasing dietary inclusion. This was assumed due to the increased proportion of canola seed-based lipid flowing out into the intestine, thereby decreasing the relative proportion of bacterial lipid flow with increasing dietary lipid. Hence, based on this study, it was concluded that dietary lipid was not the source of decreased G:F associated with HLP feeding. However, the changes to the digesta kinetics (i.e. rumen retention time associated with a lipid supplemented diet) is still a possibility.

Most of the fibre incorporated into the HLP was from non-forage fibre sources such as oat hulls and the hulls associated with off-grade cereal grain. Due to the inherent nature of low digestibility with high lignin content of hulls (Thompson et al., 2002), an experiment was undertaken by Johnson et al. (2018) to improve oat hull digestibility through alkaline treatment with calcium oxide (CaO). In that study, the authors reported that CaO treatment improved the in situ digestibility of oat hulls; however, CaO treatment failed to increase the dietary NDF digestibility suggesting that factors other than potential degradability may contribute to the lower G:F observed with HLP relative to barley-grain based diets.

As discussed above, both forage and lipid supplementation can affect digesta kinetics and alter the rumen retention time (Rodrigue and Allen, 1956; Abouheif et al., 2012). Passage rate of fibre out of the rumen is a time-dependent process (Pond et al., 1988) and it has been shown that indigestible NDF (iNDF) has a faster rumen passage rate compared to potentially digestible NDF (Lund et al., 2007). The HLP formulation contained nearly 6% of oat hulls on DM basis with a high proportion of iNDF content, which might have added on to the rapid fibre outflow rate resulting in low rumen NDF digestibility. Mean rumen retention time of fibre particles depends on the intrinsic nature of the fibre type incorporated in the diet (Tamminga et al., 1989; Lund et al., 2007). Those fibre particles which disintegrate into large particles form a denser rumen mat entraping small particles and increasing their retention time compared to fibre, which disintegrates into small cuboidal particles resulting in a less dense rumen mat and shorter rumen retention of particulate matter (Mertens, 2002). Grinding and pelleting of byproduct components in the current study might have resulted in smaller particles subsequent to rapid disintegration in the rumen, accentuating the passage of fibre components out of the rumen (Abouhief et al., 2012). In Chapter 5, a moderate increase in the proportion of barley silage (6% vs. 12% dietary DM) in growing beef heifers was observed to improve ADG without affecting DMI or digestibility of DM, OM, NDF, CP, and ether extract when fed with diets containing HLP. It is suprising that increasing the proportion of forage did not result in increased DMI and reduced ADG considering this dietary substitution decreased the energy density of the diet. The explanation for a lack of a negative response with increasing dietary forage may be due to improved ruminal mat structure and as a consequence a longer retention time of HLP within the rumen. Thus, while the greater inclusion rate of barley silage would be expected to reduce dietary energy density and digestibility, the potential for increased ruminal retention and subsequently digestibility of HLP may have offset the outcome.

7.4 Opportunities and challenges with the use of HLP

The opportunities associated with HLP use have been highlighted within this thesis including reducing risk for ruminal acidosis and decreasing the need for producers to handle multiple ingredients should they choose to use byproduct ingredients. However, there are some additional benefits that were not specifically evaluated or discussed. Firstly, HLP may be a viable alterative high energy feed source for beef producers when the feed grain prices are volatile. The

cost of HLP are much less than cereal grains, especially after the recent increase in demand for biofuels (Gorka et al., 2013). From a food security standpoint, the byproducts used within HLP are non-edible for humans and if not utilized by livestock would have ended up in landfills. Converting these byproducts into energy rich livestock feeds also helps to conserve valuable natural resources and reduce the pressure on arable land resources for the production of animal feed.

At the same time, HLP poses some challenges in terms of utilization. The greatest threat is concern over contaminants such as ergot alkaloids and their derivatives, and mycotoxins that could be present and potentially concentrated in the byproducts. According to Canadian Food Inspection Agency's (CFIA) regulatory guidance on contaminants in feed, mycotoxins and their derivatives in feed could cause nephrotoxicity, hepatotoxicity, neurotoxicity, lung disease, reduced fertility, reduced animal performance and even death. The stipulated maximum level of aflatoxin in all individual feed ingredients is 20 ppb and that of ergot alkaloids is less that 2 ppm. If care is not taken to screen incoming ingredients to avoid inclusion of these contaminants, they could pose serious health issues to beef cattle.

Another issue to address is the unpredictability of nutrient composition of the byproducts. The chemical composition of byproduct ingredients varies between batches based on variety, year, climate, maturity and the processing undergone. Previous studies have been conducted to evaluate variability within a byproduct source and have identified large differences in digestibility (Thompson et al., 2002). Such information would suggest that nutritive analysis of a composite sample from each batch of the ingredients would be necessay to mainitain a supply of HLP pellet with consistent nutritive value. However, this is not easily accomplished during the production process given the quantities of ingredients utilized, the continuous flow and mixing between batches of the same ingredient, and that such differences would require real-time formulation changes. Another important challenge with the HLP pellet is related to pellet quality. Recent research has indicated that pellet binders may not be effective at increasing pellet durability or reducing the percentage of fines with high-byproduct pellets (Wood et al., 2019) and that pellet size may influence the utilization of byproduct pellets (Kelln et al., 2019). The previous points are further exacerbated as the HLP contain a relatively high lipid incorporation rate further challenging pellet quality (Behnke, 1994).

7.5 Conclusion

In conclusion, partially replacing barley grain with a HLP is an effective alternative to reduce the incidence of low rumen pH and may reduce feed cost. However, based on the results of the studies within this thesis and those conducted using similar formulations for HLP, it can be expected that the use of HLP will reduce G:F relative to barley grain. Phase- feeding HLP in the latter half of finishing could be adopted without negatively affecting, DMI, ADG, HCW or G:F; however, the reduced duration of feeding associated with phase-feeding decreases the positive economic benefit of HLP use. In terms of the reduction in G:F, data within this thesis suggest that low ruminal retention of HLP is the driving factor for the reduced G:F given that increasing dietary lipid below 6% of dietary DM did not alter ruminal nutrient digestibilities other than the lipid fraction nor did it alter microbial protein flow out of the rumen. Moreover, increasing the proportion of dietary fibre did not decrease digestibility, as would be expected, suggesting that the increased forage may have stimulated greater retention time for HLP and hence digestibility. It was also observed that insulin sensitivity decreased with advancing DOF in finishing cattle, irrespective of the diet. Decreased insulin sensitivity may be associated with reduced G:F and should be further evaluated in future studies.

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