

**DEVELOPMENT OF AN EFFICIENCY RANKING SYSTEM FOR BEEF  
COWS AND A COMPARISON OF THE DIGESTIVE PHYSIOLOGY  
BETWEEN EFFICIENT AND INEFFICIENT COWS**

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By

JUSTIN J. DELVER

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Dean of the College of Graduate and Postdoctoral Studies  
University of Saskatchewan  
116 Thorvaldson Building, 110 Science Place  
Saskatoon, Saskatchewan, S7N 5C9 Canada

## ABSTRACT

Beef cows ( $n = 100$ ) were used in a 2-yr selection system based on cow rump fat thickness at calving, calving date, and calf weaning weight (% dam BW). The 9 most (ME) and least efficient (LE) cows were used to compare feed intake and ruminal fermentation using four 26-d periods with decreasing dietary nutrient density. There were no phenotype  $\times$  diet interactions for variables of primary interest. Rump fat and calf weaning weight were greater and calving date was earlier for ME than LE ( $P \leq 0.032$ ). The ME cows were lighter ( $P < 0.001$ ) but had similar DMI ( $P = 0.93$ ) to LE cows, resulting in greater DMI (%BW;  $P < 0.001$ ). Ruminal contraction amplitude height and area ( $P \leq 0.015$ ), and ruminal digesta weight were greater for LE than ME cows ( $P = 0.043$ ). Ruminal aNDFom passage was greater for ME cows than LE cows ( $P = 0.047$ ) but the rate of aNDFom degradation did not differ ( $P = 0.69$ ). Total tract digestibility did not differ. Efficient cows had greater rump fat, weaned heavier calves, ate more relative to their BW, had smaller ruminal digesta mass, and greater ruminal passage of aNDFom without reducing digestibility.

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## TABLE OF CONTENTS

PERMISSION TO USE.....	i
ABSTRACT.....	ii
ACKNOWLEDGEMENTS.....	iii
TABLE OF CONTENTS.....	iv
LIST OF TABLES.....	vi
LIST OF FIGURES.....	viii
LIST OF ABBREVIATIONS.....	ix
CHAPTER 1: INTRODUCTION.....	1
CHAPTER 2: LITERATURE REVIEW.....	2
2.1 Measures of efficiency in beef cattle.....	2
2.1.1 Gain-to-Feed.....	2
2.1.2 Kleiber ratio.....	3
2.1.3 Residual feed intake.....	3
2.1.4 GOLD indicators.....	7
2.1.5 Phenotypic selection.....	9
2.2 Reproductive fitness.....	10
2.2.1 Physiology of beef cow reproduction.....	11
2.2.2 Cow physiology and its effects on reproduction fitness.....	12
2.3 Energy metabolism/balance.....	13
2.4 Regulation of dry matter intake.....	14
2.4.1 Physical rumen distention.....	15
2.4.2 Hepatic oxidation.....	16
2.5 Ruminal passage rate.....	17
2.5.1 Dry matter intake and ruminal digesta weight.....	18
2.5.2 Physiological state.....	20
2.5.3 Ruminal motility.....	21
2.6 Conclusion.....	22

CHAPTER 3: DEVELOPMENT OF AN EFFICIENCY RANKING SYSTEM FOR BEEF COWS AND EFFECTS ON FEED INTAKE, RUMINAL FERMENTATION AND NDF TURNOVER, AND APPARENT TOTAL TRACT DIGESTIBILITY .....	24
3.1 Introduction .....	24
3.2 Materials and Methods .....	25
3.2.1 Management of Cows under Extensive Feeding Conditions .....	25
3.2.2 Phenotypic Selection .....	26
3.2.3 Preparation and Management of the Selected Cows .....	26
3.2.4 Experimental Design .....	29
3.2.5 Data and Sample Collection .....	29
3.2.6 Ruminal Fermentation .....	31
3.2.7 Ruminal Motility .....	32
3.2.8 Ruminal NDF Turnover .....	33
3.2.9 Apparent Total Tract Digestibility .....	33
3.2.10 Statistical Analysis .....	34
3.3 Results .....	34
3.4 Discussion.....	49
3.4.1 Development of a Novel Efficiency Classification System for Beef Cattle .....	49
3.4.2 Lack of Interactions between the Efficiency Phenotype and Dietary Treatment.....	50
3.4.3 Differences in Digestive Physiology among LE and ME Cows .....	51
3.4.4 Effects of Dietary Composition.....	55
3.4.5 Conclusion.....	57
CHAPTER 4: GENERAL DISCUSSION .....	58
4.1 Importance of feed efficiency for cow-calf producers .....	58
4.2 Phenotypic selection of efficient cattle compared to other measures of efficiency .....	58
4.3 Practical applications and management required for the phenotypic selection of efficient cows .....	60
4.4 Using NIR estimated NDF digestibility as a secondary selection method.....	61
4.5 Future directions of this research.....	63
CHAPTER 5: CONCLUSION .....	65
LITERATURE CITED .....	66

## LIST OF TABLES

<b>Table 3.1</b> Rump fat and calving date for 86 cows over 2 consecutive years and the ranking score used.....	26
<b>Table 3.2</b> Calf weaning weight for the 86 cows evaluated over 2 consecutive years and ranking score for calf weaning weight.....	28
<b>Table 3.3</b> Ingredient and chemical composition of the high quality (HQ), medium high-quality (MHQ), medium quality (MQ), and low quality (LQ) diets fed to 18 mature beef cows in over 4 consecutive 28-d periods. ....	30
<b>Table 3.4</b> Pearson correlation coefficients and the respective <i>P</i> -value for calf weaning weight, rump fat thickness, and calving date from 86 cows measured over two years.....	36
<b>Table 3.5</b> Pearson correlation coefficients for year 1 and 2 weaning weight, rump fat thickness, calving date, and total scores in a herd of 86 cows measured over two consecutive years. ....	37
<b>Table 3.6</b> Rump fat measured at calving, calving interval, and calf weaning weight for cows phenotypically classified as least-efficient (LE; n = 9) and most-efficient (ME; n = 9) when measured over two years. ....	38
<b>Table 3.7</b> Start and ending BW, and rib and rump fat measurements of beef cows phenotypically classified as least-efficient (LE; n = 9) or most-efficient (ME; n = 9) and fed a high-quality (HQ), medium-high quality (MHQ), medium quality (MQ), or low quality (LQ) diet during 4 consecutive 28-d periods. ....	40
<b>Table 3.8</b> Sorting behaviour and DM and nutrient intake for beef cows phenotypically classified as least-efficient (LE; n = 9) or most-efficient (ME; n = 9) and fed a high-quality (HQ), medium-high quality (MHQ), medium quality (MQ), or low quality (LQ) diet during 4 consecutive 28-d periods. ....	41
<b>Table 3.9</b> Ruminal pH, short-chain fatty acid (SCFA) concentrations, and ammonia concentration from beef cows phenotypically classified as least-efficient (LE; n = 9) or	

most-efficient (ME; n = 9) and fed a high-quality (HQ), medium-high quality (MHQ), medium quality (MQ), or low quality (LQ) diet during 4 consecutive 28-d periods. .... 43

**Table 3.10** Ruminal motility, digesta pool sizes, and NDF turnover for beef cows phenotypically classified as least-efficient (LE; n = 9) or most-efficient (ME; n = 9) and fed a high-quality (HQ), medium-high quality (MHQ), medium quality (MQ), or low quality (LQ) diet during 4 consecutive 28-d periods. .... 45

**Table 3.10 (Continued)** Ruminal motility, digesta pool sizes, and NDF turnover for beef cows phenotypically classified as least-efficient (LE; n = 9) or most-efficient (ME; n = 9) and fed a high-quality (HQ), medium-high quality (MHQ), medium quality (MQ), or low quality (LQ) diet during 4 consecutive 28-d periods..... 46

**Table 3.11** Fecal output, apparent total tract digestibility, urine output, and nitrogen balance for beef cows phenotypically classified as least-efficient (LE; n = 9) or most-efficient (ME; n = 9) and fed a high-quality (HQ), medium-high quality (MHQ), medium quality (MQ), or low quality (LQ) diet during 4 consecutive 28-d periods. .... 48



## LIST OF FIGURES

<b>Figure 4.1</b> Histogram of the NDF digestibility of 49 beef cows in a pen feeding experiment on a high-forage diet estimated using NIR through previously created calibrations (Jancewicz et al. 2017).....	62
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## LIST OF ABBREVIATIONS

ADF = Acid detergent fiber

aNDFom = NDF assay with amylase and sodium sulfite, corrected for ash content

BCS = Body condition score

BW = Body weight

CP = Crude protein

DM = Dry matter

DMI = Dry matter intake

EEI = Energy efficiency index

G:F = Gain to feed

HD = Greatest NDF digestibility

HOT = Hepatic oxidation theory

HQ = High quality

$K_d$  = Ruminal degradation rate of aNDFom

$K_p$  = Ruminal passage rate of aNDFom

KR = Kleiber ratio

LD = Least NDF digestibility

LE = Least efficient

LQ = Low quality

ME = Most efficient

MHQ = Medium-high quality

MQ = Medium quality

NDF = Neutral detergent fiber

$NE_g$  = Net energy of gain

$NE_m$  = Net energy of maintenance

NIR = Near infrared spectroscopy

OM = Organic matter

PD = Potentially digestible

RFI = Residual feed intake

SCFA = Short chain fatty acid

uNDF = indigestible neutral detergent fiber

## CHAPTER 1: INTRODUCTION

Beef cattle producers are under pressure to improve the economic, social, and environmental sustainability of beef cattle production. Improving the feed efficiency of cattle has been a focus of the industry for decades and continues to offer an opportunity to improve sustainability. Feed efficiency of growing cattle has been well researched and vast improvements have been made; however, less progress has been made on improving feed efficiency for the breeding herd. This is partly due to the difficulty in measuring inputs and outputs of a beef cow over her lifetime, especially when cows are extensively managed for much of their life (Arthur and Herd 2008). The lack of progress presents an opportunity to further improve the efficiency and productivity of the entire beef production chain, as the cow herd consumes about 72% of the metabolizable energy that is consumed from conception to slaughter of finished cattle (Jenkins and Ferrell 2002). Improving the efficiency of the breeding herd requires a review of efficiency measures that are currently in use and improvements that can be made in relation to the specific goals of the cow-calf sector.

Unlike in growing cattle, where the goal is to optimize the conversion of feed into growth, the primary goal in breeding herds is to produce a weaned calf requiring a focus on reproductive health and fertility (Cushman et al. 2013). Reproductive fitness is correlated to cow body composition and energy balance suggesting that maintenance energy and metabolism may be important factors in feed efficiency and the reproductive health of the cow (Osoro and Wright 1992; Cantalapiedra-Hijar et al. 2018). As in growing cattle, feed efficiency cannot be fully examined without analyzing feed intake and what drives intake in cattle. The beef cow is often expected to survive on low-quality forages for part of the year, and different measures of efficiency may find conflicting results on the effect of intake on the efficiency of the cow (Arthur and Herd 2008; Reis et al. 2021).

The purpose of this review was to compare current measures of efficiency, mostly applicable to growing cattle, and their use in the cow-calf sector. Identifying limitations of these measures of efficiency may allow for a novel method of evaluating efficiency in beef cows, especially in respect to the reproductive fitness, DMI, and performance attributes that are unique to the cow-calf sector.

## CHAPTER 2: LITERATURE REVIEW

### 2.1 Measures of efficiency in beef cattle

Improving feed efficiency has been a focus of the animal production industries to increase productivity, profitability, and mitigate environmental concerns for many decades (Byerly 1967). Measuring the feed efficiency of an animal differs among different stages of an animal's life. In growing cattle, the feed conversion ratio, or the inverse, the gain-to-feed (G:F) ratio has been used extensively. The Kleiber ratio (KR) is also a measure of efficiency used in growing cattle that utilizes average daily gain and metabolic body weight (Kleiber 1961). More recently, residual feed intake (RFI) has become another common measure of feed efficiency with purported benefits that its ranking is independent of animal body weight (BW) and growth making it a useful measurement for cattle that are not growing, like mature breeding cows and bulls (Arthur and Herd 2008). Although RFI does allow for the ranking of feed efficiency in a mature breeding cow, because of the complex range of feeding, environmental, management, and physiological conditions a cow is subjected to over a year, a one-time measurement of feed efficiency may not be representative of lifetime efficiency. By identifying phenotypic traits in cows that correlate to lifetime productivity and efficiency, a new measure of feed efficiency that is specific to cows in a cow-calf operation may be developed.

#### 2.1.1 Gain-to-Feed

The gain-to-feed ratio is one of the most common measures of efficiency because it directly relates outputs to inputs. This is especially useful in growing animals and when comparing animals at similar stages of growth and BW that are being fed diets of similar nutrient composition. Methods to overcome limitations for cattle not fed the same diet include the use of corn equivalent feed units as a standard for feed intake (Byerly 1967), or the KR which doesn't require feed intake and accounts for BW (Kleiber 1961). One of the limitations of G:F and the KR is that they are only applicable to growing cattle. As such, selecting efficient dams and sires for a cow herd requires G:F to be calculated while they are still in a growth phase and it is not clear if most efficient growth translates to more efficient reproductive and maintenance energy use. Bishop et al. (1991) divergently selected bulls that had high or low G:F ratios and bred cows using these bulls. This selection and breeding program was replicated four times using different sires to follow the offspring and determine the genetic and phenotypic correlation among other

traits. The genetic correlations were estimated using heritability values from literature and the experimentally measured traits. The genetic correlations showed that genes that impact feed efficiency may also impact subcutaneous fat deposition, rate of gain, BW, and feed intake (Bishop et al. 1991). The phenotypic correlations were similar to the genetic correlations, where cattle that had greater G:F were fatter, had greater average daily gain, and had greater carcass quality grades, but lesser yield grades (Bishop et al. 1991). Although G:F is a practical tool for evaluating feed efficiency in growing cattle, it is not applicable to mature cows because they are not in a growing phase.

### **2.1.2 Kleiber ratio**

Unlike G:F which measures the efficiency of feed use, the KR measures growth efficiency which is correlated to feed conversion and efficiency. Kleiber (1961) used the ratio of average daily gain to metabolic body weight, calculated as  $(\text{body weight})^{0.75}$ , to determine how efficiently an animal is growing relative to its basal maintenance requirements. The KR can be used as a measure of feed efficiency under the assumption that metabolic body weight is related to the basal maintenance requirements, and hence, animals that have a greater KR are more efficiently utilizing feed for growth and maintenance (Kleiber 1961). Crowley et al. (2011) used data from 94,936 crossbred beef cows to determine genetic correlations between the KR that was measured while the cows were in a growth phase, and weaning weights, BW, fertility, and calving performance. The KR was genetically correlated with the weaning weight of calves as well as the age at first calving (Crowley et al. 2011). Greater KR resulted in heavier weaning weights of calves, but delayed the age at first calving, which the authors attributed to a later onset of puberty (Crowley et al. 2011). The KR also lacks applicability for use in the cow herd as it relies on average daily gain, and cows are no longer in a significant growth phase.

### **2.1.3 Residual feed intake**

Residual feed intake is another measure of feed efficiency that was first suggested by Koch et al. (1963). The approach used makes RFI rankings independent of both weight and growth. Residual feed intake is defined as the difference between an animal's expected feed intake and their actual intake at a given level of performance (Koch et al. 1963). The expected intake can be calculated as either the average intake of the group of animals being evaluated or

based on a formula for animals at their current BW and average daily gain (Arthur and Herd 2008). Using these calculations, more efficient cattle have a lower or negative RFI value because they are eating less than is predicted for the level of performance. Recently, much of the RFI research that has been conducted focuses on the physiological basis behind the differences in efficiency, with feed intake, digestion, body composition, metabolism, and thermoregulation being the main focuses (Arthur and Herd 2008; Herd and Arthur 2009). Residual feed intake has also been suggested to be useful in measuring the efficiency of mature beef cows because it is independent of growth (Fitzsimons et al. 2014).

Feed intake is inherently tied to RFI and variations in feed intake and feeding behaviour play a role in the differences in RFI (Herd and Arthur 2009). Feed intake may affect differences in RFI as animals that are eating more will have greater maintenance energy requirements, through increased digestive organ weight, increased energy expenditure in the tissue, and greater energy expenditure from eating activities (Herd and Arthur 2009; Robinson and Oddy 2004). Robinson and Oddy (2004) calculated the RFI on 1481 growing cattle to compare genetic correlations on feeding behaviour, feed intake, and RFI. The number of daily eating sessions and time spent eating were both positively genetically correlated to RFI, but were not genetically correlated with feed intake, suggesting that some of the genes that affect feeding behaviour may also affect RFI (Robinson and Oddy 2004). Although feed intake is important to some of the variations in RFI ranking, the digestion of the feed can also be used to explain some of the variation (Herd and Arthur 2009).

Feed intake and digestibility are often related, as feed intake increases above maintenance requirements, ruminal and total tract digestibility decreases (Robinson et al. 1985). Total tract digestibility of nutrients in cattle of varying RFI rankings has shown inconsistent results for whether RFI is negatively correlated to digestibility or not correlated at all. de La Torre et al. (2019), Johnson et al. (2019), and McDonnell et al. (2016) all found negative correlations between RFI and at least organic matter digestibility. Low-RFI heifers in a study by de La Torre et al. (2019) had greater dry matter and organic matter digestibility, but NDF digestibility did not differ. The cows were fed at 95% ad libitum intake during the digestibility portion of the study which may have inflated the digestibility results. However, it is also interesting to note that the cows that were divergently selected for RFI when they were heifers, and then had digestibility measurements taken 22 months after, no longer showed any differences in intake (de La Torre et

al. 2019). This suggests that RFI ranking may not be consistent over time, cow age, or possibly diet. During the initial RFI measurement period, the heifers feed intake was measured using automatic gates, which can be accessed by one animal at a time and measures weight disappearance. Feed sorting and cow hierarchy could have affected the actual nutrient intake of each animal during this period, and cows were housed individually during the metabolism portion of the study eliminating this effect. Like de La Torre et al. (2019), Johnson et al. (2019) also found low RFI cows had greater dry matter and organic matter digestibility, but they also had greater NDF and ADF digestibility. The digestibility measurements were at least partially independent of DMI, suggesting that the differences in digestibility are a result of some other mechanisms (Johnson et al. 2019). The adjustment for dry matter digestibility improved the RFI model by accounting for 6 to 8% of the variation (Johnson et al. 2019). Not all data supports the theory that total tract digestibility contributes to the variation in RFI. Cruz et al. (2010) and Lawrence et al. (2011) found no difference in dry matter digestibility among steers and heifers, respectively, that differed in RFI ranking.

Fat and muscle differ in the amount of energy required for deposition and maintenance, hence differences in the composition of gain and body mass may account for some of the variation in RFI. Studies that have compared body fat and RFI rankings in growing heifers (Kelly et al. 2010) and steers (Nkrumah et al. 2004) generally show that high-RFI animals have more body fat and low-RFI animals are leaner. Fat requires more energy to deposit which may help support that low-RFI animals are more energetically efficient as they deposit more muscle and less fat. Concerns have been raised that the lower body fat may affect carcass quality grade in finished cattle and fertility in mature breeding cows (Kelly et al. 2010; Lawrence et al. 2011). However, Nkrumah et al. (2004) found no difference in marbling score or carcass weight of high-, medium-, or low-RFI steers, although the low-RFI steers had greater lean meat yield and less grade fat than high-RFI steers. Lawrence et al. (2011) compared body condition score (BCS), fat thickness, and skeletal measurements in gestating beef heifers that differed in RFI. In contrast to other studies, there was no difference in subcutaneous fat thickness between high- and low-RFI groups, although initial muscle depth was greater in the low-RFI group (Lawrence et al. 2011). There was also no difference in BCS or skeletal measurements between RFI groups. Cruz et al. (2010) also found no difference in hot carcass weight, quality grade, backfat, or carcass fat between high- and low-RFI steers. Arthur et al. (2005) divergently selected high- and low-RFI

cows over 3 breeding seasons and found that low-RFI cows had less subcutaneous rib fat than high-RFI cows. Basarab et al. (2011a) found no difference in backfat thickness at the start of a postweaning measurement of RFI in heifers but found low RFI heifers had less backfat at the end. Basarab et al. (2011a) also showed that the low RFI heifers had lower pregnancy and calving rates, which suggests that RFI may influence fertility. Adjusting for the backfat thickness of the heifers partially eliminated the difference in pregnancy and calving rates, which led the authors to suggest including a backfat correction in RFI calculations to eliminate the negative effect on fertility (Basarab et al. 2011a). Contradictory, Basarab et al. (2011b) found that low-RFI cows had greater subcutaneous backfat thickness. Basarab et al. (2011b) did not directly measure the RFI of the cows; however, instead measuring the RFI of the progeny of the cows and using the progeny RFI ranking to classify the cows. This likely affected the results as it was examining the relationship between progeny RFI and dam productivity (Basarab et al. 2011b). Body composition, and especially body fat has been shown to be positively correlated in growing heifers and steers, which may be a cause of concern regarding lower fertility in low-RFI cows, and a backfat correction is a recommended practice to eliminate this effect.

Variation in RFI could also be attributed to differences in maintenance energy requirements, which could be a result of differences in metabolism and heat production (Cantalapiedra-Hijar et al. 2018). In a study by Nkrumah et al. (2006), RFI was negatively correlated to metabolizable and retained energy and positively correlated to heat production. Limited studies however on heat production using oxygen consumption and its relationship to RFI suggest that more studies are needed to understand the biological mechanisms behind differences in maintenance energy requirements and the partial efficiency of metabolizable energy use for growth, and whether this is related to feed efficiency in beef cows (Nkrumah et al. 2006; Cantalapiedra-Hijar et al. 2018).

Although RFI is more applicable to mature breeding cows than G:F and the KR, practical challenges associated with the collections and measurement of RFI have limited the implementation of it as a popular measurement in cow-calf operations (Arthur and Herd 2008). These challenges include the high cost and difficulty of measuring individual feed intake, especially of grazing cattle. Durunna et al. (2011, 2012) also showed that both growing steers and heifers changed RFI ranking in two consecutive feeding periods on the same diet. The reranking of cattle on consecutive feeding periods is especially important in the context of



mature beef cows, which, unlike growing cattle that may be fed the same or similar diet in the same environment over most of its growth period, are expected to thrive under a variety of feed, management, environmental, and physiological conditions throughout the year. Despite these concerns, RFI has remained one of the few tools available to identify efficient cows that are no longer in a growing phase.

#### **2.1.4 GOLD indicators**

Record keeping and evaluating herd performance is important for a producer to determine yearly trends, profitability, and production in relation to provincial or national averages, or within their own herd from year-to-year. The GOLD acronym stands for the growth of calves; number of open cows; length of the calving season; and calf death loss and are a set of performance indicators that can be used to evaluate herd performance (Kaliel et al. 2008). These data are easy to measure, but relies on the accurate recording, as well as analysis of the data at the end of the year. The GOLD indicators also set a benchmark of what should be targeted for each variable for producers and are used to evaluate herd-based performance. It is reasonable to assume that some minor adaptations could be made to evaluate the performance of individuals within a herd.

The growth of calves can be calculated as either weaning weight as a percent of dam BW, or weight of calf weaned per weight of cow exposed, and the benchmarks of 43% or 0.4 kg of weaned weight per kg of cow exposed, respectively have been proposed (Kaliel et al. 2008). The weight of weaned calves is an important economic trait for producers because sale of weaned calves is the main revenue source of cow-calf operation (Boyda 2022). The growth of calves up to weaning is influenced by both dam and sire genetics, environment, and nutrition of the cow and calf. There are also differences between the weaning weight of bull, steers, and heifer calves, with bulls weighing more (Rollins and Guilbert 1954). The lactating ability of the cows is also a major contributor to the growth rate of the calf and weaning weight (Rollins and Guilbert 1954). Utilizing growth rate of calves, a producer can identify poor producing cows through the individual weaning weight of a calf as a percent of cow BW or determine herd level production by looking at weight of weaned calves per BW of exposed cow (Kaliel et al. 2008).

The number of open cows and the length of the breeding season are both measures of fertility in the herd and beyond growth, the proportion of cows that have a calf is the most

impactful variable affecting potential revenue. The number of open cows relates to the herd fertility, where a more fertile herd will have a fewer number of open cows, and the length of the breeding season measures the fertility of the bred cows, where a shorter breeding season implies greater fertility (Kaliel et al. 2008). Both measures also rely on the length of the breeding season, but the benchmark for open cows is <4% of the herd exposed, and the calving season should be 63 days or shorter (Kaliel et al. 2008). Minimizing open cows can be accomplished through proper nutritional management, bull selection, and disease prevention. Kaliel et al. (2008) also indicated that BCS as an important cow trait to be measured and recorded. Cow BCS and fat cover have a large effect on early rebreeding (Osoro and Wright 1992). Cows that were in greater body condition had a shorter calving interval (Osoro and Wright 1992). Earlier calving cows have many benefits as they are more likely to stay in their early calving group in subsequent years, will wean older and heavier calves at weaning, will have greater lifetime productivity, and have increased longevity (Osoro and Wright 1992; Hess et al. 2005; Cushman et al. 2013; D'Occhio et al. 2019).

The final component of the GOLD indicator is calf death loss: mostly a measure of herd health (Kaliel et al. 2008). The benchmark for calf death loss is 4% between birth and weaning. Death loss of calves can have significant costs as the cow no longer has a revenue stream for the year unless she is culled. Some death loss is unavoidable; however, certain management practices can help minimize death loss. The heritability of calf survivability to weaning is negligible with heritability estimates of  $-0.01 \pm 0.13$  (Dearborn et al. 1973). Thus, management strategies are most important to ensure calf survivability. To reduce calf losses, producers should focus on reducing dystocia via selection of sires that have lower birth weights (Larson and Tyler 2005). Concentrating most cows into the beginning of the calving season can also help prevent disease and calf death, as calves born later in the season are exposed to more pathogens from calves that were born earlier (Larson and Tyler 2005).

The GOLD indicators are an important tool for a producer to measure their production against benchmarks and to improve their own herd performance over time. The growth of calves, number of open cows, length of the calving season, and calf death loss are correlated and improving one of them is likely to have a positive effect on the others. By modifying the GOLD indicators to evaluate individual cow performance, such as comparing calf weaning weight as a

percent of dam BW, individual cows that are more productive can be selected for, or less productive cows can be culled.

### **2.1.5 Phenotypic selection**

Determining efficient beef cows is difficult, especially when it comes to measuring individual feed intake. By identifying phenotypic traits that correlate to more efficient beef cows without having to measure feed intake, a more applicable method of selecting efficient mature beef cows may be possible. The phenotypic traits that may be likely candidates for use can be identified through correlation with previous efficiency measures, like RFI, or by identifying the goals of a mature beef cow and what phenotypic traits are most likely to correspond to those goals. Using correlations with RFI could be difficult due to the limited number of studies using mature beef cows, as well as the reranking that can occur with RFI, especially of concern in mature breeding cows (Durunna et al. 2011, 2012). Some potential traits that could be investigated are BCS or fat deposition, calf weaning weights, calving date or interval, cow BW, and milk yield (Bitencourt et al. 2020; Terry et al. 2021; Reis et al. 2021). Another concern with RFI when used in cow-calf operations, is that cows are expected to perform on a variety of feeding conditions, including low-quality forages that are likely fed through the winter, and it is possible that cows that have greater intake and or digestibility may perform better.

Rather than directly measuring feed intake, utilizing a model to estimate intake could also resolve the challenge of costliness when measuring RFI. Reis et al. (2021) used a measure of efficiency in beef cows called the energy efficiency index (EEI), which is the ratio of metabolizable energy required for maintenance by the cow to calf weaning weight. The metabolizable energy required for maintenance was calculated using the cattle value discovery system for beef cow model which uses cow BW adjusted for conceptus weight and physiological stage in its calculations (Reis et al. 2021). More efficient cows have a lower EEI because they require less energy/unit of weaned calf weight. This method was negatively correlated to calving interval, peak milk yield, calf weaning weight, and calf weaning weight as a ratio of cow BW; and was positively correlated with cow BW and BCS during lactation (Reis et al. 2021). Although there was a positive correlation between EEI and BCS, low EEI cows did not differ from high EEI cows for BCS and they had more internal fat suggesting that fat deposits may alter estimation of maintenance requirements. Similarly, calving interval did not differ between

the low and high EEI cows, although numerically the low EEI cows had a longer calving interval. In a study by Bitencourt et al. (2020), they found that cows that calved earlier in the calving season had greater pregnancy rates and heavier calves at weaning than cows that calved later, although the later calving cows did produce more milk. This suggests that cows that calve earlier in the breeding season are more reproductively fit than those that calve later and produce heavier calves at weaning. The latter results were similar to Reis et al. (2021) who reported a negative correlation between calving interval and the ratio of calf weaning weight to cow BW. Weaning weights were greater for the more efficient cows, both on a kg basis and as a ratio of cow BW; however, they also had greater predicted peak milk yield, contrary to Bitencourt et al. (2020) which could explain the greater weaning weights (Reis et al. 2021). Interestingly, cow DMI did not differ between the low and high EEI cows in both late lactation and late gestation, which differs greatly from RFI, especially considering the low EEI cows were also lighter so they would have greater intake as a proportion of their BW (Reis et al. 2021). The similarity in DMI could be part of the reason that the low EEI cows were able to wean heavier calves with greater peak milk yield. In addition, maintenance requirements would be expected to be lower for low EEI cows because they were lighter and may be able to divert more energy towards their calf. This suggests that phenotypic traits that relate to cow efficiency likely focus on reproductive fitness, greater weaning weights, and lower cow maintenance requirements and may be more important than traits that focus on feed intake as a driver of maintenance.

## **2.2 Reproductive fitness**

The goal in a cow-calf herd is for cows to consistently produce weaned calves, and hence, their reproductive fitness is one of the most important traits to be a productive cow. Reproductive fitness is also related to cow longevity, as cows that can consistently become pregnant are likely to remain in the herd. Greater longevity results in more calves weaned/cow and likely a greater total for the weight of the calves weaned diluting the production costs during the first 2 years of her life. Reproductive fitness is generally not a focus of most measures of efficiency as once a cow is not successfully bred, she is culled, and fertility is poorly heritable (Cammack et al. 2009). Most of the work that has focused on reproductive fitness centers around heterosis and hybrid vigor (Terry et al. 2021). Despite this, reproductive fitness should remain a

goal of efficiency measurements for breeding cows as it drives lifetime productivity and profitability (Cushman et al. 2013).

### **2.2.1 Physiology of beef cow reproduction**

The reproductive cycle of a cow has a few major events beginning with the onset of puberty prior to breeding, estrus and ovulation, fertilization, embryonic and fetal development, parturition, and successful return to estrus prior to the following breeding season. Each of these events is important to the productivity and longevity of a cow in the herd. The sire also plays a vital role in successful reproduction, but for the purposes of this review only the female contribution to reproduction will be examined.

The onset of puberty in heifers should ideally begin 1 to 3 months prior to the start of breeding, or about 12 to 14 months of age for a 24-month calving date (Byerley et al. 1987). The onset of puberty in heifers is controlled through a cascade of hormones. Prior to puberty the hypothalamus has a high sensitivity to estradiol, which results in negative feedback on luteinizing hormone (Pohler et al. 2020). As the heifer approaches puberty there is a decrease in the sensitivity to estradiol negative feedback through a reduction in estradiol receptors, which increases the pulse frequency of luteinizing hormone and encourages follicular development (Pohler et al. 2020). There is also an increase in progesterone prior to a heifers first ovulation which helps establish normal estrous cycles (Pohler et al. 2020). The plane of nutrition of cows is important in the regulation of the onset of puberty, as a low plane of nutrition delays, and a high plane of nutrition advances the onset of puberty (Pohler et al. 2020). Puberty is an important event in establishing the lifetime productivity of a cow. Cushman et al. (2013) compared the lifetime productivity of heifers that either calved in the first 21 days of the calving period, or those that calved later. Cushman et al. (2013) found that heifers that calved earlier in their first year had greater lifetime kg of calves weaned and stayed in the herd longer than those that calved later.

Once a cow has reached puberty, she begins her estrous cycle which lasts about 21 days and is regulated through hormones. The estrous cycle consists of the follicular stage, which leads into the onset of estrus; the estrus stage, which initiates estrous behaviour and ends with the release of the oocyte; and the luteal phase, which begins with ovulation and the formation of the corpus luteum (Pohler et al. 2020). The estrous cycle is vital for the release of the egg,

preparation for fertilization, and exhibition of estrus behaviours to communicate readiness to breed. The return to estrus of a post-partum cow is similar to that of a pre-pubertal heifer, where immediately after parturition the hypothalamus is highly sensitive to circulating estradiol which inhibits luteinizing hormone release, and over time the luteinizing hormone pulse frequency increases until the first ovulation is reached (Pohler et al. 2020). After fertilization of the oocyte, the zygote goes through mitotic division to form a blastocyst which travels and attaches to the uterine epithelium, chemically signals to the dam to prevent return to estrus and undergoes placentation (Pohler et al. 2020).

### **2.2.2 Cow physiology and its effects on reproduction fitness**

One of the most important goals of a cow post-partum is to return to estrus so she can be rebred, and in heifers the earlier onset of pregnancy can increase her lifetime return of weaned calves (Hess et al. 2005; Cushman et al. 2013). Cows that fail to return to estrus in time calve later the following year or may be culled due to reproductive failure. As such, improving a cow's ability to return to estrus can have a significant impact on productivity. A successful return to estrus can be measured either by examining calving date, where an earlier calving date shows a quicker return to estrus, or through calving interval, where a shorter calving interval signifies a quicker return to estrus (MacGregor and Casey 1999). MacGregor and Casey (1999) compared calving date and calving interval to determine which was a better indicator for reproductive performance. They found that calving interval had a negative relationship with previous calving date leading to bias unless calving interval was corrected for the previous calving date. In contrast, calving date did not require a correction (MacGregor and Casey 1999). The importance of calving date is especially prominent in heifers as they approach their first calving event. Heifers that calved in the first 21 days of the calving season tended to calve early in the subsequent years (Cushman et al. 2013). The earlier calving heifers also had heavier calves at weaning in their first year and greater longevity. Heavier calves along with greater longevity resulted in heifers that calved in the first 21 days of the calving season producing a lifetime weaned weight of calves that equated to an extra calf in their lifetime relative to those calving 22 days or later (Cushman et al. 2013). This demonstrates the importance of reproductive fitness and the benefit of earlier calving cows.

Adequate body condition of a cow and increasing plane of nutrition helps cows to recover from parturition and return to estrus (D'Occhio et al. 2019). The BCS of cows at calving is especially important to the reproductive fitness, and ability to return to estrus (Osoro and Wright 1992; D'Occhio et al. 2019). Cows that calved in a BCS of  $\geq 3$  had a shorter calving interval than cows than cows in a BCS of  $\leq 2.5$  on a 5-point scale (Osoro and Wright 1992). Morrison et al. (1999) managed 3 groups of cattle to a BCS of  $\leq 4$ , 5 to 6, and  $\geq 7$ , on a 9-point scale until the start of the last trimester of pregnancy where the 3 groups were then fed to calve at the same BCS of 5.1. Post-partum the cows were managed as a single group. There were no differences among the 3 groups for pregnancy rate, days to conception, calf birth weight, or 205-d adjusted calf weaning weight (Morrison et al. 1999). It's likely that part of the reason BCS at calving is so important to reproductive performance is due to leptin (D'Occhio et al. 2019). Leptin is a hormone that is released from adipose tissue, that among other effects, helps control the onset of puberty in heifers through receptors in the hypothalamus that promotes GnRH and luteinizing hormone secretion (D'Occhio et al. 2019). Body condition score and adipose tissue influence reproductive fitness and the ability to return to estrus in both heifers and multiparous cows.

### **2.3 Energy metabolism/balance**

The efficiency of metabolizable energy use varies depending on the physiological function the energy is being used for due to a variety of factors (Tedeschi et al. 2010). This led to the development of the partial efficiency of energy use for maintenance ( $NE_m$ ) and growth ( $NE_g$ ). The  $NE_m$  was calculated as the slope of the regression of negative recovered energy on metabolizable energy intake, and  $NE_g$  is the slope of the positive regression (Tedeschi et al. 2010). The  $NE_g$  can be altered by changes in the level of intake, nutrient intake, and the physiological function that the energy is being utilized for, such as protein versus fat deposition (Tedeschi et al. 2010).

Body composition and composition of gain plays an important role in determining the maintenance energy requirements of cattle. For cattle fed at maintenance requirements, protein turnover accounts for a significant portion of total body energy expenditure with estimates of about 30% (Carvalho et al. 2019). The efficiency of metabolizable energy use for deposition of protein and fat have varied from 12 to 22% and 56 to 122%, respectively (Tedeschi et al. 2010). Despite the wide range, the consensus is that the deposition of fat is more energetically efficient

than storing energy as protein (Tedeschi et al. 2010). The lower efficiency of protein deposition likely relates to protein turnover, it is also widely variable depending on the physiological stage, feed level and quality, and amino acid profile which can also affect protein turnover (Tedeschi et al. 2010).

Variation in energy metabolism has been suggested as a potential source of the differences between more and less efficient animals, especially for RFI and the KR (Kleiber 1961; Cantalapiedra-Hijar et al. 2018). Metabolism by the portal drained viscera and liver, along with protein turnover of skeletal muscle, account for a significant portion of the energy use in ruminants, and hence likely represents an important factor in differences in animal efficiency (Huntington 1989; Carvalho et al. 2019). This is especially apparent when the oxygen expenditure (40 to 50% of whole body) is compared to the mass (7 to 13% of whole body) of the portal drained viscera, demonstrating their disproportionately high metabolic rate (Huntington 1989). The disproportionate metabolic rate suggests that small changes in energy metabolism or the efficiency of energy metabolism in these tissues may have significant changes in the overall efficiency of the animal. Portal drained viscera refers to the gastrointestinal tract, spleen, pancreas, and gut associated fat. The metabolism of the portal drained viscera as well as the liver responds directly to changes in levels of feed intake (Huntington 1989). When metabolizable energy intake increases in cattle, there is a positive effect on blood flow to the portal drained viscera, supporting the relationship between DMI and portal drained viscera metabolism. The increase in blood flow helps to facilitate transportation of digested nutrients from the gastrointestinal tract into the blood, through the liver, and the rest of the body (Huntington 1989).

## **2.4 Regulation of dry matter intake**

The regulation of feed intake in ruminants is a complex interaction of many variables involving neural and hormonal feedback loops. Accurate estimation of dry matter intake (DMI) is important to ensure diets meet the nutritional requirements of cattle in various physiological states, environmental conditions, and diet composition (NASEM 2016). Feed intake in cattle is likely the single most important factor in controlling their production, and accounts for twice as much variation in energy availability as digestibility does (Mertens 1994). The control of feed intake in cattle is thought to be a combination of physical rumen distention, which is more important in low-quality feeds with slower passage rate, and metabolic feedback, which is more



important in energy dense feeds where rumen fill is not the limiting factor (Fisher 2002). It is also important to note that there are distinct differences between short-term and long-term control of feed intake (Mertens 1994). Dry matter intake is regulated by a complex interaction of many factors, including both physical ruminal fill and metabolic feedback (Forbes 1996), this review will focus on one theory at a time for simplicity.

#### **2.4.1 Physical rumen distention**

Physical distention, especially of the reticulo-rumen, is widely accepted as an important regulator of DMI, especially on low digestibility, high fill diets (Allen 1996; Roche et al. 2008). The physical distention theory works on the premise that as ruminal fill increases, stretch receptors in the rumen and reticulum wall are stimulated and send signals through the vagus nerve to the hypothalamus signaling satiety (Mertens 1994). Some factors that affect ruminal distention are passage rate out of the rumen and ruminal retention time, ruminal digestibility, and feed particle size. Reducing the particle size of forages that were fed to sheep or cattle increased their voluntary DMI (Osborn et al. 1976). This response was shown with forages that were either ground or pelleted and the magnitude of response was greater in mature than immature forages (Osborn et al. 1976). The greater increase in voluntary intake when low-quality forages are ground than high-quality forages is consistent with the physical distention theory as voluntary intake is limited more by physical distention in low-quality forages (Allen 1996).

The neutral detergent fiber (NDF) content of feed has been identified as a chemical constituent that helps to predict DMI because of its role in ruminal fill (Mertens 1987). Mertens (1987) showed that dairy cows consistently ate 1.1 to 1.3% of their BW in dietary NDF, suggesting that  $1.2 \pm 0.1\%$  of BW could be near maximal NDF intake and that DMI could be estimated from NDF concentration in the diet, assuming physical fill is limiting. Dado and Allen (1995) added inert fill in the form of water filled containers to cows fed either a 25% or 35% NDF diet. They estimated that DMI was limited by ruminal fill in diets that were  $\geq 28.5\%$  NDF, and at concentrations below that ruminal fill was not the limiting factor controlling DMI (Dado and Allen 1995). However, Dado and Allen (1995) were careful to note that this limit may only apply to cows that are similar in physiological state and diet composition to those in the study, as differences in rumen volume or NDF digestibility could affect DMI. Increasing the rumen fill through the addition of inert fill has shown inconsistent results, with decreased voluntary DMI in

some studies but no effect in other studies (Dado and Allen 1995; Allen 1996). One explanation for the inconsistency is that the rumen has reserve capacity, because the physical ruminal fill and ruminal passage rate were not at capacity prior to the inert fill addition (Dado and Allen 1995). These inconsistent results show the complex interaction between ruminal fill and the metabolic control of DMI. Schettini et al. (1999) compared whether increasing the mass or volume of the rumen via inert fill would influence DMI. They found that DMI was lower in steers that had inert fill added than the control (Schettini et al. 1999). In addition to this, increasing both the volume and the mass of the rumen contents via inert fill further decreased DMI, although there was no interaction effect.

#### **2.4.2 Hepatic oxidation**

Ruminal fill does not explain control of DMI when cattle are fed high energy diets that have high fermentability, rapid passage rate, and shorter retention time so maximum ruminal capacity is not met (Roche et al. 2008). Research in nonruminant species has shown that oxidation of fuel in the liver can regulate feeding via signals sent through the vagus nerve, and similar effects have been observed in ruminants (Allen et al. 2009). This metabolic regulation of feed intake has been called the hepatic oxidation theory (HOT), and helps to increase the understanding of DMI regulation, especially of meal termination.

Some of the challenges associated with HOT is that much of the work is done on non-ruminants and they utilize different metabolites for ATP production in the liver. Specifically, ruminants do not oxidize plasma glucose in the liver (Allen et al. 2009). When glucose is infused into nonruminants it elicits a hypophagic response; however, in ruminants, infusion of glucose had no effect on feed intake, as glucose uptake by the liver of ruminants is negligible (Allen et al. 2009). Rather than glucose, ruminants utilize propionate for gluconeogenesis and energy through the tricarboxylic acid cycle as well as butyrate for oxidation. Interestingly, despite abundant supply, the liver of ruminants does not utilize acetate as an oxidizable substrate because it has low activity of acetyl CoA synthetase (Allen et al. 2009).

In a study that compared feeding ground high-moisture corn with more rapid starch fermentation to dry ground corn on DMI, Oba and Allen (2003a) found that DMI was depressed for cows fed the high-moisture corn diet. This is contradictory to the DMI response expected with high-forage diets as increasing digestibility (NDF digestibility) generally increases DMI

due to more rapid disappearance of feed out of the rumen (Allen 1996). The dichotomy between factors that promote and inhibit feed intake under high forage and high grain diets further supports the idea that ruminal fill does not always account for changes in DMI, and that the HOT contributes to regulation of DMI. For situations where the HOT primarily regulates DMI, an increase in rapidly fermented starch causes an increase in total SCFA, acetate, propionate, and butyrate production in the rumen. Absorption of SCFA has been reported to increase fuel supply to the liver, especially the hepatic oxidation of propionate causing the most potent hypophagic effects (Oba and Allen 2003a). When propionate or acetate were infused into the mesenteric vein of steers, only propionate caused a decrease in feed intake (Elliot et al. 1985). The reduction in metabolizable energy intake from an intra-ruminal infusion of propionate was greater than the metabolizable energy that was supplied by the propionate infusion (Oba and Allen 2003b). This demonstrates that propionate's role in satiety is beyond the energy it supplies and implicates it as part of a fuel-specific mechanism in regulating DMI (Oba and Allen 2003b; Allen et al. 2009). The HOT helps to fill in the gap that ruminal fill cannot explain in the regulation of feed intake, and the role nutrient digestion and metabolism play in controlling hunger and satiety (Allen et al. 2009).

## **2.5 Ruminal passage rate**

The passage rate of digesta out of the rumen is a complex process that is not fully understood but involves both feed and animal factors (Firkins et al. 1998). Feed that enters the rumen can be removed through two processes: it can either be digested and absorbed into the bloodstream through the rumen epithelium; or it can be passed through the reticulo-omasal orifice into the omasum and onto the lower gastrointestinal tract for further digestion and absorption, or excretion. This process is important not only because it creates room in the rumen for more feed to be ingested, but also because it inherently relates to the rate of ruminal degradation (Firkins et al. 1998). The longer the retention time of feed in the rumen, the more access rumen microbes get to the feed and extent of ruminal degradation increases to a theoretical maximum. For example, with NDF, increasing residence time in the rumen will not result in complete digestion of NDF. The residual NDF remaining has been defined as undigested NDF (uNDF), and measurement of uNDF is commonly done utilizing a 240-h in vitro ruminal incubation (Raffrenato and van Amburgh 2011). Another important role of passage

rate is not just the flow of undigested feed out of the rumen, but also the passage of rumen microbes, and in turn microbial protein into the lower gastrointestinal tract where it can be utilized by cattle (Firkins et al. 1998). The flow of microbial protein out of the rumen is important in providing high quality protein to the cow. However, the ruminal rate of passage is difficult to measure, and several techniques have been developed either using solid and liquid phase markers or total rumen evacuations (Firkins et al. 1998).

It was previously thought that digesta flow out of the rumen was limited by particle size of feed, and the density of those particles in the rumen. In this model, once feed was small enough to fit through the reticulo-omasal orifice, < 3.8 mm, it was able to exit the rumen (Osbourn et al. 1976). This was further supported by the fact that DMI and passage of feed out of the rumen increased when forages were pelleted or ground (Osbourn et al. 1976). However, Okine and Mathison (1991) fed four non-lactating dairy cows up to 1.7 times maintenance requirements and found the proportion of particles that were > 4 mm in the duodenum and feces increased with DMI. The study of Okine and Mathison (1997) highlights that limits to the minimum particle size required for passage may be altered as DMI increases. Many of the particles that are retained in the rumen are also below the minimum size required to pass through the reticulo-omasal orifice, which can be attributed to the ruminal mat, which acts as a filter to hold smaller particles in the rumen for longer (Firkins et al. 1998). The feed traits that affect the formation of the rumen mat include both the particle size and the specific gravity of the feed, where larger and more buoyant feeds held more of the small particles in the rumen mat (Firkins et al. 1998).

### **2.5.1 Dry matter intake and ruminal digesta weight**

Dry matter intake and ruminal passage rate are interconnected, especially on forage-based diets where ruminal fill may be the main regulator of feed intake (Allen 1996). Robinson et al. (1987) found that as DMI was reduced, the ruminal passage rate of NDF also declined at an increasing rate, and the ruminal rate of digestion of NDF followed the inverse trend and increased. Despite the lower rate of passage, the ruminal pool of NDF also decreased as DMI decreased (Robinson et al. 1987). Huhtanen and Kukkonen (1995) also showed a lower ruminal passage rate of NDF when bulls had a decreased DMI.

Research has also been conducted to determine the effect that ruminal volume and mass has on the ruminal passage rate. Schettini et al. (1999) added inert fill to the rumen at varying volumes and masses to determine its effect on passage rate, ruminal digesta weight, and digestibility. Increasing the volume of the ruminal content increased the ruminal passage rate of digesta, but increasing the mass of the ruminal content did not affect passage rate (Schettini et al. 1999). Contrary to this, Whetsell et al. (2004) found that the addition of inert fiber to the rumen and increasing the mass of that fiber decreased particle passage rate out of the rumen on both a forage and concentrate based diet. Whetsell et al. (2004) suggested that the decrease in particle passage rate was likely related to the decrease in DMI that they observed, although a decrease in DMI was also observed by Schettini et al. (1999). Whetsell et al. (2004) observed a much larger decrease in particle passage rate when steers were fed a concentrate-based diet compared to a forage diet (31% vs 8% decrease, respectively). Okine et al. (1989) observed an increase in ruminal passage rate of digesta in steers fed at a calculated maintenance level that had weight added to their rumen. The contradictory results suggests that more research is needed to determine the mechanisms behind ruminal mass and digesta passage rate.

There was no difference in total tract digestibility when ruminal volume was increased on a forage-based diet or when ruminal mass was increased on forage-based or concentrate-based diet (Schettini et al. 1999; Whetsell et al. 2004). When ruminal volume was increased via inert fill on a forage diet, passage rate increased, which would suggest a shorter retention time in the rumen and hence a lower digestibility; however, digestibility coefficients did not differ (Schettini et al. 1999). It is likely that the post ruminal digestion compensated for the lower ruminal digestibility, although without measuring site of digestion it is difficult to confirm (Schettini et al. 1999). Okine et al. (1989), also did not observe a difference in total tract digestibility coefficients when ruminal passage rate increased and noted that the long particle length of the forage they fed, may have allowed it enough retention time in the rumen to be sufficiently degraded before it was small enough to pass through the reticulo-omasal orifice. Generally, the relationship between ruminal passage rate and degradation is inverse, although post-ruminal digestion may play an important role (Firkins et al. 1998).

### 2.5.2 Physiological state

The physiological state that a cow is in plays an important role in its DMI capacity. As described previously, DMI potential for forage-based diets are inherently tied to ruminal digestibility and passage rate. These two factors become especially important in gestating cows where rumen capacity is limited by the size of the fetus and uterus. In a comparison of pregnant and non-pregnant beef cows approaching parturition, Hanks et al. (1993) found that pregnant cows had greater ruminal particulate passage rate, but no difference in DM digestibility. Stanley et al. (1993) also observed ruminal digesta kinetics in pregnant beef cows as they approached parturition and immediately after. They noted that DMI increased as parturition approached, had a short decline on the day of calving, and then continued to increase above prepartum levels and peaked 22 days post-partum (Stanley et al. 1993). Measurements ended 22 days post-partum, and it is likely that DMI continued to increase until peak milk. Indigestible acid detergent fiber (ADF) passage rate followed a quadratic trend, increasing until its peak 6 days post-partum, then declining. Meanwhile, the rumen capacity and DM fill of the rumen decreased to their minimum 5 days pre-partum, then increased again postpartum. The increasing ruminal passage rate as parturition approaches, combined with the decreasing capacity of the rumen, suggests that passage rate is important in facilitating the increase in DMI as fetal growth limits rumen capacity (Stanley et al. 1993). The authors suggest a couple mechanisms through which increased passage rate may be facilitated, one is that fetal growth causes an increase in intra-ruminal pressure enhancing the sensitivity of ruminal tension receptors. It may also be controlled hormonally, as parturition approaches, estradiol and prolactin are secreted at higher rates, both of which can increase gut motility and passage rate (Stanley et al. 1993).

Lactation has an impact on DMI, and hence may also affect the ruminal passage rate of feed (Hartnell and Satter 1979). Dry matter intake is greater for up to 44 weeks into lactation, than during the dry period (Hartnell and Satter 1979). During the same time, DM digestibility also increased, although the diet did change from a forage based to a more concentrate-based diet during the start of lactation. Dry matter and total rumen fill were greater during lactation than during the dry period, as is expected as the intake increases, as well as the fetus is no longer restricting rumen capacity (Hartnell and Satter 1979; Stanley et al. 1993). Despite the increase in DMI; ruminal passage rate of liquid, hay, and grain did not differ between the dry and lactating period, although, the authors did note that there was variation between individual animals

(Hartnell and Satter 1979). This is contradictory to Stanley et al. (1993), but it is important to note that the passage rate measured by Hartnell and Satter (1979) is confounded by both DMI and the varying ratios of hay to grain between the dry period and different stages of lactation.

### **2.5.3 Rumen motility**

Feed characteristics play an important role in determining passage rate in cattle; however, animal factors are also significant, and ruminoreticulum motility is especially important in the mixing and passage of digesta (Okine et al. 2011). Digesta particle size was thought to be one of the most important factors influencing ruminal passage rate; however, when Okine and Mathison (1991) increased DMI to 1.7 times maintenance, the percentage of large particles increased in the dorsal and ventral sac, reticulum, and duodenum without a change in the rate of particle breakdown. This suggests that the animal has some control of passage rate beyond modification of ruminal digesta particle size, via control of feed passing through the reticulo-omasal orifice (Okine et al. 2011).

Reticular and ruminal motility are evaluated by measuring contraction frequency, duration, and amplitude. One of the difficulties of determining the effect of reticulo-ruminal motility on passage rate is that passage rate can be confounded by DMI. To overcome this challenge, weights in the form of inert fill are often added to the ruminoreticulum to modify motility (Okine et al. 1989). When either 9 or 18 kg was added to the ventral sac of steers, the duration of reticular contractions linearly increased, and the amplitude decreased (Okine et al. 1990). The frequency of reticular contraction increased quadratically and was greatest when 9 kg was added to the rumen. The increased duration of reticular contractions was associated with an increase in fecal particle size and was more important than frequency or amplitude in the distribution of fecal particle size (Okine et al. 1990). The increase in passage in relation to contraction duration likely results primarily from an increase in digesta passing through the reticulo-omasal orifice per contraction, rather than an increase in contractions (Okine et al. 2011). Further supporting the theory that cattle have control over passage rate and size of particles passing out of the rumen (Okine et al. 2011).

## 2.6 Conclusion

Current measures of efficiency, especially G:F and the KR are of limited use in the cow-calf herd because they relate only to a growing animal and beef cows are at maintenance for the majority of their lives. However, the measurement of G:F and the KR in growing heifers may have some relation to feed efficiency of the adult cow. Residual feed intake may offer a more suitable measure of efficiency in the beef cow because it is independent of both growth and BW. Adoption of residual feed intake is limited by the cost and difficulty of measuring individual feed intake, especially of grazing animals, concerns around correlations between RFI and body fat which may negatively impact reproduction, and the significant effect that different feeds, environmental and management conditions, and physiological state can have on the reranking of animals. Using data from previous research, along with incorporating unique goals of the cow-calf sector, a novel approach to evaluating efficiency in beef cows may be identified.

The reproductive fitness of the beef cow is among the most important traits in a productive and profitable cow. Cows that can produce heavier calves consistently and for a longer period will have a greater lifetime production and profitability, and reproductive fitness is a vital aspect of this. More fertile cows generally calve earlier in the calving season, which also relates to heavier weaned calves, and are in better body condition. The energy metabolism of cows plays an important role in fat deposition, BCS, and reproduction. Energy metabolism has also been shown to account for some of the variation in RFI, suggesting it may also be an indicator, or source of efficiency in cows. Understanding the regulation mechanisms of feed intake in cattle continues to be a focus of research, not only to be better able to predict intakes of grazing cows on pasture, but to uncover the underlying biological mechanisms behind the variation that is observed in individual intakes. One such mechanism is the role that ruminal passage rate of digesta has on feed intake, and vice versa. The development of an efficiency index for beef cows will have to incorporate the goals and challenges of a cow-calf herd. The GOLD indicators provide a potential base upon which to begin identifying traits that could relate to the efficiency of the individual beef cow.

The objectives of this thesis were to develop a ranking system to classify efficiency of beef cows and to evaluate whether efficient and inefficient cows differ in their ability to utilize forage. The hypothesis was that more efficient cows will have greater DMI than inefficient cows



due to greater ruminal turnover rates and motility, and smaller ruminal digesta mass. Furthermore, these responses will be consistent across diets of varying quality.

## **CHAPTER 3: DEVELOPMENT OF AN EFFICIENCY RANKING SYSTEM FOR BEEF COWS AND EFFECTS ON FEED INTAKE, RUMINAL FERMENTATION AND NDF TURNOVER, AND APPARENT TOTAL TRACT DIGESTIBILITY**

### **3.1 Introduction**

Beef cattle are often managed in extensive grazing systems during the fall and winter where they typically consume low-quality forages. The ability of cows to maintain body condition with minimal supplementation has helped cow-calf producers impose low-cost production systems. Thus, cows that efficiently utilize low quality forage as nutrients to maintain their body reserves, support reproductive success, and wean a heavy calf are more profitable (Cushman et al. 2013). There are several approaches that have been used to quantify feed efficiency for the cow-calf sector; however, the reliance on gain as a key metric in many efficiency systems limits applicability. Residual feed intake has been promoted as a potential efficiency measure for cows, although adoption of RFI is limited by the high cost of identifying low-RFI animals, difficulty in measuring individual feed intake, and practical limitations with measurement of RFI using high-forage diets (Arthur and Herd 2008). Furthermore, cattle may change their RFI classification when evaluated in consecutive feeding tests, even when fed the same diet (Durunna et al. 2012) and having multiple cows consume feed from the same bunks prevents a full understanding of the composition of the diet consumed by individuals. As such, efficiency factors that result in a stable outcome and allow for evaluation when fed high-forage diets are needed for beef cattle.

The ability of a cow to produce a calf on an annual basis has a strong influence on profitability of cow-calf operations. In addition, cows that calve early within the calving season produce calves that are heavier at the time of weaning due to more days available for growth. These cows have a greater duration for uterine involution and resumption of estrus prior to the start of the breeding season and as a result are less likely to be culled due to reproductive failure (Lesmeister et al. 1973; Cushman et al. 2013). Maintenance of, and the trajectory for, body condition score as parturition approaches and in early lactation impact the duration of the post-partum interval. Cows that approach parturition with an adequate body condition score have a shorter post-partum interval than those that lose body condition as parturition approaches (Osoro

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and Wright 1992; Hess et al. 2005). Measures of efficiency for the cow-calf sector should include the aforementioned factors as they affect lifetime productivity and profitability (Rahnefeld et al. 2011; Scholljegerdes and Summers 2016; Snelling et al. 2019; Broleze et al. 2020).

The objectives of this study were to develop a ranking system to classify efficiency of beef cows and to evaluate whether efficient and inefficient cows differ in their ability to utilize forage. The hypothesis was that efficient cows will have greater DMI than inefficient cows due to greater ruminal turnover rates and motility, and smaller ruminal digesta mass. Furthermore, these responses will be consistent across diets of varying quality.

### **3.2 Materials and Methods**

Use of cows in this research was approved by the University of Saskatchewan Research Ethics Committee (protocol 20200079) and followed the guidelines of the Canadian Council on Animal Care (Ottawa, ON, Canada).

#### **3.2.1 Management of Cows under Extensive Feeding Conditions**

Two years of data collection were conducted to complete the phenotype assessment. One hundred Black Angus heifers were managed in an extensive production system utilizing tame pasture mixes for grazing during the summer, stockpiled forage during the fall, and whole-crop barley in a swath grazing system over the winter (2018 to 2020). Cows were housed in large drylot pens during calving. Cows were checked for pregnancy during the fall of each year and estimated fetus ages were recorded. Calving date, calf sex, calving difficulty (0 for unassisted, 1 for assisted), and calf BW were measured within 24 h of parturition. In addition cow BW, cow BCS on a scale of 1 to 5, and cow rump and rib fat thickness using ultrasonography (Aloka SSD-500; 17 cm 3.5 MHz linear transducer: Aloka UST-5044-3.5; Hitachi Aloka Medical Ltd. Tokyo, Japan) with rib fat measured between the 12<sup>th</sup> and 13<sup>th</sup> rib and rump fat measured at the apex of the biceps femoris muscle between the hook and pin bones (Realini et al. 2001) were recorded at calving and weaning. Due to cow culling in year 1 and missing data, the final selection was based on 86 cows.

### **3.2.2 Phenotypic Selection**

Cows were ranked using percentile scoring systems in each of the two years based on: cow rump fat depth at calving; calving date; and calf weaning weight as a percent of cow body weight. The total score of the 3 attribute percentiles were then summed for each cow within each year. Cow rump fat at calving was measured using ultrasonography and was weighted at a maximum of 10 points. Rump fat was used as an indicator of the ability of cows to maintain body condition score under extensive winter grazing management. Cows were also ranked on a percentile basis for day of calving within the calving season with cows calving earliest receiving a maximum of 8 points (Table 3.1). The year 2 calving date was based on the gestational age of the calf determined at pregnancy checking to place emphasis on rebreeding and to allow for completion of the subsequent phase of the study. Calf weaning weight as a percent of cow body weight was conducted independently for heifer and steer calves and was unadjusted for age for a maximum of 6 points each (Table 3.2). Cows that were open at pregnancy check or had a calf die before weaning were deducted 2 points. The cumulative percentile scores were plotted to evaluate cows that were above (most efficient; ME) or below (least efficient; LE) the 50<sup>th</sup> percentile in each year. Using this phenotypic scoring system, the 10 cows with the greatest and least scores (n=20) were selected.

### **3.2.3 Preparation and Management of the Selected Cows**

The 20 ME and LE cows were moved to the University of Saskatchewan Livestock Research Building (Saskatoon, SK, Canada) and were group housed in an outdoor pen on a free choice grass hay diet. Prostaglandin (Lutalyse, Zoetis, Parsippany-Troy Hills, NJ, USA) and dexamethasone were used to abort the fetus (Johnson et al. 1981) to avoid confounding effects of pregnancy on ruminal fermentation, digesta passage, and apparent total tract digestibility. Cows were evaluated for pregnancy 7-days after prostaglandin and dexamethasone treatment and cows that did not abort were treated again and rechecked. Cows were then surgically fit with a 7.6-cm ruminal cannula (model 4C, Bar Diamond Inc., Parma, ID, USA). Twenty-one days after surgery, the cannulas were replaced with a 9-cm cannula (model 9C, Bar Diamond Inc.) and the cows were provided an additional 29 d for recovery and training. Two cows were removed from the study due to aggressive behaviour resulting in 9 ME and 9 LE cows. Cows were housed in individual pens (9 m<sup>2</sup>) with a rubber mat on the floor. Pens were scraped daily and washed every 2 d apart from during collections when washing was not permitted. Environmental enrichment

**Table 3.1** Rump fat and calving date for 86 cows over 2 consecutive years and the ranking score used.

Variable	Year 1	Year 2
<b>Rump fat</b>		
Thickness, mm		
Minimum	2.0	2.0
Mean	3.7	4.3
Maximum	6.0	8.0
SD	0.8	1.2
Score <sup>1</sup>		
Minimum	0.00	0.00
Mean	3.25	3.69
Maximum	10.00	9.88
SD	2.81	2.89
<b>Calving date<sup>2</sup></b>		
Time from herd calving start, days		
Minimum	0	0
Mean	27	20
Maximum	76	44
SD	14	14
Score <sup>1</sup>		
Minimum	0.00	0.00
Mean	5.17	5.55
Maximum	8.00	7.96
SD	1.55	1.93

<sup>1</sup>Score was calculated based on percentile ranking in the herd.

<sup>2</sup>Year 2 calving date is predicted by gestation length via ultrasound pregnancy checking.

**Table 3.2** Calf weaning weight for the 86 cows evaluated over 2 consecutive years and ranking score for calf weaning weight.

Variable	Year 1	Year 2
Calf weaning weight <sup>1</sup> , % of dam BW		
Bull calves		
Minimum	30.0	24.0
Mean	44.1	37.7
Maximum	59.0	51.0
SD	6.2	5.7
Heifer calves		
Minimum	0.0	20.0
Mean	39.9	34.8
Maximum	53.0	46.0
SD	9.2	5.5
Calf weaning weight score <sup>2</sup>		
Bull calves		
Minimum	0.00	0.00
Mean	2.87	2.85
Maximum	6.00	6.00
SD	1.82	1.77
Heifer calves		
Minimum	-2.00	0.00
Mean	2.98	2.80
Maximum	6.00	6.00
SD	1.92	1.82

<sup>1</sup>Cows that did not calve or did not have a live calf at weaning were deducted 2 points from weaning weight.

<sup>2</sup>Score was calculated based on percentile ranking in the herd with a maximum score of 6 for cows with either bull or heifer calves.

was provided via nose-to-nose contact with neighbouring cows and a suspended ball in each pen. If weather and sampling permitted, cows were provided with 3 h of outdoor access in a group pen. Cows were fed daily at 1000 h and the refusals were removed prior to the feeding time. Mineral and urea were combined and supplied on a daily basis using a separate feeder. Cows had ad libitum access to water in their pens.

### **3.2.4 Experimental Design**

Cows were blocked into 1 of 2 wings of the barn and randomly assigned to a pen with 5 ME and 4 LE cows in block 1 and 4 ME and 5 LE cows in block 2. The experiment consisted of 4-consecutive 26-d periods with all cows offered the same diet within each period. Diets were formulated using Nutritional Dynamic System (RUM&N, Reggio Emilia, Italy) and progressively decreased in quality as indicated by reduced silage inclusion, increased straw inclusion, and chemically with increasing NDF, uNDF, and decreasing  $NE_m$  (Table 3.3). Crude protein was formulated to be adequate for non-pregnant and non-lactating cows among all diets. For the diets, hay and straw were chopped through a 15.2-cm primary and 5.1-cm secondary screen, respectively, using a Haybuster H1100E (DuraTech Industries, Jamestown, ND, USA) and blended using a Keenan Mechfiber320 mixer wagon (Alltech Farming Solutions Ltd., Borris, Co. Carlow, Ireland). Five minutes of mixing time from last ingredient addition was used to ensure a homogenous mix was produced. Silage and blended hay-straw samples were collected every 4 and 8 days, respectively, and dried for 72 h in a forced air oven at 55°C to determine the DM concentration to ensure diets were mixed accurately on an as is basis.

### **3.2.5 Data and Sample Collection**

Cow body weight, rib fat, and rump fat thickness were recorded on d -1 and 1, and d 26 of each period. Cow rib and rump fat was measured using ultrasonography with rib fat measured between the 12<sup>th</sup> and 13<sup>th</sup> rib and rump fat measured at the apex of the biceps femoris muscle between the hook and pin bones (Realini et al. 2001). Subcutaneous fat was determined by the same person throughout the study to ensure consistent measurements.

Feed intake was monitored throughout the study to ensure ad libitum intake of feed by targeting 15% of offered feed being refused. The amount of feed offered and refused were weighed and used for data analysis from d 14 to 21. A subsample of refusals (10% of the total weight) from each day were collected and composited to yield a single sample for each cow in each period.

**Table 3.3** Ingredient and chemical composition of the high quality (HQ), medium high-quality (MHQ), medium quality (MQ), and low quality (LQ) diets fed to 18 mature beef cows in over 4 consecutive 28-d periods.

	Diet quality			
	High	Med-Hi	Med	Low
Ingredient, % DM				
Barley silage	99.78	32.5	17.04	11.93
Grass hay	-	42.5	41.08	37.43
Wheat straw	-	25.0	41.82	50.15
Urea	0.22	-	0.06	0.49
Chemical composition <sup>1</sup> , % DM				
DM, %	38.7 ± 0.40	59.8 ± 0.58	71.5 ± 0.60	79.2 ± 0.36
OM	93.4 ± 0.06	93.4 ± 0.45	93.3 ± 0.69	92.8 ± 0.72
CP	11.5 ± 0.56	11.2 ± 0.00	10.8 ± 0.85	10.8 ± 0.55
ADF	23.1 ± 0.49	35.5 ± 0.55	39.3 ± 1.63	42.6 ± 1.95
NDF	41.0 ± 0.78	56.9 ± 1.17	62.5 ± 3.40	64.3 ± 1.40
aNDFom	40.7 ± 0.92	55.7 ± 1.10	61.3 ± 3.48	62.9 ± 1.28
Lignin	3.4 ± 0.13	4.9 ± 0.36	5.7 ± 0.26	6.0 ± 0.04
uNDF	10.7 ± 1.01	18.0 ± 1.58	20.0 ± 1.70	21.0 ± 0.17
Starch	17.3 ± 3.53	4.2 ± 0.86	3.1 ± 0.07	5.6 ± 4.87
Ether extract	2.8 ± 0.20	1.8 ± 0.14	1.7 ± 0.30	1.6 ± 0.13
NE <sub>m</sub> , Mcalkg	1.69 ± 0.000	1.37 ± 0.016	1.24 ± 0.049	1.18 ± 0.016
NE <sub>g</sub> , Mcal/kg	1.08 ± 0.000	0.79 ± 0.016	0.66 ± 0.049	0.62 ± 0.016

<sup>1</sup>Data presented are the means and the standard deviation (n = 2)



Individual feed ingredient samples (200 g/d) were collected from d 14 to 21 and a period composite was prepared. Feed ingredients and feed refusals were stored at -20°C until they were removed for particle size separation using the Penn State Particle Separator with sieve openings of 19-, 8-, and 4-mm, and a pan (Nasco, Newmarket, ON, Canada). Sorting indices were calculated for each cow as the actual intake of particles retained on each screen as a percentage of the predicted intake (Leonardi and Armentano 2003). The predicted intake of each screen was based on the particle size of the feed offered and the amount of feed offered. The feed ingredients and refusals were also dried in a forced air oven at 55°C for 72 h to determine DM before being ground using a hammer mill (Christie-Norris Laboratory Mill, Christie-Norris Ltd, Chelmsford, UK) to pass through a 2.5-mm screen. Samples were then re-ground to pass through a 1-mm screen and analyzed for organic matter (OM), crude protein (CP), starch, ash free neutral detergent fiber (aNDFom), acid detergent fiber (ADF), lignin, and undigestible neutral detergent fiber (uNDF) at Cumberland Valley Analytical Services (Waynesboro, PA, USA). Ash was analyzed according to method 942.05 of AOAC (2000) with the modifications of using 1.5-g sample weight, 4-h ash time, and using hot weight. The OM was calculated as ash subtracted from 100%. Crude protein was determined using method 990.03 of AOAC (2000) with a Leco FP-528 Nitrogen Combustion Analyzer (St. Joseph, MI, USA). Starch was analyzed according to Hall (2009) with a correction for free glucose and water-soluble carbohydrates according to Dubois et al. (1956). Ether extract was determined according to AOAC (2000) method 2003.05 using the Tecator Soxtec System HT 1043 Extraction unit (Tectator, Foss, Eden Prairie, MN, USA). The aNDFom was determined according to van Soest et al. (1991) except Whatman 934-AH glass micro-fiber filters with 1.5- $\mu$ m particle retention were used and samples were ashed at 535°C in a furnace for 2 h. Method 973.18 of AOAC (2000) was used to determine ADF but Whatman 934-AH glass micro-fiber filters with 1.5- $\mu$ m particle retention replaced the fritted glass crucible. Lignin and uNDF were determined according to Goering and Van Soest (1970) with the uNDF content determined as the aNDFom left after 240 h in vitro digestion.

### **3.2.6 Ruminal Fermentation**

Ruminal digesta collection was initiated on d 17 at 0700 h and continued every 12 h with a 4-h offset among days. Thus, samples were collected at 0700 and 1900 h on d 17, 1100 and 2300 h on d 18, 1500 h on d 19, and 0300 h on d 20. Ruminal digesta samples (250 mL/region)

were collected at the ruminal-fluid ruminal-mat interface from the cranial central, central, and caudal central regions of the rumen. The ruminal digesta from each region were combined and strained through two layers of cheesecloth. Ten milliliters of ruminal fluid was then added to 2 mL of metaphosphoric acid (25% wt/vol) or 1% sulfuric acid for analysis of short chain fatty acids (SCFA) or ammonia, respectively. The ruminal fluid samples were stored at -20°C before being thawed. A composite sample was prepared by transferring 1.5 mL from each time point for each cow within each period. The SCFA concentration was determined using gas chromatography with a flame ionization detector (Agilent 6890; Agilent Technologies Canada Inc., Mississauga, ON, Canada; Khorasani et al. 1996).

Ruminal pH was measured using the strained ruminal fluid at each sampling timepoint described above. The hand-held pH meter (Accumet AP110; Fisher Scientific, Pittsburgh, PA, USA) was standardized in buffers 4 and 7 prior to each sampling. The mean, maximum, and minimum pH values were calculated.

### **3.2.7 Ruminal Motility**

Ruminal motility was measured in 5 cows/block on d 22 and 4 cows/block on d 23 from 1100 h to 1500 h. Motility was measured by placing a weighted balloon (Party City, Saskatoon, SK, Canada) filled with 1 L of water into the ventral sac of the rumen. The balloon was connected to a disposable blood pressure transducer (MLT0699; ADInstruments Inc., Colorado Springs, CO, USA) as described by Egert et al. (2014). The pressure transducer was connected to a recording device (PowerLab 9/35, ADInstruments Inc.) through bridge amplifiers (FE224; ADInstruments Inc.) which took a mV reading every 200 ms and was calibrated to 20 mmHg and 100 mmHg prior to recording (MLA6595; ADInstruments Inc., Colorado Springs, CO, USA). Rumen pressure data were analyzed using LabChart Pro software (ADInstruments Inc.) for contraction frequency, time between contractions, contraction duration, contraction amplitude, and total contraction area (Pereira et al. 2022). Contraction frequency, time between contractions, contraction duration, and contraction amplitude were measured by calculating the integral of the smoothed pressure signal, filtering to remove noise, using cyclic measurement detection with filtering using a high pass cutoff of 0.01 Hz, and a minimum peak height of 3.5432 to 11.1200 mmHg. The minimum peak height used was adjusted for each cow in each

period to ensure contractions were detected. Total contraction area was calculated by summing the areas from each contraction event.

### **3.2.8 Ruminal NDF Turnover**

Ruminal NDF turnover was determined by completely evacuating the rumen of all digesta at 0700 h (prior to feeding) on two consecutive days (d 24 and 25; Linton and Allen 2008). Ruminal digesta was weighed, thoroughly mixed, and two 5-L samples were collected before the digesta was returned to the rumen. Each 5-L sample was separated into the liquid and solid portions using a wine press (Harvest Bounty Wine Press, Pleasant Hill Grain LLC, Hampton, NE; Karnati et al. 2007). The liquid and solid portion were weighed before being dried for 120 h at 55°C in a forced-air oven. The duplicate samples of the dried solid portion from each evacuation were composited and sent to Cumberland Valley Analytical Services (Waynesboro, PA, USA) for determination of uNDF and aNDFom, as previously described. The ruminal rate of aNDFom passage ( $k_p$ ; %/hr) was assumed to be equal to the ruminal rate of uNDF passage and the ruminal rate of aNDFom degradation ( $k_d$ ; %/hr) was calculated as (intake of potentially degradable aNDFom / ruminal pool size of potentially degradable aNDFom) -  $k_p$  (Dado and Allen 1995). Intake of uNDF and aNDFom was calculated from d 24 DMI and the composited feed and refusal uNDF and aNDFom concentrations. The ruminal pool size was the product of ruminal solid fraction DM weight and the ruminal solid fraction uNDF and aNDFom concentrations.

### **3.2.9 Apparent Total Tract Digestibility**

Foley bladder catheters (24 Fr 75 mL Bardex Lubricath Catheter, C. R. Bard Inc., Covington, GA, USA) were inserted and infused with 80 mL of saline solution on d 16 of each period, cows were tethered, and cows were provided with 1 d to acclimatize before collections began. Total fecal collections began on d 17 of each period at 0700 h and continued for 96 h. Pens were scraped every 4 h and the weight of the feces was weighed at each timepoint. A representative sample of feces was collected (2% of the collected weight) and used to prepare a composite for each cow. Fecal samples were stored in a plastic container at -20°C. After compositing, the fecal samples were thawed and dried in a forced-air oven at 55°C for 120 h to determine DM concentration. Dried samples were ground to pass through a 2.5-mm screen using a hammer mill (Christie-Norris Laboratory Mill, Christie-Norris Ltd, Chelmsford, UK). The

ground fecal samples were sent to Cumberland Valley Analytical Services (Waynesboro, PA, USA) for determination of OM, CP, starch, aNDFom, ADF, lignin, and uNDF, as previously described.

Total urine output was collected during the same period as fecal output. Urine was collected in 20-L carboys filled with 300-mL of HCl. Urine was mixed and weighed daily at 0700 h and a 30-mL subsample was collected and stored at -20°C. Daily urine subsamples were then composited based on daily urine output. Urine pH was tested in the carboys daily to ensure that the 300 mL of HCl was sufficient to maintain pH below 4. The composited urine samples were analyzed for urine N using a LECO FP-528 analyzer (LECO Instruments ULC, Mississauga, ON, Canada).

### **3.2.10 Statistical Analysis**

All statistical analysis was conducted using the Statistical Analysis Systems software (SAS version 9.4, SAS Institute, Inc. Cary, NC, USA). The mixed procedure of SAS was used, and the model included the fixed effects of phenotype, diet, and the 2-way interaction, and the random effect of block. Means were declared to be different when  $P < 0.05$ . Sorting behaviour was also analyzed using a two-tailed T-test to determine if individual treatment means differed from 100 with significance being declared when  $P < 0.05$ . Correlation and regression of cow rump fat at calving, calving date, calf weaning weight, and yearly selection point totals were analyzed using the CORR procedure and REG procedure of SAS, respectively.

### **3.3 Results**

Rump fat thickness of the 86 cows ranged from 2.0 to 6.0 mm with a mean of  $3.7 \pm 0.8$  mm in year 1 and 2.0 to 8.0 mm with a mean of  $4.3 \pm 1.2$  mm in year 2 (Table 3.1). The minimum rump fat thickness score was 0.00 for both year 1 and 2. The rump fat score had a maximum of 10.00 with a mean of  $3.25 \pm 2.81$  in year 1 and a maximum of 9.88 with a mean of  $3.69 \pm 2.89$  in year 2. Calving date, which was measured as the difference between a cow's calving date and the date of the first cow to calve in year 1, and the difference in a cow's gestational age and the oldest gestational age in year 2. Calving date ranged from 0 to 76 d with a mean of  $27 \pm 14$  d in year 1 and ranged from 0 to 44 d with a mean of  $20 \text{ d} \pm 14 \text{ d}$  in year 2. The minimum calving date score was 0.00 in both year 1 and 2 and the maximum score was 8.00 and

7.96 in year 1 and 2, respectively. The mean score in year 1 was  $5.17 \pm 1.55$  and  $5.55 \pm 1.93$  in year 2.

The weaning weight of bull calves as a percent of cow BW ranged from 33.0 to 59.0% in year 1 and 24.0 to 51.0% in year 2 (Table 3.2). The mean bull calf weaning weight was  $44.1 \pm 6.2\%$  of the dams BW in year 1 and  $37.7 \pm 5.5\%$  in year 2. The weaning weight of heifer calves in year 1 ranged from 0.0 to 53.0% and in year 2 ranged from 20.0 to 46.0%. The mean weaning weight of heifer calves was  $39.9 \pm 9.2\%$  of dams BW and  $34.8 \pm 5.5\%$  of dams BW in year 1 and 2, respectively. The score for bull calf weaning weight ranged from 0.00 to 6.00 in years 1 and 2, with a mean of  $2.87 \pm 1.82$  and  $2.85 \pm 1.77$  in year 1 and 2, respectively. The minimum score for heifer calf weaning weight was -2.00 in year 1 and 0.00 in year 2 with a maximum of 6.00 in both years. The mean score for heifer calf weaning weight was  $2.98 \pm 1.92$  and  $2.80 \pm 1.82$  in year 1 and 2, respectively.

Calving date of the 86 cows over 2 years of extensive grazing management was not correlated with rump fat thickness at calving or calf weaning weight (Table 3.4;  $P \geq 0.45$ ). Calf weaning weight as a percent of cow BW was negatively correlated to rump fat thickness at calving ( $P = 0.001$ ). The year 1 weaning weight score was positively correlated with year 2 weaning weight and year 1 total score (Table 3.5;  $P \leq 0.003$ ) and tended to be negatively correlated with year 2 rump fat ( $P = 0.062$ ). Year 1 weaning weight was not correlated to year 1 rump fat and calving date, or year 2 calving date and total points ( $P \geq 0.67$ ). Year 1 rump fat was not correlated to year 1 calving date, or year 2 weaning weight and calving date ( $P \geq 0.13$ ) but was positively correlated to year 2 rump fat and year 1 and 2 total points ( $P \leq 0.017$ ). The year 2 weaning weight was not correlated with year 2 calving date ( $P = 0.44$ ) but was positively correlated with Year 1 and 2 total points. Year 2 weaning weight also tended to be negatively correlated with year 2 rump fat ( $P = 0.085$ ). Year 2 rump fat and calving date were positively correlated with year 2 total points ( $P < 0.001$ ), Year 1 and 2 total points were also positively correlated ( $P = 0.010$ ).

Rump fat measured at calving, calving date, calf birth weight, and calf weaning weight as a percent of cow BW and on a kg basis of the 9 LE and 9 ME cows during 2 consecutive years of extensive management were not affected by the phenotype  $\times$  year interaction (Table 3.6;  $P \geq 0.22$ ). Rump fat thickness was greater in ME cows than LE cows ( $P < 0.001$ ) and was greater in year 2 than year 1 ( $P = 0.024$ ). Calving date did not differ between years ( $P = 0.49$ ) but was

**Table 3.4** Pearson correlation coefficients and the respective *P*-value for calf weaning weight, rump fat thickness, and calving date from 86 cows measured over two years.

Variable	Calf weaning weight, % dam BW	Rump fat thickness <sup>1</sup>	Calving date <sup>2</sup>
Calf weaning weight, % dam BW	1	-0.248 (0.001)	0.059 (0.45)
Rump fat thickness		1	0.058 (0.46)
Calving date			1

<sup>1</sup>Cow rump fat was measured using ultrasonography during calving.

<sup>2</sup>Calving date is the difference in days between a cows calving date and the first cow to calve for year 1 and the difference between a cow's estimated gestation length at pregnancy checking and the longest cow's estimated gestation length in year 2.

**Table 3.5** Pearson correlation coefficients for year 1 and 2 weaning weight, rump fat thickness, calving date, and total scores in a herd of 86 cows measured over two consecutive years.

Variable	Year 1				Year 2			
	Weaning weight <sup>1</sup>	Rump fat <sup>2</sup>	Calving date <sup>3</sup>	Total points	Weaning weight	Rump fat	Calving date	Total points
Year 1								
Weaning weight	1	-0.035 (0.75)	0.047 (0.67)	0.505 (<0.001)	0.320 (0.003)	-0.202 (0.062)	-0.001 (1.00)	0.001 (0.99)
Rump fat		1	-0.085 (0.44)	0.706 (<0.001)	-0.166 (0.13)	0.419 (<0.001)	0.022 (0.84)	0.257 (0.017)
Calving date			1	0.431 (<0.001)	0.440 (<0.001)	-0.126 (0.25)	0.086 (0.43)	0.167 (0.12)
Total points				1	0.244 (0.024)	0.157 (0.15)	0.057 (0.60)	0.276 (0.010)
Year 2								
Weaning weight					1	-0.187 (0.085)	0.085 (0.44)	0.398 (<0.001)
Rump fat						1	-0.045 (0.68)	0.667 (<0.001)
Calving date							1	0.530 (<0.001)
Total points								1

**Table 3.6** Rump fat measured at calving, calving interval, and calf weaning weight for cows phenotypically classified as least-efficient (LE; n = 9) and most-efficient (ME; n = 9) when measured over two years.

Variable	Phenotype		Year		SEM <sup>1</sup>	P value		
	LE	ME	1	2		Phenotype	Year	Phenotype × year
Rump fat <sup>2</sup> , mm	3.5	4.7	3.9	4.3	0.18	<0.001	0.024	0.56
Calving date <sup>3</sup> , d	30	14	20	23	4.0	<0.001	0.49	0.45
Calf birth weight, kg	34	35	31	38	1.6	0.33	<0.001	0.22
Calf weaning weight, kg	211	231	220	222	9.3	0.032	0.79	0.54
Calf weaning weight <sup>4</sup> , % dam BW	35.5	43.8	42.2	37.2	2.05	<0.001	0.018	0.54
Calf sex, n								
Male	9	10	12	7	-	-	-	-
Female	9	8	6	11	-	-	-	-

<sup>1</sup>Greatest SEM for the 2-way interaction is presented.

<sup>2</sup>Cow rump fat was measured using ultrasonography during calving.

<sup>3</sup>Calving date is the difference in days between the calving date and the first cow to calve for year 1 and the difference between a cow's estimated gestation length at pregnancy checking and the longest cow's estimated gestation length in year 2.

<sup>4</sup>Calf weaning weight was corrected for sex according to (Minyard and Dinkel 1965) and then calculated as a percent of the dam body weight.



earlier for the ME cows ( $P < 0.001$ ). Calf birth weight did not differ between phenotypes ( $P = 0.33$ ) but was greater in year 2 than year 1 ( $P > 0.001$ ). Calf weaning weight as a percent of cow BW and on a kg basis were both greater for ME than LE cows ( $P \leq 0.032$ ) but only calf weaning weight as a percent of cow BW was greater in year 1 than 2 ( $P = 0.018$ ). Low efficiency cows had 9 bull calves and ME cows had 10, with 12 of the bull calves being born in year 1 and 7 in year 2. Nine heifer calves were born to the LE cows and 8 to the ME cows. In year 1, 6 heifer calves were born and in year 2, 11 were born.

While unintended but not controlled by the experimental design, starting BW (643 kg and 595 kg;  $P < 0.001$ ; Table 3.7) and ending BW (633 kg and 618 kg;  $P < 0.001$ ) were both greater for LE than ME cows, respectively. Starting BW was lightest when cows were fed the HQ diet relative to all other diets ( $P < 0.001$ ). Diet had no effect on ending BW ( $P = 0.18$ ) and there was no phenotype  $\times$  diet interaction for starting or ending BW ( $P > 0.98$ ). Likewise, there were no phenotype  $\times$  diet interactions for measures of rib or rump fat thickness ( $P > 0.17$ ). There was no phenotype effect on the change in rib or rump fat thickness ( $P > 0.51$ ). Starting rib fat did not differ between phenotypes ( $P = 0.14$ ) but starting rump fat was thicker for ME than LE cows ( $P = 0.019$ ). Ending rump fat was also thicker for ME than LE cows ( $P = 0.019$ ) while ending rib fat followed the same tendency ( $P = 0.070$ ). Starting rib and rump fat were thinnest for the HQ diet, intermediate in the MHQ diet, and thickest in the MQ, and LQ diets ( $P < 0.001$ ). Ending rib and rump fat were thinnest when fed the HQ diet and thickest for the MHQ, MQ, and LQ diets ( $P < 0.025$ ). Rib and rump fat change were greatest while cows were fed the HQ diet, intermediate for the MHQ diet, and least for the MQ and LQ diets ( $P < 0.001$ ).

There were no interactions between phenotype and diet on measures of DMI ( $P \geq 0.36$ ; Table 3.8). While DMI (kg/d) was not affected by phenotype ( $P = 0.93$ ), when reported as a percentage of BW, ME cows had greater DMI than LE cows (2.16% and 2.00%, respectively;  $P < 0.001$ ). In addition, DMI (kg/d and % BW) were greatest for cows fed the HQ and MHQ diets, intermediate when fed the MQ diet, and least for the LQ diet ( $P < 0.001$ ). Phenotype had no effect on NDF intake (kg/d,  $P = 0.99$ ); however, similar to DMI, when reported as percentage of BW, ME cows had a greater intake than LE cows (1.14% and 1.06%, respectively;  $P < 0.001$ ). Neutral detergent fiber (kg/d) and uNDF (% BW) intake were greatest when fed the MHQ diet, and decreased as diet quality decreased, although the least intake occurred when fed the HQ diet

**Table 3.7** Start and ending BW, and rib and rump fat measurements of beef cows phenotypically classified as least-efficient (LE; n = 9) or most-efficient (ME; n = 9) and fed a high-quality (HQ), medium-high quality (MHQ), medium quality (MQ), or low quality (LQ) diet during 4 consecutive 28-d periods.

Variable	Phenotype		Diet				SEM <sup>1</sup>	P value		
	LE	ME	HQ	MHQ	MQ	LQ		Phenotype	Diet	Phenotype × diet
BW, kg										
Start	643	595	571 <sup>b</sup>	625 <sup>a</sup>	631 <sup>a</sup>	649 <sup>a</sup>	16.3	<0.001	<0.001	0.98
End	663	618	625	631	649	656	16.0	<0.001	0.18	0.99
Rib fat, mm										
Start	6.1	6.8	2.6 <sup>c</sup>	6.4 <sup>b</sup>	8.2 <sup>a</sup>	8.4 <sup>a</sup>	0.69	0.14	<0.001	0.86
End	7.4	8.4	6.4 <sup>b</sup>	8.2 <sup>a</sup>	8.4 <sup>a</sup>	8.6 <sup>a</sup>	0.77	0.070	0.025	0.99
Change	1.4	1.6	3.9 <sup>a</sup>	1.8 <sup>b</sup>	0.2 <sup>c</sup>	0.1 <sup>c</sup>	0.59	0.51	<0.001	0.86
Rump fat, mm										
Start	7.3	8.8	2.6 <sup>c</sup>	8.0 <sup>b</sup>	10.6 <sup>a</sup>	11.1 <sup>a</sup>	1.03	0.019	<0.001	0.64
End	9.1	10.8	8.0 <sup>b</sup>	10.6 <sup>a</sup>	11.1 <sup>a</sup>	10.1 <sup>a</sup>	1.08	0.020	0.020	0.90
Change	1.8	2.0	5.4 <sup>a</sup>	2.6 <sup>b</sup>	0.4 <sup>c</sup>	-0.9 <sup>c</sup>	0.79	0.73	<0.001	0.17

<sup>1</sup>Greatest SEM for the 2-way interaction is presented.

<sup>a,b,c</sup>Means with different superscripts in a row are different ( $P < 0.05$ ).

**Table 3.8** Sorting behaviour and DM and nutrient intake for beef cows phenotypically classified as least-efficient (LE; n = 9) or most-efficient (ME; n = 9) and fed a high-quality (HQ), medium-high quality (MHQ), medium quality (MQ), or low quality (LQ) diet during 4 consecutive 28-d periods.

Variable	Phenotype		Diet				SEM <sup>1</sup>	P value		
	LE	ME	HQ	MHQ	MQ	LQ		Phenotype	Diet	Phenotype × diet
DMI, kg	13.0	13.0	14.3 <sup>a</sup>	14.6 <sup>a</sup>	12.4 <sup>b</sup>	10.7 <sup>c</sup>	0.39	0.93	<0.001	0.82
DMI, % BW	2.00	2.16	2.40 <sup>a</sup>	2.34 <sup>a</sup>	1.94 <sup>b</sup>	1.64 <sup>c</sup>	0.059	<0.001	<0.001	0.36
NDF intake, kg/d	6.90	6.90	5.78 <sup>d</sup>	7.95 <sup>a</sup>	7.36 <sup>b</sup>	6.50 <sup>c</sup>	0.206	0.99	<0.001	0.87
NDF intake, % BW	1.06	1.14	0.97 <sup>c</sup>	1.27 <sup>a</sup>	1.16 <sup>b</sup>	1.00 <sup>c</sup>	0.033	<0.001	<0.001	0.80
uNDF intake, % BW	0.33	0.35	0.25 <sup>d</sup>	0.41 <sup>a</sup>	0.37 <sup>b</sup>	0.33 <sup>c</sup>	0.010	<0.001	<0.001	0.82
Sorting index <sup>2</sup> , %										
19 mm screen	84.0 <sup>z</sup>	85.0 <sup>z</sup>	102.4 <sup>az</sup>	91.9 <sup>bz</sup>	75.5 <sup>cz</sup>	68.2 <sup>dz</sup>	3.27	0.66	<0.001	0.72
8 mm screen	105.1 <sup>z</sup>	105.2 <sup>z</sup>	99.7 <sup>cz</sup>	106.2 <sup>bz</sup>	108.7 <sup>az</sup>	106.1 <sup>bz</sup>	0.91	0.85	<0.001	0.89
4 mm screen	102.4	102.8 <sup>z</sup>	97.3 <sup>bz</sup>	98.6 <sup>b</sup>	106.6 <sup>az</sup>	107.9 <sup>az</sup>	1.95	0.71	<0.001	0.28
Pan	108.8 <sup>z</sup>	106.9 <sup>z</sup>	101.1 <sup>c</sup>	96.0 <sup>dz</sup>	113.3 <sup>bz</sup>	121.0 <sup>az</sup>	2.23	0.24	<0.001	0.68

<sup>1</sup>Highest SEM for the 2-way interaction is presented.

<sup>2</sup>Sorting index was calculated as actual intake of retained particles on each screen / predicted intake (Leonardi and Armentano, 2003).

<sup>a,b,c</sup>Means with different superscripts in a row are different ( $P < 0.05$ ).

<sup>z</sup>Indicates difference from 100 ( $P < 0.05$ ) using two-tailed t-test.

( $P < 0.001$ ). Undigestible neutral detergent fiber intake represented as a percentage of BW was greater for ME than LE cows ( $P < 0.001$ ).

The only sorting index value that did not differ from 100 was the fraction on the pan when cows were fed the HQ diet ( $P > 0.050$ , Table 3.8). Phenotype did not affect sorting of any of the fractions ( $P \geq 0.24$ ). Particles retained on the 19-mm screen were preferentially consumed when fed the HQ diet and were increasingly selected against as diet quality decreased ( $P < 0.001$ ). Particles retained on the 8-mm screen were selectively consumed to the greatest extent when cows were fed the MQ diet, intermediate and selected for when fed the MHQ and LQ diets, and selected against when fed the HQ diet ( $P < 0.001$ ). Cows fed the MQ and LQ diets selected for particles retained on the 4-mm screen while those fed the HQ and MHQ diets selected against these particles ( $P < 0.001$ ). Fine particles were most greatly selected for when fed the LQ diet, with less preferential selection when fed the MQ diet, not selected or refused when fed the HQ diet, and selected against in the MHQ diet ( $P < 0.001$ ). There were no phenotype  $\times$  diet interactions in any of the fractions ( $P \geq 0.28$ ).

Phenotype and the phenotype  $\times$  diet interaction did not affect mean, minimum, and maximum ruminal pH or total SCFA concentration ( $P \geq 0.11$ , Table 3.9). Mean and minimum ruminal pH were greatest when fed the LQ and MQ diets which did not differ, intermediate for the MHQ diet, and least for the HQ diet ( $P < 0.001$ ). Maximum ruminal pH was greatest when fed the LQ diet, the LQ and MQ diet did not differ and the MQ and MHQ did not differ, although the LQ and MHQ diets were different, and the HQ diet was the least ( $P < 0.001$ ). Total ruminal SCFA concentration was not affected by phenotype ( $P = 0.12$ ) or the phenotype  $\times$  diet interaction ( $P = 0.78$ ); however, concentrations were greatest when fed the HQ diet, with no difference between the HQ and MHQ diet, MHQ and MQ diet, or the MQ and LQ diet ( $P < 0.001$ ). There were no phenotype or phenotype  $\times$  diet interaction effects ( $P \geq 0.33$ ) on the molar proportions of SCFA except for isovalerate which was affected by the phenotype  $\times$  diet interaction (data not shown;  $P < 0.001$ ) where the LE cows (2.1%) had a greater molar proportion than the ME cows (1.4%) fed the HQ diet. The molar proportion of acetate was greatest for cows fed the LQ diet and concentrations decreased as diet quality increased ( $P < 0.001$ ). For propionate, butyrate, and isobutyrate, molar proportions were greatest when fed the HQ diet, intermediate for the MHQ diet, and least when fed the MQ and LQ diets, although MHQ and MQ diet did not differ for isobutyrate ( $P > 0.001$ ). Valerate was greatest for cows fed

**Table 3.9** Ruminal pH, short-chain fatty acid (SCFA) concentrations, and ammonia concentration from beef cows phenotypically classified as least-efficient (LE; n = 9) or most-efficient (ME; n = 9) and fed a high-quality (HQ), medium-high quality (MHQ), medium quality (MQ), or low quality (LQ) diet during 4 consecutive 28-d periods.

Variable	Phenotype		Diet				SEM <sup>1</sup>	P value		
	LE	ME	HQ	MHQ	MQ	LQ		Phenotype	Diet	Phenotype × diet
Ruminal pH										
Mean	6.99	7.02	6.85 <sup>c</sup>	6.98 <sup>b</sup>	7.10 <sup>a</sup>	7.11 <sup>a</sup>	0.038	0.20	<0.001	0.82
Min	6.76	6.79	6.56 <sup>c</sup>	6.71 <sup>b</sup>	6.90 <sup>a</sup>	6.92 <sup>a</sup>	0.057	0.47	<0.001	0.79
Max	7.26	7.31	7.14 <sup>c</sup>	7.26 <sup>b</sup>	7.36 <sup>ab</sup>	7.38 <sup>a</sup>	0.050	0.11	<0.001	0.97
Total SCFA, mM	102.82	100.06	108.02 <sup>a</sup>	103.29 <sup>ab</sup>	99.24 <sup>bc</sup>	95.22 <sup>c</sup>	2.463	0.12	<0.001	0.78
Ruminal SCFA, mol/100 mol										
Acetate	67.7	67.6	57.5 <sup>d</sup>	69.1 <sup>c</sup>	71.5 <sup>b</sup>	72.4 <sup>a</sup>	0.52	0.64	<0.001	0.77
Propionate	17.7	17.9	19.7 <sup>a</sup>	17.6 <sup>b</sup>	17.0 <sup>c</sup>	16.9 <sup>c</sup>	0.25	0.53	<0.001	0.97
Butyrate	10.5	10.7	16.1 <sup>a</sup>	9.8 <sup>b</sup>	8.5 <sup>c</sup>	8.0 <sup>c</sup>	0.41	0.58	<0.001	0.45
Isobutyrate	0.8	0.8	0.9 <sup>a</sup>	0.8 <sup>b</sup>	0.8 <sup>bc</sup>	0.7 <sup>c</sup>	0.02	0.57	<0.001	0.74
Isovalerate	1.2	1.0	1.7 <sup>a</sup>	1.0 <sup>b</sup>	0.9 <sup>bc</sup>	0.8 <sup>c</sup>	0.08	<0.001	<0.001	<0.001
Valerate	1.3	1.3	2.0 <sup>a</sup>	1.2 <sup>b</sup>	1.0 <sup>c</sup>	0.9 <sup>d</sup>	0.04	0.39	<0.001	0.81
Caproate	0.8	0.8	2.0 <sup>a</sup>	0.6 <sup>b</sup>	0.4 <sup>c</sup>	0.3 <sup>c</sup>	0.04	0.33	<0.001	0.43
NH <sub>3</sub> -N, mg/dL	5.14	4.94	5.59 <sup>ab</sup>	3.69 <sup>c</sup>	4.97 <sup>b</sup>	5.92 <sup>a</sup>	0.666	0.52	<0.001	0.57

<sup>1</sup>Highest SEM for the 2-way interaction is presented.

<sup>a, b, c</sup>Means with different superscripts in a row are different ( $P < 0.05$ ).

the HQ diet and decreased as diet quality decreased from HQ to LQ ( $P < 0.001$ ). Caproate was greatest when fed the HQ diet and least for the MQ and LQ diets ( $P < 0.001$ ). Ruminal ammonia concentrations were not affected by phenotype ( $P = 0.52$ ) or the phenotype  $\times$  diet interaction ( $P = 0.57$ ) but were greatest when fed the HQ and LQ diets, intermediate for the MQ diet, and least for the MHQ diet with no difference between the HQ and MQ diets ( $P < 0.001$ ).

Ruminal contraction frequency, duration, and time were not affected by phenotype, diet, or the phenotype  $\times$  diet interaction ( $P \geq 0.11$ , Table 3.9). Ruminal contraction height and peak area were not affected by the phenotype  $\times$  diet interaction ( $P \geq 0.27$ ) but ruminal contraction height was greater in LE than ME cows ( $P = 0.015$ ) and was also greater when fed the HQ and MHQ diets than the MQ and LQ diets ( $P < 0.001$ ). The ruminal contraction peak area was also different among phenotypes ( $P = 0.009$ ) and diets ( $P = 0.036$ ) where the LE cows had a greater peak area than ME cows and the HQ diet was greater than the MQ and LQ diets with the MHQ diet not different from the HQ, MQ, and LQ diets.

Total, solid, and liquid ruminal digesta weights whether reported on an as is or DM basis were not affected by the phenotype  $\times$  diet interaction ( $P \geq 0.84$ , Table 3.10). However, total digesta and the solid digesta fraction reported on an as is basis ( $P = 0.043$  and  $P < 0.001$ , respectively) and DM basis ( $P = 0.013$  and  $P = 0.018$ , respectively) were greater for LE cows than the ME cows. The liquid fraction did not differ on an as is basis ( $P = 0.48$ ) but tended to have a greater quantity of DM for the LE cows than ME cows ( $P = 0.097$ ). Total ruminal digesta weight (as is basis) was greatest when fed the LQ diet and decreased as diet quality increased ( $P < 0.001$ ). The weight of the solid ruminal digesta fraction (as is basis) was greatest when fed the HQ and MQ diets, least for the MHQ diet, and the LQ diet did not differ from the other diets ( $P = 0.032$ ). The liquid fraction digesta weight when reported on an as is ( $P < 0.001$ ) and DM ( $P < 0.001$ ) basis were greatest when fed the LQ diet, intermediate for the MQ and MHQ diets, and least in the HQ diet. For both the total and solid rumen digesta weight (DM basis) the LQ and MQ diets were the greatest, the HQ diet was the least, and the MHQ diet did not differ ( $P < 0.001$  and  $P = 0.024$ , respectively).

The aNDFom pool size was greater for LE than ME cows ( $P = 0.028$ , Table 3.10) and did not differ between the MQ and LQ diets, the LQ and MHQ, and the MHQ and HQ diets, with HQ differing from the MQ and LQ diets, MHQ differing from MQ, and LQ differing from HQ ( $P < 0.001$ ). In the aNDFom fraction, the potentially digestible aNDFom did not differ between

**Table 3.10** Ruminal motility, digesta pool sizes, and NDF turnover for beef cows phenotypically classified as least-efficient (LE; n = 9) or most-efficient (ME; n = 9) and fed a high-quality (HQ), medium-high quality (MHQ), medium quality (MQ), or low quality (LQ) diet during 4 consecutive 28-d periods.

Variable	Phenotype		Diet				SEM <sup>1</sup>	P value		
	LE	ME	HQ	MHQ	MQ	LQ		Phenotype	Diet	Phenotype x diet
Ruminal motility										
Frequency, min <sup>-1</sup>	1.66	1.75	1.75	1.66	1.71	1.7	0.09	0.14	0.76	0.89
Contraction duration, s	52.5	50.2	48.8	51.9	53.3	51.4	3.5	0.35	0.59	0.84
Contraction time, s	18.9	18.1	17.5	19	19.1	18.3	0.99	0.11	0.11	0.96
Contraction height, mmHg	22.2	18.9	25.2 <sup>a</sup>	21.9 <sup>a</sup>	18.0 <sup>b</sup>	16.9 <sup>b</sup>	2.38	0.015	<0.001	0.27
Contraction area, mmHg×s	168	139	179 <sup>a</sup>	154 <sup>ab</sup>	144 <sup>b</sup>	136 <sup>b</sup>	19.6	0.009	0.036	0.56
Ruminal digesta, kg as is										
Total	76.61	72.64	63.43 <sup>d</sup>	71.77 <sup>c</sup>	78.55 <sup>b</sup>	84.75 <sup>a</sup>	2.72	0.043	<0.001	0.87
Solid fraction	32.61	29.88	32.69 <sup>a</sup>	28.98 <sup>b</sup>	32.66 <sup>a</sup>	30.66 <sup>ab</sup>	1.513	<0.001	0.032	0.95
Liquid fraction	44.03	42.75	30.74 <sup>c</sup>	42.79 <sup>b</sup>	45.89 <sup>b</sup>	54.16 <sup>a</sup>	2.657	0.48	<0.001	0.84

<sup>1</sup>Highest SEM for the 2-way interaction is presented.

<sup>2</sup>Potentially degradable aNDFom calculated as aNDFom – uNDF.

<sup>3</sup>Ruminal rate of aNDFom passage.

<sup>4</sup>Ruminal rate of aNDFom degradation.

<sup>a, b, c</sup>Means with different superscripts in a row are different ( $P < 0.05$ ).

**Table 3.10 (Continued)** Ruminal motility, digesta pool sizes, and NDF turnover for beef cows phenotypically classified as least-efficient (LE; n = 9) or most-efficient (ME; n = 9) and fed a high-quality (HQ), medium-high quality (MHQ), medium quality (MQ), or low quality (LQ) diet during 4 consecutive 28-d periods.

Variable	Phenotype		Diet				SEM <sup>1</sup>	P value		
	LE	ME	HQ	MHQ	MQ	LQ		Phenotype	Diet	Phenotype x diet
Ruminal digesta, kg DM										
Total	8.85	8.26	7.86 <sup>b</sup>	8.39 <sup>ab</sup>	9.01 <sup>a</sup>	8.95 <sup>a</sup>	0.346	0.013	<0.001	0.99
Solid fraction	7.97	7.42	7.20 <sup>b</sup>	7.53 <sup>ab</sup>	8.11 <sup>a</sup>	7.94 <sup>a</sup>	0.334	0.018	0.024	0.99
aNDFom	5.74	5.37	5.12 <sup>c</sup>	5.44 <sup>bc</sup>	5.93 <sup>a</sup>	5.74 <sup>ab</sup>	0.239	0.028	<0.001	0.99
PD aNDFom <sup>2</sup>	2.52	2.45	2.71 <sup>a</sup>	2.45 <sup>b</sup>	2.56 <sup>ab</sup>	2.20 <sup>c</sup>	0.131	0.42	<0.001	0.9
uNDF	3.22	2.92	2.41 <sup>c</sup>	2.99 <sup>b</sup>	3.37 <sup>a</sup>	3.54 <sup>a</sup>	0.15	<0.001	<0.001	0.84
Liquid fraction	0.89	0.83	0.66 <sup>c</sup>	0.86 <sup>b</sup>	0.90 <sup>b</sup>	1.02 <sup>a</sup>	0.046	0.097	<0.001	0.73
Ruminal digesta, % BW										
Total weight, kg as is	11.72	11.93	10.61 <sup>d</sup>	11.42 <sup>c</sup>	12.29 <sup>b</sup>	12.97 <sup>a</sup>	0.322	0.3	<0.001	0.74
Total weight, kg DM	1.36	1.37	1.32	1.34	1.41	1.38	0.053	0.86	0.23	0.99
aNDFom k <sub>p</sub> <sup>3</sup> , %/hr	2.89	3.11	3.00 <sup>b</sup>	3.52 <sup>a</sup>	2.90 <sup>b</sup>	2.57 <sup>c</sup>	0.163	0.047	<0.001	0.85
aNDFom k <sub>d</sub> <sup>4</sup> , %/hr	5.3	5.22	4.31 <sup>c</sup>	5.60 <sup>ab</sup>	5.25 <sup>b</sup>	5.88 <sup>a</sup>	0.347	0.69	<0.001	0.58

<sup>1</sup>Highest SEM for the 2-way interaction is presented.

<sup>2</sup>Potentially degradable aNDFom calculated as aNDFom – uNDF.

<sup>3</sup>Ruminal rate of aNDFom passage.

<sup>4</sup>Ruminal rate of aNDFom degradation.

<sup>a, b, c</sup>Means with different superscripts in a row are different ( $P < 0.05$ ).



phenotypes ( $P = 0.42$ ) but the uNDF pool size was greater for LE cows ( $P < 0.001$ ) than ME cows. The potentially digestible aNDFom pool size was greatest for cows fed the HQ diet, intermediate for the MHQ diet, and least when fed the LQ diet with MQ only differing from LQ ( $P < 0.001$ ). The ruminal uNDF fraction was greatest when fed the LQ and MQ diets, intermediate for the MHQ diet, and least when fed the HQ diet ( $P < 0.001$ ). The total ruminal digesta DM and weight on an as is basis, when presented as a % BW, did not differ between phenotypes or the phenotype  $\times$  diet interaction ( $P \geq 0.30$ ), and only differed among diets on an as is basis where ruminal digesta weight (% DM) was greatest when fed the LQ diet and decreased as diet quality increased ( $P < 0.001$ ). The rate of aNDFom passage and degradation were not affected by the phenotype  $\times$  diet interaction ( $P \geq 0.58$ ); however, ME cows had greater rate of aNDFom passage from the rumen than LE cows ( $P = 0.047$ ). In addition, the aNDFom passage rate was greatest when fed the MHQ diet, intermediate for the HQ and MQ diets, and least for the LQ diet ( $P < 0.001$ ). The rate of aNDFom degradation was not different between phenotypes ( $P = 0.69$ ) but was greatest when fed the LQ diet, intermediate for the MHQ diet, and least when fed the HQ diet with MHQ only differing from the HQ diet ( $P < 0.001$ ).

The daily fecal DM output was not affected by phenotype or the phenotype  $\times$  diet interaction ( $P \geq 0.62$ ) but was greatest when fed the MHQ and MQ diets and least for the LQ diet with HQ not differing from the other diets ( $P < 0.001$ , Table 3.11). Apparent total tract digestibility of DM, OM, CP, aNDFom, ADF, starch, and ether extract did not differ among phenotype or the phenotype  $\times$  diet interaction ( $P \geq 0.23$ ) but did differ between diets ( $P < 0.001$ ). The apparent total tract digestibility of DM and OM were greatest when fed the HQ and MHQ diets, intermediate for the MQ diet, and least when fed the LQ diet. Apparent total tract digestibility of CP was greatest when fed the MHQ and MQ diets and least for the HQ and LQ diets. The apparent total tract digestibility of aNDFom was greatest when fed the MHQ diet, intermediate when fed the LQ diet, and least when fed the HQ diet with the MHQ diet only differing from HQ. The apparent total tract digestibility of ADF was greatest when fed the MHQ diet, intermediate for the MQ and LQ diets, and least for the HQ diet. Starch total tract digestibility was greatest when fed the MHQ and LQ diets, intermediate for the MQ diet, and least in the HQ diet. Ether extract total tract digestibility only differed when fed the HQ diet, which was greater than the MHQ, MQ, and LQ diets.

**Table 3.11** Fecal output, apparent total tract digestibility, urine output, and nitrogen balance for beef cows phenotypically classified as least-efficient (LE; n = 9) or most-efficient (ME; n = 9) and fed a high-quality (HQ), medium-high quality (MHQ), medium quality (MQ), or low quality (LQ) diet during 4 consecutive 28-d periods.

Variable	Phenotype		Diet				SEM <sup>1</sup>	P value		
	LE	ME	HQ	MHQ	MQ	LQ		Phenotype	Diet	Phenotype × Diet
Fecal output, kg DM	4.56	4.50	4.56 <sup>ab</sup>	4.75 <sup>a</sup>	4.59 <sup>a</sup>	4.21 <sup>b</sup>	0.192	0.62	<0.001	0.85
Apparent total tract digestibility, %										
DM	64.62	64.95	67.86 <sup>a</sup>	67.52 <sup>a</sup>	63.07 <sup>b</sup>	60.69 <sup>c</sup>	0.826	0.55	<0.001	0.68
OM	66.44	66.71	69.34 <sup>a</sup>	69.10 <sup>a</sup>	65.12 <sup>b</sup>	62.73 <sup>c</sup>	0.780	0.61	<0.001	0.59
CP	65.23	64.82	63.79 <sup>b</sup>	66.72 <sup>a</sup>	66.05 <sup>a</sup>	63.55 <sup>b</sup>	0.912	0.53	<0.001	0.99
aNDFom	60.13	60.67	54.13 <sup>c</sup>	63.56 <sup>a</sup>	62.92 <sup>ab</sup>	61.01 <sup>b</sup>	1.043	0.43	<0.001	0.61
ADF	54.90	55.63	50.37 <sup>c</sup>	58.77 <sup>a</sup>	55.94 <sup>b</sup>	55.97 <sup>b</sup>	1.135	0.34	<0.001	0.63
Starch	96.00	96.51	93.33 <sup>c</sup>	97.74 <sup>a</sup>	96.02 <sup>b</sup>	97.93 <sup>a</sup>	0.833	0.36	<0.001	0.64
Ether extract	64.40	66.73	73.49 <sup>a</sup>	62.25 <sup>b</sup>	65.33 <sup>b</sup>	61.19 <sup>b</sup>	2.861	0.23	<0.001	0.46
Urine output, kg	10.93	10.30	13.31 <sup>a</sup>	10.39 <sup>b</sup>	9.97 <sup>b</sup>	8.80 <sup>c</sup>	0.564	0.086	<0.001	0.90
Urinary N output, g/d	92.3	87.4	96.0 <sup>a</sup>	87.3 <sup>b</sup>	90.0 <sup>ab</sup>	86.0 <sup>b</sup>	4.33	0.054	0.036	0.94
Urinary N, %	0.86	0.88	0.74 <sup>c</sup>	0.85 <sup>b</sup>	0.91 <sup>b</sup>	0.98 <sup>a</sup>	0.053	0.54	<0.001	0.99
Fecal N output, g/d	84.1	84.6	94.8 <sup>a</sup>	88.8 <sup>b</sup>	82.0 <sup>b</sup>	72.6 <sup>c</sup>	3.55	0.81	<0.001	0.91
Fecal N, %	1.85	1.88	2.08 <sup>a</sup>	1.85 <sup>b</sup>	1.79 <sup>c</sup>	1.73 <sup>d</sup>	0.032	0.095	<0.001	0.37
Total N output, % of intake	73.3	71.8	72.8 <sup>b</sup>	66.4 <sup>c</sup>	71.3 <sup>b</sup>	79.7 <sup>a</sup>	1.75	0.15	<0.001	0.98
N balance, g/d	66.0	68.9	71.2 <sup>b</sup>	88.9 <sup>a</sup>	69.3 <sup>b</sup>	40.4 <sup>c</sup>	4.84	0.30	<0.001	0.99

<sup>1</sup>Highest SEM for the 2-way interaction is presented.

<sup>a, b, c</sup>Means with different superscripts in a row are different ( $P < 0.05$ ).

## **3.4 Discussion**

### **3.4.1 Development of a Novel Efficiency Classification System for Beef Cattle**

Efficiency of mature breeding beef cows is more difficult to define than for growing cattle due to a lack of easily identified and measured variables that can be used to denote cow performance. Measures of cow efficiency usually relate to feed intake, sometimes measured during a growing phase and assumed to extend to later life stages of life or has been based on the performance of their calves prior to weaning (Arthur and Herd 2008; Callum et al. 2019). While evaluating feed consumption is logical considering that feed accounts for up to 41 to 60% production costs in Canada (Canfax Research Services 2020), such approaches rarely consider the assessment of output variables that drive reproductive success and profitability for cow-calf operations. In the present study, a novel ranking system was used to characterize efficiency of cows based on a relatively long-term assessments including body condition at calving, timing of calving within the calving season, and weaning weight of heifers and steers as a proportion of cow BW. Specifically, rump fat measured at calving was used as an indicator of the ability to maintain body condition over winter. Rump fat depth was used instead of body condition score given the quantitative nature of rump fat and that rump fat and body condition score are positively correlated and both indicative of body fat reserves (Looper et al. 2010). Past research has indicated that a greater body condition score at calving has been reported to hasten the post-partum interval (Osoro and Wright 1992; Hess et al. 2005). Rump fat also received the greatest weighting in the current scoring system as it was assumed to be a response directly impacted by nutrient intake and nutrient utilization of the cow under extensive winter grazing conditions.

The second efficiency criterion was calving date within the calving season. Cows that calve earlier in the current calving season tend to also calve earlier in the following year, are older when they are first diagnosed as open, stay in the herd longer, and wean calves that are older and heavier (MacGregor and Casey 1999; Cushman et al. 2013). Others have suggested to use calving interval as an indicator (Hess et al. 2005); however, use of calving interval prevents selection of cows within a single season. The third component of the efficiency selection was calf weaning weight when represented as a percent of the dams body weight. Given differing growth potential for heifer and steer calves (Minyard and Dinkel 1965), values were established independently for dams with heifer and steer calves. While distinct performance indicators were

used, it was recognized that these factors may be, at least, partially autocorrelated. As such, the ranking criteria were weighted to place greater emphasis on direct measures of the cow and lesser weighting on factors where management might confound outcomes. Despite the assumption that traits might be highly autocorrelated, the post-hoc correlation analysis did not yield such findings. We observed that calf weaning weight was negatively correlated with rump fat thickness; however, neither calf weaning weight and calving date, or rump fat thickness and calving date were correlated. The correlation between rump fat thickness and calf weaning weight was -0.248, and most of the correlation appears to come from year 2. There was also a correlation, although only 0.276, between year 1 and 2 total points, which suggests that the phenotypic selection is at least partially consistent from year to year. Due to the relatively low correlation however, at least two years of data is recommended to ensure more consistent and accurate selection.

The results of our combined efficiency ranking yielded cows that had greater rump fat, calved earlier in the calving season, and weaned heavier calves as a percentage of cow BW. For example, ME cows had 4.7 mm of rump fat at calving compared to the LE cows that had 3.5 mm. In addition to greater rump fat at calving, cows selected as ME had greater starting and ending rump fat than LE cows during the intensive portion of this study, regardless of the diet fed highlighting consistency in this measurement outcome. The thicker rump fat in the ME cows may have contributed to their greater reproductive fitness (Whitman 1974; D'Occhio et al. 2019). Correspondingly, ME cows calved earlier with a mean calving date on d 14 relative to the start of calving compared to a mean of 30 d for LE cows. Sex corrected calf weaning weight was also greater for ME cows than LE cows whether considered on a calf BW basis (510 and 464 kg, respectively) or calf BW represented as a percent of cow body weight (43.8 and 35.5%, respectively). Despite the greater weaning weights, calf birth weight did not differ between ME and LE cows further supporting that calves born earlier are heavier at the time of marketing (Cushman et al. 2013).

### **3.4.2 Lack of Interactions between the Efficiency Phenotype and Dietary Treatment**

In the present study we characterized DMI, ruminal fermentation characteristics, ruminal pool size and motility, and apparent digestibility for LE and ME cows using 4 consecutive 28-d periods where the quality of the diet progressively decreased. The use of multiple diets was to

determine whether phenotypic responses would differ by diet quality as previous studies have reported that diet may influence the efficiency ranking, at least for RFI (Durunna et al. 2011, 2012). We did not observe phenotype × dietary interactions for any of the primary response variables observed. The lack of interactions infer that long-term selection based on performance over 2 annual cycles can be used to identify cows that express a consistent phenotypic response, regardless of dietary characteristics.

### **3.4.3 Differences in Digestive Physiology among LE and ME Cows**

Measures of efficiency for growing cattle generally classify efficient cattle as those that gain more while consuming less feed (Koch et al. 1963; Arthur and Herd 2008); and it has been extrapolated to suggest that cows may have lesser feed requirements for maintenance functions (Herd and Arthur 2009). In the present study, ME cows did not have a lesser DMI than LE cows, as they consumed more when DMI was expressed as a percent of cow BW. Reis et al. (2021) calculated an energy efficiency index as the ratio of metabolizable energy required by the cow for maintenance, gestation, and lactation to calf weaning weight, where high efficiency cows had a lower energy efficiency index. Reis et al. (2021) also found that high and low efficiency cows did not differ for DMI despite high efficiency cows having lighter BW. High efficiency cows in this study were lighter at the start and end which is consistent with previous studies that found heavier cows had longer gestation lengths, younger calves at weaning, and had lower cumulative lifetime production (Snelling et al. 2019). The greater DMI (% BW) of the ME cows contradicts DMI observed when RFI is used to classify high and low efficient cattle, even on high-forage diets (Arthur and Herd 2008; Fitzsimons et al. 2014).

As could be expected, aNDFom intake followed patterns observed for DMI with no difference between ME and LE cows when reported as kg/d, but ME cows ate more aNDFom and uNDF as a percent of BW. The greater aNDFom, uNDF, and DM intake as a percent of cow BW for ME relative to LE cows indicates that metabolizable energy intake and potentially metabolizable protein supply may have been proportionally increased, especially when paired with the lack of apparent total tract digestibility differences.

In the present study, differences in DMI (% BW) between the ME and LE cows can partially be explained by differences in ruminal digesta mass and rate of passage. High efficiency cows had smaller total and solid ruminal digesta weights on both an as is and DM basis. This

smaller ruminal digesta mass, coupled with greater rates of aNDFom passage may have allowed the smaller ME cows to consume the same DMI as the LE cows when reported on a kg/d basis, but greater DMI as a percent of BW. It is possible that the lower rate of aNDFom passage without differences in degradation rate and digestibility may have limited DMI for the LE cows as a larger ruminal digesta volume and mass generally decrease DMI (Schettini et al. 1999; Whetsell et al. 2004). Supporting the previous theory, ME cows had smaller ruminal pools of aNDFom and uNDF, despite consuming the same amount of aNDFom (kg/d). Interestingly, the potentially degradable aNDFom pool size was not different between the ME and LE cows and sorting indices were not different, suggesting that ME cows may have a greater ability to selectively retain potentially degradable aNDFom in the rumen. Lund et al. (2007) reported that dairy cattle selectively retain digestible NDF in the rumen, most likely through differences in the distribution of digestible and indigestible NDF in the plant and differences in buoyancy and size of the plant components. It may be possible that the selective retention of potentially digestible aNDFom further contributed to enhanced energy intake supporting rump fat accretion. However, there were no differences in total tract digestibility of aNDFom or the ruminal aNDFom  $K_d$  despite greater ruminal aNDFom  $K_p$  for the ME cows. Okine and Mathison (1991) reported that the ruminal rate of passage also increased as nonlactating dairy cows fed above maintenance requirements. However, in the study by Okine et al. (1989) the fractional rate of NDF degradation decreased at increasing levels of maintenance requirements. Okine and Mathison (1991) further reported that greater NDF degradation occurred post-ruminally as cows were fed above maintenance requirements, which may explain why there was no difference in total tract digestibility of aNDFom despite the greater ruminal aNDFom  $K_p$  for ME cows in this study. The greater ruminal aNDFom passage rate may have increased microbial protein flow out of the rumen, contributing to a greater microbial efficiency for the ME than LE cows (Sniffen and Robinson 1987). Although speculative, the lower urinary N output of ME cows and numerically lower total N output, helps support the theory of greater microbial efficiency due to greater ruminal passage rate in the ME cows.

In addition to greater DM and aNDFom intake as a proportion of BW, it is likely that differences in performance between the ME and LE cows may be related to differences in their maintenance energy requirements. Using the equations in NASEM (2016) the  $NE_m$  balance of the ME and LE cows could be calculated for each diet using mean BW and DMI, and the  $NE_m$  of

the diet. The calculated  $NE_m$  balance was 15.88, 11.00, 6.02, and 3.09 Mcal for the ME cows, and 14.58, 10.39, 5.82, and 2.79 Mcal for LE cows in the HQ, MHQ, MQ, and LQ diets, respectively. While not evaluated statistically, these data suggest that there was potential for a greater maintenance energy balance for the ME cows given the lesser BW but similar DMI and total tract digestibility when compared to LE cows.

Ruminal motility is an important factor regulating the mixing of digesta within the rumen and passage of digesta out of the rumen (Okine et al. 2011). High-efficiency cows had lower amplitude and contraction peak area than LE cows. The ME cows in this study had a smaller ruminal digesta mass, and hence less ruminal distention which plays an important role in the regulation of ruminal motility (Dado and Allen 1995). Deswysen et al. (1987) suggested that an increase in strong ruminal contractions may be indicative of weaker or less efficient reticular contractions. Strong primary contractions of the rumen are involved in the movement of feed to the cranial region of the reticulo-rumen which may limit consumption of new feed. Thiago et al. (1992) reported that despite greater intensity of ruminal contractions on a hay vs. silage diet, the fractional rate of passage from the rumen was not greater further suggesting factors beyond ruminal contraction frequency and amplitude may play a role in particle passage out of the rumen. While contractions are indicative of mixing in the rumen, we did not assess rumination activity, size of the omasal orifice, or fibrous particles in the feces and as such, are unable to conclude whether reticular motility or other factors regulating ruminal NDF residence time in the rumen were causative for the change in aNDFom turnover.

Despite ME cows having a greater ruminal passage rate for aNDFom and DMI (% BW), they did not differ in the rate of aNDFom degradation or for total-tract digestibility of DM, OM, CP, aNDFom, ADF, starch, or ether extract relative to LE cows. This further suggests that greater DMI as a function of BW rather than greater digestibility may be the primary factor resulting in greater fat thickness of ME cows. However, ME cows had a greater ruminal rate of passage, but no difference in ruminal rate of NDF degradation or total tract digestibility. That said, the aNDFom turnover model evaluated (Linton and Allen 2008) only considers potentially degradable aNDFom and undegradable aNDFom using 240 h of in vitro incubation to assess these values. It may be possible LE and ME may have differed in the passage of potentially digestible aNDFom. For example, the CNCPS model (Raffrenato and van Amburgh 2011) characterizes aNDFom into rapidly digestible, potentially digestible, and undigested aNDFom

pools. A shift for the passage rate of individual pools could facilitate the lack of difference for aNDFom digestibility between ME and LE while still allowing for greater rates of aNDFom passage out of the rumen. Alternatively, greater passage of potentially degradable aNDFom could suggest greater post-ruminal digestion for ME than LE cows. Okine and Mathison (1991) reported that with increasing DMI, ruminal retention time decreased, but lower digestive tract retention time increased resulting in an increase in total tract NDF digestibility. Okine and Mathison (1991) further suggested that as DMI increases, the digestion of feed post-ruminally becomes more important. In the present study we were unable to assess site of digestion and other than measuring apparent total tract digestibility, did not evaluate fecal characteristics to determine if large intestinal fermentation may have differed. Other studies that have compared digestibility responses among efficiency groups have found conflicting results. De La Torre et al. (2019) compared high- and low-RFI beef cows and found that low-RFI cows had greater DM and OM digestibility but were not different for NDF digestibility. Johnson et al. (2019) reported greater DM, OM, and NDF digestibility in low-RFI growing beef heifers, while McDonnell et al. (2016) only observed differences in OM digestibility. Other studies have found no differences in diet digestibility between RFI classifications (Cruz et al. 2010; Lawrence et al. 2011) or have attributed differences in digestibility to be related to the lesser DMI rather than efficiency classification (Cantalapiedra-Hijar et al. 2018). Although ME cows had a greater DMI (% BW) and ruminal aNDFom  $k_p$ , total tract digestibility did not differ between ME and LE cows, suggesting that diet digestibility is not likely to be affected by the efficiency classification used in this study.

Ruminal fermentation did not differ between efficiency classifications with only the proportion of isovalerate being affected by the phenotype  $\times$  diet interaction. High efficiency cows had greater proportions of isovalerate when fed the HQ diet but did not differ from LE cows when fed the MHQ, MQ, or LQ diets. McDonnell et al. (2016) also saw greater proportions of isovalerate in low-RFI growing heifers fed either grass silage, ryegrass pasture, or a 70:30 TMR of corn silage: concentrate. The differences in isovalerate proportions were relatively small and it is not clear how the proportion of isovalerate may help explain outcomes given that rates of SCFA production and clearance, and the ruminal volume were not known. Studies comparing ruminal fermentation among RFI groups have reported inconsistent results. Despite the inconsistent results from RFI in relation to ruminal fermentation patterns, the results from our



study were supported as there were no differences for the ruminal rate of degradation of aNDFom or apparent total tract digestibility of any of the nutrients evaluated.

#### **3.4.4 Effects of Dietary Composition**

In the present study, cattle were fed common diets within a period and a clear dietary sequence from those expected to have high digestibility to those with low digestibility were imposed. As such, diet and period of the study are inherently confounded. That said, as could be expected, DMI was affected by diet. Given that aNDFom and uNDF intake were least for HQ, greatest for MHQ, and decreased from HQ to MQ and that the ruminal uNDF pool size increased as the expected fermentability of the diet decreased, it is likely that metabolic regulators of intake may have limited DMI when fed HQ and that physical fill may have regulated intakes for all other diets (Allen et al. 2009).

Ruminal fermentation patterns followed expected outcomes for a forage-based diet with lowest ruminal pH when cows were fed the HQ diet with pH generally increasing as diets were formulated to be less digestible. Corresponding to ruminal pH changes, the molar proportions of SCFA decreased as diet quality decreased, likely indicative of reduced rates and extents of ruminal fermentation and that these diets increased the ruminal liquid pool size that may have diluted the SCFA concentration. The molar proportions of acetate and propionate increased and decreased, respectively, as diet quality decreased yielding results consistent with previous studies (Sutton et al. 2003; Penner et al. 2009; Walsh et al. 2009). As diet quality decreased molar proportions of butyrate, isobutyrate, valerate, isovalerate, and caproate decreased, in agreement with Walsh et al. (2009) who reported similar results when increasing the ratio of barley straw to grain in silage.

Despite the greatest DMI and smallest ruminal digesta mass, the ruminal rate of NDF passage was less than the MHQ diet and similar to the MQ diet. This may be due to the assumption that the rate of uNDF passage is equivalent to the rate of NDF passage out of the rumen. The uNDF may have been associated with more large particles in the HQ diet which would cause them to have a greater retention time in the rumen and lower the  $K_d$ . The ruminal rate of degradation of NDF was also the least in the HQ diet; likely a result of the greater DMI and smaller ruminal digesta mass. Dry matter intake was likely regulated by rumen fill in both the MQ and LQ diets because they had the smallest intakes but greatest total and solid DM

ruminal digesta masses. This suggests that about 9 kg of DM is the maximum mass that the cows in this study could hold in their rumen. Because of this slow ruminal turnover, cows fed the LQ diet had the slowest ruminal rate of passage and greatest ruminal rate of NDF degradation from the long ruminal retention time. The greater  $K_d$  of cows fed the MQ diet than the HQ diet is likely a result of lesser DMI and greater ruminal digesta mass.

Feed sorting was observed in almost every fraction in all four diets, with only the < 4 mm fraction in the HQ diet and the 4-8 mm fraction in the MHQ diet not being sorted. In general, as diet quality decreased, cows sorted more strongly against long particles and for finer particles. In the HQ diet cows sorted for > 19 mm particles and did not sort the < 4 mm particles, as opposed to the MHQ diet where they sorted against both > 19 mm and < 4 mm particles. The minimal sorting in both the HQ and MHQ diets may be because the diets were lower in DM, which can help minimize sorting (Miller-Cushon and DeVries 2017). The MQ and LQ diets both had significant sorting against > 19 mm particles and sorting for < 19 mm particles. The MQ and LQ diets were both greater in aNDFom and lesser in energy than the MHQ and HQ diets, and the cows were likely sorting for the particles with greater energy available. Dairy cows have been shown to preferentially sort for finer particles which have greater proportions of energy and lower NDF, which was also observed in the beef cattle fed the MQ and LQ diets in this study (Lawrence et al. 2011).

The only measures of ruminal motility that differed among diets were ruminal contraction amplitude and contraction area, but it should be noted that ruminal contraction amplitude and area are inherently autocorrelated. The ruminal contraction amplitude and area were greatest for the HQ and MHQ diet, suggesting that contraction height and peak area are driven by DMI rather than ruminal digesta weight. We speculate that contraction characteristics such as amplitude and contraction duration may be affected by ruminal digesta mass and the insulating effect it may have to alter the contraction signal to the pressure transducer. Future research is needed to quantify the impact of contraction force and frequency on mixing of ruminal digesta differing in weight and dry matter concentration.

Dry matter and OM apparent total tract digestibility both decreased as diet quality decreased, as was expected (Jung and Allen 1995). However, aNDFom and ADF digestibility only followed this trend when fed the MHQ, MQ, and LQ diets. When cows were fed the HQ diet aNDFom and ADF digestibility were less than the MHQ, MQ, and LQ diets. Dry matter

intake, but also ruminal aNDFom Kp were greatest when cows were fed the HQ diet suggesting that the high turnover rate when fed the HQ diet may have limited aNDFom and ADF digestibility.

### **3.4.5 Conclusion**

A phenotypic selection utilizing cow rump fat at calving, calving date, and calf weaning weight allowed for the ranking of efficient and inefficient cows in a herd over two years. High efficiency cows weighed less, had thicker rump fat, calved earlier, and had heavier calf weaning weights than LE cows. In addition to greater performance under extensive management, the ME cows had consistent responses across diets of varying forage quality as there were no phenotype × diet interactions. High efficiency cows may have had greater energy retention, considering the ME cows were lighter over the course of the study and had similar DMI and total-tract digestibility suggesting more energy was partitioned to body condition, reproduction, and lactation. The ability of the ME cows to consume more DMI as a percent of BW was driven by greater ruminal aNDFom passage rate, smaller ruminal digesta mass, and potentially by differences in ruminal motility.

## CHAPTER 4: GENERAL DISCUSSION

### 4.1 Importance of feed efficiency for cow-calf producers

Feed costs make up 40 to 60% of a cow-calf producer's total costs, with much of the cost coming from the winter feeding of forages (Canfax Research Services 2020; Boyda 2022). The general goal of cow-calf operations is to utilize low-cost forages and pastures unsuitable for crop production with minimal supplementation to maintain cow condition and produce weaned calves. The majority of revenue in a cow-calf operation comes from the sale of weaned calves (Boyda 2022). Increasing the utilization of forages to produce weaned calves can help increase the profits of a cow-calf operation by reducing feeding cost. The GOLD indicators are a common benchmark used which stands for the growth of calves (total pounds weaned / # of calves weaned), open cows (# open cows and heifers / # exposed females), length of calving period (days from first to last calf born), and death loss of calves (# dead calves / live births) (Beef Cattle Research Council 2022b). Utilizing modified GOLD indicators, individual phenotypic traits were identified that likely related to more productive cows. The goal was to select cows that would thrive under extensive winter and summer management based on phenotypic traits that were easy to measure and translated into cows that utilized forage more efficiently to produce pounds of weaned calves. In the present study, backfat thickness at calving, day of calving within the calving season, and the sex-dependent weight of the calf as a function of weaning weight were used to classify cows. All variables except for backfat thickness, are easily measured and BCS could be used as a proxy for backfat thickness. We also utilized a weighted ranking system to prioritize variables that were influenced most by the cow. To my knowledge, this is the first time such a system has been developed and implemented.

### 4.2 Phenotypic selection of efficient cattle compared to other measures of efficiency

There are several ways to measure and classify feed efficiency in cattle with the gain-to-feed ratio (G:F), Kleiber ratio (Kleiber 1961), and residual feed intake (RFI; Koch et al. 1963) being some of the most common. The G:F ratio is commonly used because body weight gain and feed intake can both be easily measured, especially in growing cattle, at least at a pen level. Gain-to-feed is not appropriate for measuring cow efficiency; however, as cows are not in a growth phase. Gain-to-feed is a direct measure of revenue and costs in growing cattle, unlike in mature cows where revenue is from the lifetime sale of their weaned calves (Boyda 2022).

Moreover, individual feed intake is difficult, inaccurate, and expensive to measure under grazing systems. Unlike G:F, the Kleiber ratio does not use feed intake to calculate efficiency, rather it uses average daily gain and metabolic body weight (Tedeschi et al. 2006). The Kleiber ratio is useful because it doesn't require individual feed intake and measures the amount of BW gain relative to maintenance energy, represented as metabolic BW. However, like G:F, cows are not in a growth and rely heavily on maintenance energy functions, making the Kleiber ratio inappropriate for measuring cow efficiency.

Koch et al. (1963) first suggested RFI as a measure of feed efficiency. Residual feed intake is calculated as the difference between actual feed intake and the average observed feed intake with corrections for body weight and weight change (Arthur and Herd 2008). The expected feed intake is most commonly calculated through regression of feed intake based on test period metabolic BW and average daily gain or it can be calculated from equations based on feeding standards (Arthur and Herd 2008). A lower RFI is suggested to represent a more efficient animal as they are eating less than would be expected for their size and growth. Residual feed intake has the benefit of being adjusted for BW, gain, and more recently for backfat which makes it useful for animals that are not growing, like cows in a cow-calf operation (Basarab et al. 2011a). However, RFI has challenges limiting its adoption as a measure of cow efficiency. As with G:F, individual feed intake is difficult and expensive to measure under grazing systems. In addition, cows are expected to perform over a wide variety of feeding, management, environmental, and physiological conditions, and the RFI ranking has been shown to be inconsistent across diets and even over time when fed the same diet (Durunna et al. 2011, 2012). Finally, the measurement approach ignores the potential for cows to sort components of the diet such that dietary composition might differ among cows fed from the same bunk. Due to these challenges, a method to evaluate efficiency that was easy to measure, applicable to cow-calf operations, and did not require individual feed intakes was developed. Consistency among periods and across a variety of forage-based diets was assessed and the lack of interaction among efficiency classification and diet highlight that the approach used identifies high-efficiency cows that perform better under a wide range of dietary conditions. The lack of dietary effect on responses for low and high efficient cows differentiates this efficiency ranking system from G:F, the KR, and RFI approaches. Most importantly, the measurements required are cheap, easy, and

practical providing a useful tool for producers to use in the selection of efficient and inefficient cattle in their herd.

#### **4.3 Practical applications and management required for the phenotypic selection of efficient cows**

Phenotypic selection can be a useful tool for producers, not just for identifying efficient cows, but also in the selection of cows to be kept or culled in a herd. Local adaptation to conditions is critical for success and during difficult years where producers are looking at reducing herd numbers, this selection could be especially useful in identifying the least efficient cows that could be culled. Results from this study show that while there was no difference in feed costs between ME and LE (13.0 and 13.0 kg, respectively) cows, the ME cows weaned calves that were 20 kg heavier. Using the average price of weaned calves from 2016 to 2020 ( $\$0.91 \text{ kg}^{-1}$ ) ME cows had a  $\$18.24 \text{ yr}^{-1}$  greater profit than LE cows (Boyda 2022). In addition to greater yearly profit, the greater rump fat and earlier calving date suggests that the ME cows may also have greater longevity, further increasing lifetime profitability from the ME cows (Osoro and Wright 1992; Cushman et al. 2013). Due to the relatively easy measurements required, the selection can be made quickly and easy. With that said, one of the greatest barriers to the adoption of this selection is the accurate collection, recording, and analysis of the measurements needed by producers. Record keeping is a recommended practice by the Beef Cattle Research Council (2022a) to help with management decisions to provide an overview of the operation, compare against benchmarks, and to improve profitability. The first selection criteria of the selection applied is calving date that should already be a record found in most pocket calving books and is an important component of third-party age verification programs such as that used by Verified Beef Production Plus (Canadian Cattlemen's Association n.d.). The second criteria for selection was rump fat at calving. Rump fat may be impractical for producers; however, there is a reasonable relationship between rump fat and BCS suggesting that BCS could replace rump fat as a more feasible measurement for producers to evaluate fat reserves and the long-term nutritional status (Looper et al. 2010). In western Canada, 77% of producers surveyed measured BCS using some method of assessment; however, only 13% used hands-on BCS scoring rather than visual evaluation ("Western Canadian Cow-Calf Survey" 2017) and it is not clear how many of those producers recorded BCS or used it to evaluate individual performance rather than

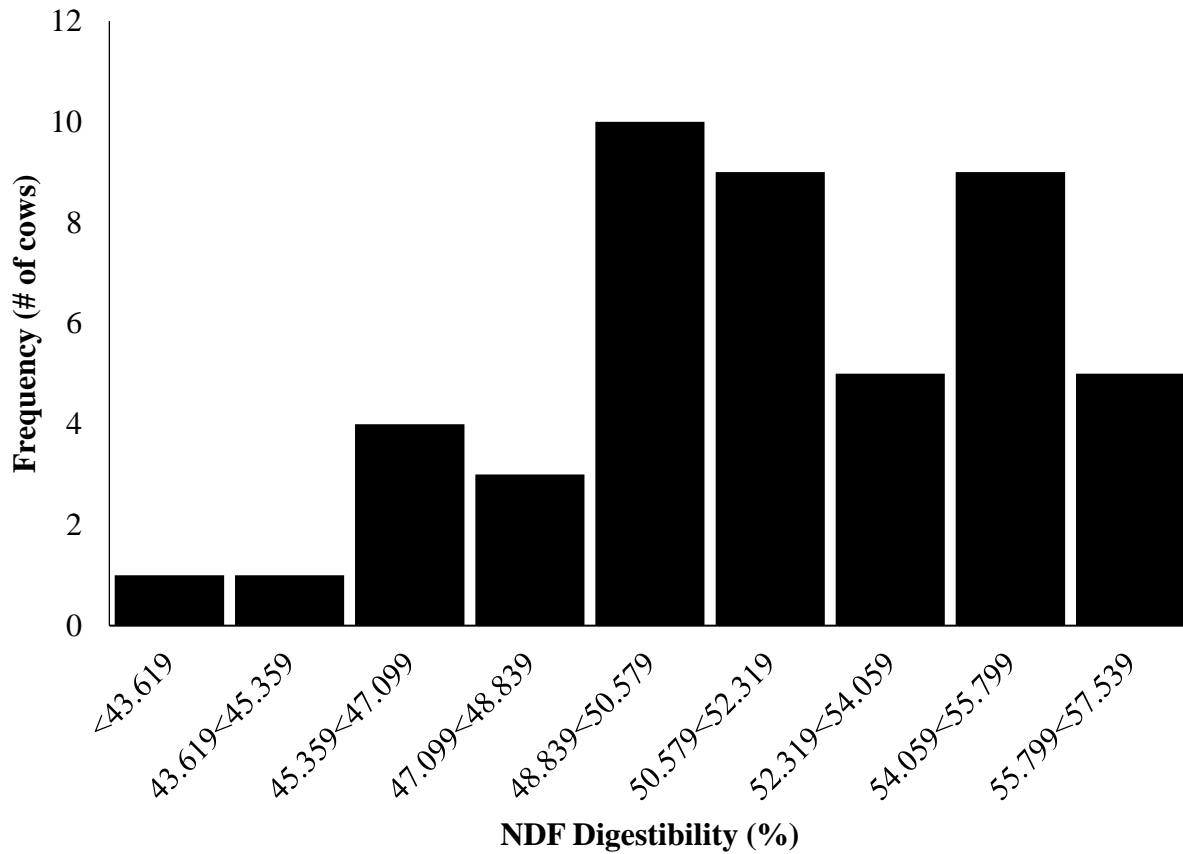
a herd-level indicator. The final measurement required for the selection developed in this thesis was calf weaning weight corrected for cow BW and sex, which requires both calf and dam body weights at weaning. Although none of the measurements required are particularly difficult or expensive to gather, the “Western Canadian Cow-Calf Survey” (2017) reported that most producers will not have all 3 measurements currently available from past years.

The results from the research conducted indicate that measurement of these variables should be extended for more than one production year. Two years of production data was originally used to ensure that the cows that were selected were consistent across years and that year was not an outlier. Although there was a significant correlation between a cow’s points in both years, the correlation coefficient was low. Despite these barriers, good record keeping is already a recommended practice, and the measurements required are not novel or difficult to perform, which should allow our selection to be useful to producers two years after adoption at the latest. While record keeping is commonly promoted, the results of this study suggest an additional step is needed to make use of those records. As such, development of easy to use data recording and management software programs could help advance the efficiency of the cow herd based on the imposed management within a farm.

#### **4.4 Using NIR estimated NDF digestibility as a secondary selection method**

While not reported in Chapter 3, cows were also separated into high and low NDF digestibility classifications. Calves from the selected ME and LE cows were weaned, and cows were randomly placed into 1 of 3 pens at the Livestock and Forage Center of Excellence (Clavet, SK, Canada). Following a 7-d acclimation period, cows were adapted to a diet consisting of 85.61% barley silage, 9.47% oat hulls, 4.08% barley straw, 0.73% limestone, and 0.11% calcium on a DM basis and fed for 28 d. Feed ingredients were sampled weekly to determine DM concentration to ensure that dietary ingredient inclusion rates matched the DM formulation. Cow body weight was recorded on two consecutive days at the start and end of the study.

Fecal grab samples were collected by observing cows in their pens and collecting fresh fecal samples over 3 days (d 26, 27, and 28). On d 28, cows that did not yield a sufficient sample quantity or had a missed daily sample were restrained in a chute, and feces were collected by rectal palpation. The fecal samples were composited equally on an as is basis to yield a 1000 g sample. Fecal samples were dried in a forced-air oven at 55°C for 72 h. Dried samples were



**Figure 4.1** Histogram of the NDF digestibility of 49 beef cows in a pen feeding experiment on a high-forage diet estimated using NIR through previously created calibrations (Jancewicz et al. 2017).



ground using a Retsch ZM 200 grinder (Haan, NRW, Germany) to pass through a sieve with 1-mm aperture openings. The ground fecal samples scanned using a near-infrared spectrometer (NIR) (Unity Spectrastar XT NIR, Unity Scientific, Milford, MA, USA) and NDF digestibility was predicted based on previously established calibrations (Jancewicz et al. 2017). Utilizing the NDF digestibility estimates (Figure 4.1), the 10 cows with the greatest and the 10 cows with the least phenotypic classification and the greatest (HD) and least (LD) NDF digestibility were selected. Ultimately, the NDF digestibility selection was not used as a fixed effect in the statistical analysis because the NDF digestibility of the HD and LD cows did not differ (60.21 and 60.67%, respectively;  $P = 0.53$ ) when they were moved to the metabolism portion of the study. In the initial NDF digestibility selection the NDF digestibility was estimated using NIR, however, the calibration used was created using diets that were much lower in forage and NDF concentrations that likely diminished the accuracy in predicting the digestibility responses for the cows in the present study.

#### **4.5 Future directions of this research**

The phenotypic selection that was used to select efficient cattle in this study was novel and demonstrated that utilizing phenotypic traits is a viable method of selecting more productive cows in a herd. However, because of its novelty, there are more questions to be answered. Although the ME cows were more efficient during both the extensive and metabolism portion of the study, the selection should be verified, and the selection weightings may need to be adjusted. A larger and longer-term case study should be conducted to compare how use of the selection criteria may influence revenue and feed cost arising from cow-calf operations. In addition, there is not available information on whether calves from more efficient cows are likely to express a similar response when maintained as replacements in the cow herd or when fed to finish. Future research is needed to determine whether selection for cow-herd level efficiency affects performance of progeny.

One of the challenges with the selection method developed in this thesis is that it takes at least two years of calving data to begin ranking cows. This indicates that heifers cannot be selected with this method. A potential solution would be to determine the heritability of the ranking, and whether replacement heifers can be selected based on their dam's ranking. Another barrier to adoption is the collection, recording, and analysis of the data needed. The creation and

distribution of a calculator to help with using the weighting and ranking system would help to minimize the time and effort needed to analyze data. The traits used in the selection may also be refined further. Because the traits that were used may be auto correlated, although not in this study, all the traits may not be required in the selection. Overall, the most important step in advancing this research is to ensure that the data and selection technique is communicated with producers so they can begin implementing this selection on their own farm.

## **CHAPTER 5: CONCLUSION**

Feed efficiency, especially of a mature breeding cow, is difficult to measure and assess. However, this research has identified an alternative way of measuring and selecting for efficiency in beef cows by utilizing phenotypic traits that are correlated with productivity of the beef cow. A greater cow rump fat at calving, earlier calving date, and heavier calf weaning weight as a percent of cow body weight were associated with more efficient cows and was consistent over time and among varying diets. This research provides the opportunity for more rigorous research to be done on this selection, its heritability, and relationship to calf performance, both in a finishing and replacement heifer program. This research could be applied immediately to cow-calf producers as a means of identifying the most and least efficient cows in their herd to improve productivity, profitability, and sustainability.

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