Identification of feed intake traits related to beef reproductive improvement

by

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A thesis submitted in partial fulfillment of the requirements for the degree of

Doctor of Philosophy

in
Animal Science

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University of Alberta

ABSTRACT

Reproductive efficiency in the Western Canadian beef cow herd has not improved over the past 3 decades, despite consistent and measurable improvement in several related areas of production. The general objective of this thesis was to evaluate the relationships between early-observation traits (feeding behaviour), weight change, and reproductive efficiency in beef cows. Estimates of total dry matter intake and the relationship between residual feed intake (adjusted for body composition; RFI_{FAT}) observed in heifers and mature cows were also evaluated as traits of interest and use to the Canadian beef industry. Chapters 3 and 4 investigated the relationship between feeding behaviours and reproductive efficiency and provided phenotypic and genetic correlations that may be of use in selecting heifers with greater reproductive potential if those heifers have feeding behaviours reported. Feeding behaviour and reproductive efficiency were both correlated with dry matter intake; feeding behaviours that promote dry matter intake may be useful in the identification of heifers with greater reproductive potential. Chapter 5 evaluates the usefulness of tracking cow weights over time and the usefulness of comparing cow weights to an idealized growth curve estimation. Generally, cows that gained weight over time were more likely to be culled for reproductive failure, and the same was true for cows that were heavier than their estimated body weight. Producers may be able to use weight-monitoring technology currently available and in development to identify cows that abort their calves after a positive pregnancy evaluation and remove them from their herd at a time when feed resources are expensive. Chapter 6 was a comprehensive and unique estimation of cow dry matter intake over time, including energy estimates based on birth, weaning, residual feed intake tests as a heifer and as a cow, and subsequent calving events with associated energy expenditures for milk production. These estimates were compared to genomic retained heterozygosity, breed composition, and winter-feeding environment to evaluate the effects of those variables on dry matter intake predictions. Chapter 7 investigated the relationship between heifer residual feed intake and residual feed intake observed in the same animals as mature cows. Residual feed intake in heifers can be used to select cows that maintain a proportion of their efficiency observed as heifers, and ultimately provides evidence that the selection of feed-efficient heifer calves as replacement animals should result in a more efficient mature cow herd.

This thesis provided evidence to support the selection of heifer replacements using feeding behaviours observed during a feed intake test, the use of weight monitoring technology to identify cows that may have had reproductive issues. This thesis also provided some of the first estimates of dry matter intake over the course of the production cycle in a large number of animals under normal production environments and provided estimates of the relationship between heifer and cow residual feed intake.

PREFACE

This thesis is an original work by Cameron Alexander Olson.

All animals were maintained at the Agriculture and Agri-Food Canada Lacombe Research and Development Centre (LRDC, Lacombe, AB, Canada) and the University of Alberta's Roy Berg Kinsella Research Ranch and were cared for according to the guidelines of the Canadian Council on Animal Care (CCAC 1993).

Chapter 3 of this thesis has been published as:

Olson, C. A., C. Li, H. C. Block, L. McKeown, and J. A. Basarab. 2020. Phenotypic and genetic correlations between feeding behaviours and feed efficiency in crossbred beef replacement females. Can. J. Anim. Sci. doi: 10.1139/CJAS-2019-0212.

Chapter 4 of this thesis has been published as:

Olson, C. A., C. Li, H. Block, L. McKeown, and J. A. Basarab. 2021. Phenotypic and genetic correlations of beef replacement heifer feeding behaviour, feed intake and feed efficiency with cow performance and lifetime productivity. J. Anim. Breed. Genet. 138:300-313. doi: 10.1111/jbg.12522.

This thesis follows the style of the Journal of Animal Science with the exception of Chapter 4, which is in the style of the Journal of Animal Breeding and Genetics.

DEDICATION

Gloria in excelsis Deo

[1]Bless the Lord, O my soul!
O Lord my God, you are very great!
You are clothed with splendor and majesty,
[2]covering yourself with light as with a garment,
stretching out the heavens like a tent.
[3]He lays the beams of his chambers on the waters;
he makes the clouds his chariot;
he rides on the wings of the wind;
[4]he makes his messengers winds,
his ministers a flaming fire.
[5]He set the earth on its foundations,
so that it should never be moved.
[6]You covered it with the deep as with a garment;
the waters stood above the mountains.
[7]At your rebuke they fled;
at the sound of your thunder they took to flight.
[8]The mountains rose, the valleys sank down
to the place that you appointed for them.
[9]You set a boundary that they may not pass,
so that they might not again cover the earth.
[10]You make springs gush forth in the valleys;
they flow between the hills;
[11]they give drink to every beast of the field;
the wild donkeys quench their thirst.
[12]Beside them the birds of the heavens dwell;
they sing among the branches.
[13]From your lofty abode you water the mountains;
the earth is satisfied with the fruit of your work.
[14]You cause the grass to grow for the livestock
and plants for man to cultivate,
that he may bring forth food from the earth
[15]and wine to gladden the heart of man,
oil to make his face shine
and bread to strengthen man's heart.
[16]The trees of the Lord are watered abundantly,
the cedars of Lebanon that he planted.
[17]In them the birds build their nests;
the stork has her home in the fir trees.
[18]The high mountains are for the wild goats;

the rocks are a refuge for the rock badgers.
[19]He made the moon to mark the seasons;
the sun knows its time for setting.
[20]You make darkness, and it is night,
when all the beasts of the forest creep about.
[21]The young lions roar for their prey,
seeking their food from God.
[22]When the sun rises, they steal away
and lie down in their dens.
[23]Man goes out to his work
and to his labor until the evening.
[24]O Lord, how manifold are your works!
In wisdom have you made them all;
the earth is full of your creatures.
[25]Here is the sea, great and wide,
which teems with creatures innumerable,
living things both small and great.
[26]There go the ships,
and Leviathan, which you formed to play in it.
[27]These all look to you,
to give them their food in due season.
[28]When you give it to them, they gather it up;
when you open your hand, they are filled with good things.
[29]When you hide your face, they are dismayed;
when you take away their breath, they die
and return to their dust.
[30]When you send forth your Spirit, they are created,
and you renew the face of the ground.
[31]May the glory of the Lord endure forever;
may the Lord rejoice in his works,
[32]who looks on the earth and it trembles,
who touches the mountains and they smoke!
[33]I will sing to the Lord as long as I live;
I will sing praise to my God while I have being.
[34]May my meditation be pleasing to him,
for I rejoice in the Lord.
[35]Let sinners be consumed from the earth,
and let the wicked be no more!
Bless the Lord, O my soul!
Praise the Lord!
Psalm 104, English Standard Version

ACKNOWLEDGEMENTS

Writing this thesis has simultaneously been a great joy and a great frustration. Joy in that I was constantly learning and bettering my understanding of how beef cattle were created and for what purpose; frustration in that I never quite seemed to get it all figured out. I look forward to many years of straining to understand everything that God has packed into these marvelous animals.

In the highs and the lows, I gratefully thank my wife for her undying support. I also extend my sincere gratitude to my committee, Drs. Basarab, Li, and Guan, for their guidance, support, and correction over the last 4 years. You have all helped to channel and focus my passion for beef cattle into a useful expenditure of energy and time. I also wish to acknowledge the time and insights of Dr. Hushton Block and Dr. David Riley, who provided their knowledge free of charge over the last 4 years.

TABLE OF CONTENTS

Page

LIST OF FIGURES

LIST OF TABLES

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This work was supervised by a doctoral committee consisting of Dr. John A. Basarab, Head of Beef Operations, Livestock Gentec (co-supervisor), Dr. Changxi Li, Agriculture and Agri-Food Canada Professor and Chair of Bovine Genomics, Department of Agriculture, Food & Nutritional Science, University of Alberta (co-supervisor), and Dr. Le Luo Guan, Professor and Associate Dean of the Faculty of Agricultural, Life and Environmental Science, University of Alberta.

The data analyzed for all chapters was made available by Dr. Basarab and Agriculture and Agri-Food Canada, Lacombe Research and Development Centre and the Roy Berg Kinsella Research Station. The analyses in Chapter 5 & 6 were conducted with the significant aid and supervision of Dr. Hushton C. Block, Agriculture and Agri-Food Canada Beef Production Systems Research Scientist, Lacombe, AB.

All other work conducted for this thesis was completed by the student independently.

Funding Sources

Graduate study was supported by a fellowship from the University of Alberta. I gratefully acknowledge in-kind contributions of animals and facilities received from Agriculture and Agri-Food Canada and Alberta Agriculture and Forestry. Technical support at the Lacombe Research and Development Centre and the Roy Berg Kinsella Research Station is also acknowledged, with special thanks to Cletus Sehn and Vernon Erickson and their staff for animal care and management.

This work was also made possible by the financial support of the Beef Cattle Research Council and the Agriculture and Agri-Food Canada Beef Cluster under Grant Number ASC-01-FDE.06.17. The contents are solely the responsibility of the author(s) and do not necessarily represent the official views of the Beef Cattle Research Council and the Agriculture and Agri-Food Canada Beef Cluster or the University of Alberta.

1. INTRODUCTION

The purpose of beef cattle husbandry is the production of beef, and producers in Western Canada should endeavour to raise cattle with economic, environmental, and social sustainability in mind. As the global population continues to expand and the appetite of the growing middle classes turns increasingly to beef, beef producers in Western Canada are in an excellent position to supply the expected demand for beef. Increasing competition for resources, including water, land, and feed commodities, means that producers must continue to strive to improve the efficiency of beef production. In this regard, the beef-finishing sector has enjoyed considerable investment in research and a large increase in knowledge, which has allowed that sector to considerably improve animal performance and efficiency. However, less attention has been given to the beef cow and her reproductive and feed efficiency, despite the well-understood fact that the cow herd accounts for approximately 72% of the feed consumed by beef cattle from birth to slaughter (Jenkins and Ferrell, 2002), and the fact that measures of reproductive efficiency have not improved in over three decades of recording (Audit, 2001; WBDC, 2015; WCCCS, 2017).

The lack of improvement in reproductive efficiency in beef cattle is largely due to very low heritability in most measures of reproduction (Berry et al., 2014). However, because of low heritability, beef producers should be able to exert considerable control over reproductive outcomes through management. Managerial control in beef cattle reproduction is challenging, especially when compared to other livestock, due largely to the extensive nature of beef cattle rearing in North America. Where dairy cattle are typically housed and handled in barns for large portions of the year, beef cattle spend as much time on large grazing pastures as possible and may only be handled by producers 1-2 times per year. As a result, the modern tools available to dairy, swine, and poultry producers like artificial insemination, embryo transfer, and hands-on practices like human involvement in parturition are unavailable to most beef cows in North America. In a survey by the BEEF magazine, artificial insemination was identified by producers as the second most important technological development in the past 50 years of beef research (Penton Research. 2013). However, among beef producers in North America, most reported that AI was used on only a small subset of their cow herds, and most of that use was in breeding heifers for the first time (USDA, 2009; WCCCS, 2017).

Further, controlling costs surrounding feed intake is important to cow-calf profitability, as feed accounts for the largest variable expense in the cow-calf operation in Alberta (Oginskyy and Boyda, 2020). Recent volatility in commodity feed markets has pushed producers to increase pressure on feed efficiency. As a result, research into the effects of residual feed intake (RFI) selection on reproductive performance is needed, in part to identify cows that should maintain or improve reproductive performance with reduced feed intake, and to ensure that escalating pressure on RFI selection does not curtail any reproductive traits. In addition, due to the long-understood close relationships between reproduction and nutritional status (Wiltbank, 1965), it is conceivable that observation of traits related to feed intake (feeding behaviour, dry matter intake, etc.) early in life could allow for simple, cost-effective proxy traits for reproductive advancement. The purpose of this thesis was to identify feed intake traits measured early in life and their potential for selection to improve the reproductive efficiency of beef females.

2. LITERATURE REVIEW

2.1. Feeding behaviour

Cattle spend as much as 17 h d^{-1} chewing, either through eating or rumination (Teller et al., 1993). The energetic cost of eating and ruminating in beef cattle has been estimated to be as high as one-third of total metabolizable energy (**ME**) derived from low-quality forages (Susenbeth et al., 1998). Energy expenditures associated with eating were positively correlated with the time spent eating, indicating that cattle lose more energy as they eat or ruminate for a longer period of time (Susenbeth et al., 1998). Further, Adam et al. (1984) concluded that, even though energy expenditure associated with eating differed between diets, the energy used was more a function of time required to eat than of diet form or amount ingested. Therefore, the feeding behavior of cattle has an impact on the overall energy status of an animal and could affect the amount of energy available for growth, reproduction, and lactation.

2.2. Evaluating feeding behaviour

2.2.1. Feeding behaviour and feed efficiency

Feeding behaviors are an evolving area and are relatively new to beef cattle research as traits for selection. Advances in remote electronic data capture from equipped feed bunks has allowed researchers access to data that was previously extremely tedious and time-consuming, or indeed impossible, to capture (Gibb et al., 1998). Technology such as GrowSafe Systems, Inc. (Calgary, Alberta, Canada) has revolutionized data capture on individual animals' feeding behaviors. Generally, feeding behaviors are now categorized into two major areas: bunk visits (**BV**), where an animal is physically present at a bunk but may or may not be eating, and meal events, where an animal is both at the bunk and there is recorded feed disappearance. Within each category there are several individual behaviors that can be identified.

Bunk visits result in four separate feeding behaviours, summarized by Jackson et al. (2016): bunk visit duration (**DUR**, sum of the lengths of all BV recorded in a day), bunk visit frequency (**FREQ**, the number of BV events recorded in a day), head-down duration (**HD**, the number of electronic identification [**EID**] readings recorded each day, multiplied by the scan rate of the GrowSafe System), and time-to-bunk (**TTB**, the average amount of time observed for an animal's EID to appear after the feed truck has delivered fresh feed). Meal events are similar but are clusters of BV events differentiated by a defined, non-feeding interval longer than non-feeding intervals within a meal (Bailey et al., 2012). Some meal events include meal duration (**MDUR**, the sum of the lengths of all meals recorded in a day), meal frequency (**MFREQ**, the number of meal events recorded in a day), meal length (**MLENGTH**, the average length of meals per day). In addition, meal size (**SIZE**, kg of feed consumed during a meal) and meal eating rate (**MER**, g/min) can also be derived from meal data (Olson et al., 2019). Feeding behaviors of cattle are generally consistent, with variation within the population, and are genetically regulated. Estimates of the heritability of these feeding behaviours are generally moderate and fall between 0.30 and 0.50, depending on the specific behaviour under discussion (Nkrumah et al., 2007; Kelly et al., 2021), making selection for genetic change possible.

2.2.2. Relationships between feeding behaviour and production traits

Feeding behaviors have been phenotypically and genetically correlated to differences in residual feed intake (**RFI**; Nkrumah et al. (2007); Lancaster et al. (2009); Durunna et al. (2011)), feed conversion ratio (**FCR**; Nkrumah et al. (2007); Lancaster et al. (2009); Durunna et al. (2011)), dry matter intake (**DMI**; Durunna et al. (2011)), average daily gain (**ADG;** Lancaster et al., 2009) and have been implemented in early detection of disease in feedlot cattle (Jackson et al., 2016). Phenotypic correlations in the literature range from 0.26 to 0.45, depending on the relationship under evaluation, and genetic correlations are similar.

Feed-inefficient cattle have been shown to have greater BV DUR, FREQ, HD time and longer, more frequent meals. Among crossbred steers classified into high, medium, and low RFI phenotypes, Nkrumah et al. (2007) found that DUR, FREQ, and HD time were greatest in high-RFI cattle. Durunna et al. (2011) confirmed these results using Angus- and Charolais-sired crossbred steers fed grower and then finisher feedlot diets, and reported that DUR, FREQ, and HD time were consistently greater in high-RFI class (inefficient) steers regardless of diet. Among developing purebred Angus bulls, Lancaster et al. (2009) reported moderate positive phenotypic correlations of meal duration, meal frequency, and HD time, indicating that as RFI increased, so did the number of visits and amount of time spent eating. The literature generally confirms that inefficient animals by any measure have more BV events, longer BV duration, greater HD time (Nkrumah et al., 2007; Durunna et al., 2011; Schwartzkopf-Genswein et al., 2011), and longer, more frequent meals (Lancaster et al., 2009) than their efficient counterparts across many breeds and cattle types.

In addition to relationships with feed efficiency, Jackson et al. (2016) used changes in feeding behaviours for the preliminary detection of bovine respiratory disease (**BRD**) among 231 yearling seedstock bulls from 5 breeds. GrowSafe bunks were used to collect feeding behavior data. Thirty bulls were diagnosed with clinical symptoms of BRD during the trial and treated with antimicrobial therapy. However, their analysis indicated changes in feeding behaviours as much as 14 d prior to observed clinical symptoms, associated with a decrease in DMI. Bulls that exhibited clinical symptoms of BRD had depressed DUR, FREQ, and HD prior to clinical symptoms, and Jackson et al. (2016) concluded that feeding behaviours could be useful in feedlot settings for the detection of BRD.

2.2.3. Feeding behaviour and reproduction

Few studies exist that explain connections between feeding behaviours and reproduction in beef cattle. Basarab et al. (2011) examined 190 commercial beef heifers over three years for connections between RFI, BF thickness, feeding behaviours, and attainment of puberty. Again, FREQ was greater in high RFI heifers than in low RFI heifers. Further, heifers that were pubertal at the beginning of the feeding trials or attained puberty within 60 days thereafter consumed more feed (r_p = -0.19), had greater DUR (r_p = -0.13) and HD (r_p = -0.23), but had less frequent bunk visits (FREQ; r_p = 0.15) than heifers that attained puberty 60 d or more after the trial started. In a study of 42 pregnant first- and second-parity Bonsmara cows, Hafla et al. (2013) found that first-parity females had greater FREQ and more bunk visits per meal relative to second-parity cows. Bunk visit duration and meal frequency were unaffected by parity, though eating rate (g/min) was greater in second-parity cows. No further investigations have been reported that specify relationships between feeding behaviours and reproductive traits in beef cattle.

2.2.4. Feeding behaviour and genetic selection

The phenotypic and genetic correlations between feeding behaviours and economically relevant feed intake and efficiency traits provide opportunity for genetic improvement (Durunna et al., 2011; Kayser and Hill, 2013; Chen et al., 2014). Similarly, feeding behaviours could be used to predict future reproductive potential when measured in developing replacement heifers. Insufficient literature in this area provides room for a knowledge gap to be investigated, and for recommendations to be made for beef cattle producers with regard to selection using feeding behaviours. Feeding behaviours are correlated with physiological traits that may be undesirable; specifically, positive phenotypic and genetic correlations between feeding behaviours and DMI (Durunna et al., 2011) and animal weight could be problematic if selection pressure is applied to increase or decrease DUR, FREQ, or HD. Therefore, it is likely that feeding behaviours should be used in selection indices, where negative effects on animal size could be mitigated, and holistic, multi-trait selection emphasised.

2.3. Dry matter intake

Accurate predictions of DMI are an essential part of making informed decisions regarding beef cattle nutrition (NASEM, 2016). Considerable challenges exist when attempting to find a precise and accurate measure of DMI in cattle, especially in beef cows grazing forages. Voluntary intake is complex and defining a framework to describe intake in beef cattle continues to be an area of investigation (Galyean and Gunter, 2016). Much of the research concerning DMI focusses on cattle in confined environments.

2.3.1. Environmental effects on DMI

Generally, the effects of temperatures above and below an animal's thermoneutral zone are well understood. In general, beef cattle DMI is expected to have a negative correlation with ambient air temperature (NASEM, 2016). Results from Delfino and Mathison (1991) indicate that the efficiency of net energy used for growth (NE_g) was poorer in Hereford × Angus steers housed outdoors for 4 months at an average temperature of -7.6˚C than in cohorts fed inside at 16.9 ˚C. The steers housed outside at low temperatures had a greater DMI, which could be due in part to the inefficiency of energy use for maintenance and growth, resulting in a metabolic demand for more feed intake. The opposite to cold stress is stress from extreme temperatures well above the thermoneutral zone. In growing feedlot steers (Hicks et al., 1990) and heifers (Colditz and Kellaway, 1972), heat stress has been shown to depress DMI. Excessive ambient temperatures also change the grazing patterns of cattle, shifting time spent grazing to early or late in the day (Blackshaw and Blackshaw, 1994). Temperature stress above and below thermoneutral can be mitigated or exacerbated by mud, wind, shade, humidity and precipitation, and steps should be taken to reasonably protect livestock from extreme elements.

2.3.2. Physiological status effects on DMI

In beef cows, reproductive activities have notable effects on DMI. Dry matter intake increases of up to 50% have been reported (NASEM, 2016) during lactation due to the associated energy demands. Among multiparous and primiparous Brangus females, each kg of milk production increased DMI by 0.33-0.37 kg, and DMI during lactation was greater in females sired by higher milk-potential bulls (Johnson et al., 2003). Further, depressions in DMI are expected prior to parturition (NASEM, 2016), and have been shown to be as severe as 14% in young (<3 years) dairy cows, and up to 28% in multiparous dairy cows older than 3 years (Marquardt et al., 1977). However, a more recent study in primiparous and multiparous crossbred Angus cows reported that DMI increased in heifers until 2 wk prepartum, and then declined, but no changes in DMI were observed in late gestation for multiparous mature cows (Linden et al., 2014). When DMI was expressed as a percentage of body weight, no differences were seen between heifers and mature cows, though Linden et al. (2014) concluded that primiparous cows were unable to consume sufficient DMI to meet the demands of growth, maintenance, and lactation post-partum, despite an increase in DMI. In a study comparing diets with required and excessive levels of metabolizable protein in Hereford-cross prepartum heifers, similar depressions were observed in the weeks leading up to parturition by Hales et al. (2018). This highlights the importance of managing beef heifer nutrition closely to ensure that nutritional status does not impede an animal's ability to rebreed quickly. Estrus also seems to depress DMI in heifers, though the decline is sharp and short lived, and is generally observed only on the day of estrus in heifers housed together (Underdahl et al., 2018).

2.3.3. Animal and feed management effects on DMI

Pasture quantity and quality can have effects on DMI. With interest in rotational grazing growing in Western Canada, it is important that producers understand the implications of pasture management on DMI in their cattle. Dry matter intake estimation is complex in feedlots, but the estimation of intake in cattle grazing pasture is further challenged by factors including selective grazing, herbage mass, structure, and composition, as well as other environmental influences and management (Galyean and Gunter, 2016). Total herbage estimates are used as an indication of how much forage should be available to cattle in a given area at a given time, with greater stocking rates indicating that a greater percentage of available forage should be harvested by the animals present (McCarthy et al., 2011). As stocking density is increased, competition between animals for available feed is also increased; this challenges animals' opportunity to realize their DMI potential. As a result, animals may suffer reduced productivity if the pastures are too densely stocked for an extended period of time (Davis et al., 2014). Among Simmental-sired calves born to F_1 Brahman-Hereford cows, calves born in high-stocking rate herds were lighter at weaning than those born in lower stocking rate herds at the same time of year (Gaertner et al., 1992). Similarly, Aiken and Bransby (1992) reported poorer ADG among steers and among cow-calf pairs maintained at greater stock densities, indicating that energy intake may not have met intake potential. Clearly, stocking rate is a major component of pasture management that can have severe repercussions if applied incorrectly.

Diet quality varies considerably through a cow's reproductive cycle, from high-protein low-fibre early summer growth to the senescent high-fibre material available in late fall and winter. Diet quality can severely affect the feed intake of beef cattle. Diets high in neutral detergent fibre (NDF) can limit the amount of forage an animal is voluntarily capable of consuming (Allen, 1996). Especially in mature forages and conserved forages for winter feeding, animals may limit feed intake below their energy needs if rumen bulk and tension signal the brain to cease eating (Allen, 2014). If the forage available to cattle is of low quality, such as what is supplied as conserved forage in the winter months in Western Canada, cattle may not be able to physically ingest sufficient nutrients to meet the demands of maintenance, pregnancy, and lactation, and may suffer productively as a result. Low-quality diets with poor crude protein levels (such as are common to feed beef cows in over the winter) should be supplemented with a high protein concentrate feed to ensure that sufficient nutrients are available to the cow for normal productive processes, including maintenance, calving, uterine involution, and rebreeding. Likewise, feedstuffs with poor energy should be supplemented with a concentrate high in energy. In the rare instance that breeding cattle are fed a concentrate-based diet, DMI is likely only inhibited by tissues communicating that energy needs are met, and the animal does not need to eat any more (NASEM, 2016). Due to the concentrated (high quality, low volume) nature of feed lot diets, rumen fill and distention are not usually implicated in limiting feed intake (Allen, 2014).

2.3.4. Methods to estimate DMI

The NASEM (2016) and previous editions (NRC, 2001) provided several widely used equations for the estimates of intake by both growing-finishing beef cattle and mature beef cows. Equations were developed for non-pregnant beef cows and for beef cows in second and final trimester of gestation (Galyean and Gunter, 2016). The NRC (2001) recommends the following equation to estimate NE_m intake requirement in beef cows:

$$Intake, NE_m\ (Mcal\ d^{-1}) = BW^{0.75} \times \left(0.04997 \times {NE_m}^2 + 0.04631\right);\ \text{Eq. 7-3}$$

Where: $BW^{0.75}$ = metabolic midweight and NE_m = net energy required for maintenance. From this value, DMI requirement can be derived by dividing estimated NE_m intake by the NE_m concentration of the diet (NRC, 2001). In the event that a cow is lactating, the daily DMI should be increased by a factor of 0.2 × daily milk production. Similar to the method described by the NASEM for growing-finishing cattle, DMI estimation for beef cows should be adjusted for low-quality forages; when TDN is less than 50%, the divisor to find DMI should be no less than 0.95. Failure to properly adjust the equation could result in biologically unrealistic estimates of DMI on those forage types (NASEM, 2016). Even with the mentioned adjustments for lactation and diet quality, the NASEM equations tend to poorly reflect DMI in extreme cases (Coleman et al., 2014). As a result, Coleman et al. (2014) suggested three equations for growing animals, dry cows, and lactating cows on high-forage diets. Data from 50 studies suggested that BW was an important factor, but not as important as physiological status in mature, non-lactating beef cows (Coleman et al., 2014). Weight was most important in growing animals, and

Coleman et al. (2014) concluded that weight became less informative of intake as animals age and reach maturity. Further, Coleman et al. (2014) suggested that calf ADG was a more realistically attainable measure of milk output than directly measured milk output, due to the challenge associated with milk output measurements in realistic beef cow environments, and suggested that calf preweaning ADG should be included in models for lactating cows. Despite these recommendations, the NASEM published the 8th edition of the Nutrient Requirements of Beef Cattle with the original equation as the official recommendation.

2.3.5. Dry matter intake and reproduction

Dry matter intake (DMI) can be measured easily in cattle consuming prepared TMR diets in dry lot environments using technology like GrowSafe and C-Lock automated feed intake systems. Dry matter intake in grazing beef cattle is extremely difficult to measure with sufficient accuracy to be scientifically useful; to collect DMI in producing beef cows in normal conditions is nearly impossible (Galyean and Gunter, 2016). As a result, no reports were found in the literature that explicitly draws on DMI to explain variation in reproductive traits. However, Holloway et al. (1979) found that cows grazing high- and low-quality fescue pasture had different intake levels. Cows on high quality pasture consumed 1.7 kg d^{-1} more than cows on low quality pasture. Cows with greater intakes gained 2.2 mm more backfat than cows with lower intakes. No differences were observed in milk production between the two grazing systems, though cows on high quality pasture weaned calves 18 kg heavier than those on low quality pasture (Holloway et al., 1979). Among 27 multiparous *B. taurus* cows, supplementation of dried distillers' grains served to improve cow intake during gestation, which may have contributed to greater birth and weaning weights (Kennedy et al., 2016). However, these improvements were not connected directly to the increase in forage DMI. A reliable estimation of cow DMI is needed for connections with reproductive traits to be fully understood.

2.4. Residual feed intake

Residual feed intake (**RFI**) has been investigated as a method to improve animal feed efficiency with little impact on economically vital production traits. Considering that nearly 70% of annual production costs in Alberta are attributable to summer and winter feed and bedding expenses (Oginskyy and Boyda, 2018, 2020), producers have an obvious inclination to attempt to improve animal efficiency. Residual feed intake is classically defined in growing animals as the difference between actual and expected feed intake over a given period of time (Koch et al., 1963), where expected feed intake is predicted from metabolic mid-trial body weight and gain. This measure of RFI is moderately heritability with estimates of heritability ranging from 0.26 to 0.43. Due to the nature of its derivation, RFI is independent of animal size and growth, which allows for selection for RFI without impacting those economically important traits. Research by Basarab et al. (2011) also indicated the value of including off-test back fat in the prediction equation, making RFI_{FAT} independent of body composition. These characteristics make RFI a unique selection tool compared to other feed efficiency metrics such as feed-to-gain ratio, which is correlated with animal size (Herd et al., 2003).

2.5. Physiological traits affecting residual feed intake

The basis of RFI selection is that there are differences between animals that may consume the same amount of feed and yet have different performance, or reversely, that there are cattle that perform similarly in terms of growth but consume considerably different amounts of feed while doing so. The use of RFI as a selection tool allows identifying cattle which consume less feed but maintain desirable performance levels – the question becomes why those animals with more favourable RFI are able to perform at the same level as those with a less favourable RFI. Herd and Arthur (2009), in a review of proposed mechanisms for variation in RFI in cattle identified 5 major areas of consideration: feed intake, digestion, body composition and metabolism, activity, and thermoregulation.

Feed intake is itself an energy sink, where as feed intake in cattle increases the amount of energy required to digest the feed also increases. Adam et al. (1984) reported differences in the energy costs of consuming diets with different energy densities in steers. Long-stem hay was consumed more slowly and had a greater energy cost of consumption compared to diets consisting of pelleted concentrates and pelleted hay. Further, Johnson et al. (1990) reported an increase in oxygen consumption by the portal-drained viscera as metabolizable energy intake increased, as well as increases in the weight of digestive organs with increased levels of feed intake. The intake of feed is also related to greater heat production (heat increment of feeding; **HIF**), and Herd and Arthur (2009) postulated that animals which consume less feed due to selection pressure for RFI should have less energy expended as HIF.

Digestibility of feeds is a factor that can be somewhat controlled by management. For example, processing grains generally increases the digestibility and improves animal performance. In bulls and heifers ranked for RFI, numerical differences in diet digestibility were observed such that high RFI cattle had poorer digestibility than low RFI cattle, which accounted for 14% of the difference in observed dry matter intake (Richardson et al., 1996). Similarly, Nkrumah et al. (2006) reported 28% lower methane production and 6% greater digestibility in calves selected for efficient RFI, and Herd et al. (2004) reported a correlation that indicated that selection for improved RFI was associated with greater diet digestibility. Obviously, improved digestibility associated with improved RFI leads to cattle that need to consume less feed to satisfy metabolic processes, because they are better able to extract the nutrients present in their diet.

Body composition is understood to affect the energy demands of cattle, and the accretion of the same weight of protein and lipid tissue has different energy costs (1.24 Vs. 9.39 kcal g^{-1} of protein and lipid tissue accreted, respectively) (Carstens and Kerley, 2009). Variation in the amounts of fat and lean gain in beef cattle can therefore affect the efficiency of nutrient utilization, such that leaner animals would be more likely to have lower RFI (Lancaster et al., 2009). Likewise, Richardson et al. (2001) showed that the body composition (chemical composition) of beef steers selected for divergent RFI was genetically correlated to RFI, such that low-RFI efficient steers had less chemical fat than high-RFI steers, though Carstens et al. (2002) concluded that the effects of body composition on RFI among crossbred steers was small.

Animal activity level is an axiom area of energy expenditure. Energetic costs of eating (intake, mastication, and rumination) may be as high as 33% of the metabolizable energy derived from the consumption of forages in cattle (Susenbeth et al., 1998). Olson (2017) reported positive phenotypic correlations between feeding behaviours collected with electronic GrowSafe feed bunks and residual feed intake in heifers fed a feedlot diet, such that RFI was greater and efficiency less in heifers with greater bunk visit frequency ($r_p = 0.24$) and duration ($r_p = 0.47$), and head-down duration ($r_p = 0.36$). Similarly, Olson et al. (2020) reported that RFI_{FAT} had positive phenotypic correlations with feeding duration ($r_p = 0.24$), head-down time ($r_p = 0.30$), and feeding frequency ($r_p = 0.20$) in a subset of the heifers from the population considered in this thesis. Basarab et al. (2011) reported that, in addition to the regression model that included average daily gain and metabolic mid-trial body weight, a model that also included off-test backfat thickness and feeding event frequency accounted for as much as 87.1% of the variation in DMI. It may be useful to include both off-test backfat and measures of animal feeding behaviour in models designed to predict cattle RFI.

Thermoregulation is the principal inefficiency in ruminants, where energy is lost due to evaporative heat loss via the respiratory tract. As yet, no studies have directly analyzed the potential relationship between respiratory rate and RFI in beef cattle. However, among dairy cows measured while lactating and while dry, respiration rates did not differ between RFI classification (respiration was measured by counting the number of flank movements in 1 minute; DiGiacomo et al., 2014). Further, temperature data collected at the shoulder and neck indicated that inefficient cows tended (*P*-value =

0.087) to have higher skin temperatures at those locations, and inefficient cows had significantly warmer udder surfaces compared to efficient cows. DiGiacomo et al. (2014) concluded that some of the differences in RFI may be attributable to thermoregulation in dairy cattle. Among Nellore bulls tested for RFI, estimated heat production did not differ, though low RFI bulls had lower heart rates than high RFI bulls (Baldassini et al., 2018). More research into the effects of respiration rate and thermoregulation needs to be done to fully elucidate the effects of thermoregulation on animal efficiency.

In an extensive review of the biochemical pathways believed to be associated with differences in animal feed efficiency, Bottje and Carstens (2009) postulated that as much as 60% of the variation between animals could be attributed to protein turnover, inefficiencies in the removal of sodium and the import of potassium ions by the sodium-potassium ATPase enzyme, and mitochondrial proton leakage. The imperfect processes of the generation of ATP in the mitochondria results in proton leak, where there is a dissipation of the mitochondrial membrane electron balance without the generation of ATP. That proton leak also leads to the production of oxidative ions that can damage proteins, fats, and genetic material associated with ATP synthesis in the mitochondria and throughout the cell. Kolath (2006) and Lancaster (2007) both reported greater efficiency of the electron transport chain in tissues harvested from cattle that were phenotypically more feed efficient (had a lower RFI). Further, among heifers tested for RFI, Kelly reported that high-RFI heifers had greater expression of mitochondrial RNA for uncoupling protein 3. Uncoupling protein 3 is associated with the protection of the cell against oxidative bodies, and so the up-regulation of this genetic material is indicative greater oxidative stress within the cell.

Taken together, there is considerable understanding of the phenotypic and biochemical causes of efficiency and inefficiency in livestock species. However, the impacts of selection for improved feed efficiency in beef cattle may have implications in other areas of production, and all aspects of beef production should be monitored for unanticipated negative effects.

2.6. Reproductive improvement in beef cattle

2.6.1. GOLD management indicators

The GOLD management indicators for beef cattle are Growth (of calves), Open rate (of cows), Length (of calving season), and Death loss (of calves) (Kaliel et al., 2008). The GOLD benchmarks have been used to measure and benchmark improvements in herd productivity at the individual, provincial, and regional level of Canada. Using these parameters, producers are able to measure their current performance against their historic performance and measure themselves against other producers in Alberta and across Canada.

2.6.2. Growth

For the purposes of benchmarking, growth is recorded using the calf's weaning weight as a percentage of the cow's body weight (Kaliel et al., 2008), which is used to measure the efficiency of the cow. A benchmark of 20 kg of calf should be produced for every 100 kg of cow weight (Kaliel et al., 2008), or any given cow should wean a calf that is approximately 40% of her own weight at weaning. Among a composite herd consisting of ¼ Charolais, ¼ Tarentaise, and ½ Red Angus cows established that the Fort Keogh Livestock and Range Research Laboratory (Miles City, MT), MacNeil (2005) reported a direct heritability of 0.20 ± 0.03 for the ratio of 200-d weaning weight to cow weight. However, MacNeil (2005) postulated that challenges may be experienced by producers attempting to select for the ratio due to a strong negative genetic correlation (-0.77 ± 0.04) between the direct and maternal effects. Selection pressure to increase the ratio could simultaneously decrease cow weight and increase weaning weight, and selection indices that include cow weight and calf wean weight might yield more control over the process (MacNeil, 2005). The low-moderate heritability of this trait also indicates that weaning weight as a percentage of dam weight can be manipulated through the environment. Practices such as creep feeding can improve weaning weights, and environmental factors such as pasture condition will variable yearly impacts.

2.6.3. Open rate

Open rate is a primary economic concern for beef cattle producers, as cows that are not pregnant at the end of the breeding season are cows that will not produce revenue for an operation through the sale of a calf (Ibendahl et al., 2004). Further, there is a considerable expense incurred in feed and maintenance to keep open cows through the winter, which highlights the importance of diagnosing pregnancy in the cowherd to identify open cows. Once a cow is identified as open, a producer can decide as to when to sell the cow for revenue by observing cull cow markets, retaining, rebreeding and selling as a fall-calving cow, or simply retaining the cow and carrying her over to the next breeding cycle. The Alberta Beef Cow-Calf Manual indicates that a benchmark of

96 cows out of 100 should be pregnant after a 63-d breeding season (Kaliel et al., 2008). As open rate among beef cows is of vital importance, considerable work has been done to investigate methods of improving it. Unfortunately, as with most reproductive measures, open rate among beef cows has low heritability ($h^2 < 0.10$; Morris et al., 2000; Minick Bormann et al., 2006; Cammack et al., 2009a; Peters et al., 2013), and genetic improvement of the trait would be very slow. Fortunately, due to the low heritability, there is a degree of control over open rate afforded to cattlemen. A full description of the effects of proper nutrition can be found in Section 2.5.7. of this thesis: "Nutrition and reproduction: The state of the art". Suffice to say that cows in adequate body condition, with sufficient access to micronutrients and water, are considerably more likely to be diagnosed as pregnant and calve following exposure to a bull than those in poor condition or lacking nutrients.

2.6.4. Length of calving season

Again, as a reproductive trait with low heritability ($h^2 = 0.05\text{-}0.09$; Meyer et al., 1990) and easily influenced by managerial manipulation, the length of the calving season is nonetheless an economically crucial benchmark. The Alberta benchmark for this GOLD standard is a 63 d breeding season, which should translate to an approximate 63 d calving season (Kaliel et al., 2008). Among respondents to the 2014 Western Canadian Cow-Calf survey, producers reported that most (55%) of their calves were born in the first 21 d of the calving season, 40% in the second and third periods of 21 d, and only 5% were born more than 63 d after the calving season started (Larson, 2015). These values are markedly improved over the results of the 1997-1998 Alberta Cow-Calf audit, which reported that 42% of calves were born in the first 21 d, and 49% were born in the second and third periods (Audit, 2001). Cows that calve earlier in the calving season wean calves that are heavier (Lesmeister et al., 1973; Funston et al., 2012; Cushman et al., 2013). Among Red Angus × Simmental beef cows housed at the Gudmundsen Sandhills Laboratory (Whitman, NE), Funston et al. (2012) reported that calves born in the first 21 d of the calving season averaged 13 kg to 34 kg heavier at weaning than calves born in the second 21 d and third 21 d periods, respectively. Further, those calves born in the first 21 d were heavier at slaughter, produced carcasses with greater backfat and a higher percentage of older carcasses graded USDA average Choice or higher, and those carcasses had a greater value. Further, heifers born in the first 21 d period of the calving season were also heavier at weaning, had higher conception rates (90% for the first 21 d vs. 86% for the second 21 d and 78% for the last 21 d [*P*-value = 0.02]), and subsequently calved earlier themselves (Funston et al., 2012). Not only are progeny born in the first 21 d more valuable market cattle, but they also perpetuate the trend for early calving to subsequent generations, enhancing the effect. Unfortunately, there is little genetic control over this trait - Berry and Evans (2014) reported heritabilities of 0.06 ± 0.013 and 0.01 ± 0.003 for the percentage of heifers and cows, respectively, that calve in the first 42 days of the calving season. Such low heritabilities are indicative of the greater influence environment can have on the length of the calving season. Obviously, if producers severely restrict their breeding season or utilize synchronised or fixed-time artificial insemination or embryo transfer, the length of the calving season can be manipulated to be drastically shorter. Likewise, producers that do not remove breeding bulls after the recommended 63 d (Kaliel et al., 2008) season ends will probably experience extended calving seasons the following year.

2.6.5. Death loss

Death loss of calves in beef herds between birth and weaning is inevitable. The benchmark for Alberta cowherds is at 4% (Kaliel et al., 2008), which is obtainable for producers in any given year but can be a challenge to maintain for consecutive years without major inputs in management and labour (Audit, 2001). An audit of Alberta cow-calf operations conducted in 1997 reported that up to 79% of calf death loss occurs in the first 2 weeks after birth, and most of those deaths are attributable to dystocia. Analysis of death loss over the entire period from birth to weaning revealed that dystocia accounted for 30.7% of the reported death loss, 33.3% of calves died for unknown reasons, 10.1% were accidental deaths and the common calf-hood issues of pneumonia, starvation, and scours accounted for 9.8%, 6.2%, and 9.9% of deaths in the 1997/1998 season, respectively (Audit, 2001). A more recent survey of producers in Western Canada indicated a slight increase in the percentage of calves that died in the 2013/2014 season (6.9% overall), but reasons remained consistent (calf-hood disease 30%, accident 29%, weather 16%, and unknown 24%; Larson, 2015). Calf death loss is barely heritable; Dearborn et al. (1973) reported heritabilities of 0.03 ± 0.13 among dams for calf survival to two weeks, and -0.01 ± 0.13 among dams for calf survival from two weeks to weaning. Among calves, heritability for surviving from two weeks to weaning was -0.04 ± 0.04 (Dearborn et al., 1973), indicating that these traits, similar to other reproductive traits, are under considerable influence from the animal's environment or perhaps non-additive genetic effects. Similarly, Cervantes et al. (2010) found low-moderate heritabilities for calf survival of 0.226 ± 0.018 among Asturiana de los Valles cattle in Spain. Therefore, improvements in death loss in any given herd will be largely dependent on management practices. Producers are encouraged to practice good herd health under the supervision of a veterinarian to reduce disease, and work to eliminate the causes of accidental, weather-related, and predator-related death loss when economically practical.

In the decades since the introduction of continental European genetics into the North American cowherd, beef producers have enjoyed measurable improvement in many areas of production (Bruns et al., 2017). Weaning weights (**WW**, calf weight at 205 d of age), yearling weights (**YW,** animal weight at 365 d of age), and carcass weights have improved in Western Canada (Audit, 2001). Advances in beef cattle nutrition have also been substantial, and the industry in Western Canada is revelling in an abundance of knowledge concerning nutrition for the cow and the calf. Today, Canadian beef cattle have a lower environmental footprint and are more efficient than they were 30 years ago, producing fewer greenhouse gasses per kilogram of beef, and generally producing more beef per animal with fewer inputs (Legesse et al., 2016). However, with a spotlight on the sustainability of beef cattle production, one area of production has remained oddly static, despite such improvements in most others: the rate of calves weaned per 100 cows exposed to breeding (**calf crop percentage**) has remained stable between 80 and 85% since auditing of the Western Canadian cowherd began in Alberta in 1988 (Audit, 2001). Calf crop percentage is a broad term that encompasses traits related to a cow's ability to become pregnant, carry a pregnancy to term, calve and wean a calf, and is therefore a reasonable and encompassing benchmark for fertility comparisons.

2.7. Economic relevance of efficient reproduction

The economic efficiency of beef cattle reproduction seems to be self-explanatory: no calf, no income. Beef cattle reproductive traits are as much as 5 times more important to the economic viability of a cow-calf operation than either growth or milk traits (Trenkle and Willham, 1977) and are the most important factors related to profitability in the cow-calf sector (Osoro and Wright, 1992).

Breakeven (**BE**) price for calves is calculated with the equation:

$$BE = \frac{(annual\ cow\ cost\ -\ value\ of\ culled\ animals)}{Avg.WW\ \times\ \%\,Calf\ Crop}$$

(Taylor and Field, 1995). Thus, with a calf crop percentage which has remained relatively stable (Audit, 2001; Larson, 2015), beef producers have relied on improving WW to boost profitability. Taylor and Field (1995) reported that calf crop percentages between high- and low-cost cow-calf operations were 84 and 83% respectively. Cow maintenance costs were $222 greater in high-cost operations than in low-cost operations, but calves in the low-cost group outweighed the high-cost calves by an average of 10.3 kg (Taylor and Field, 1995). The differences between high- and low-cost cow-calf operations primarily hinged on cow maintenance cost and calf WW.

The emphasis on animal growth performance attributes is evident in the expected progeny difference (**EPD**) traits provided by all major breed associations in Canada.

Among purebred and commercial cow-calf producers in Manitoba, Sy et al. (1997) found that purebred breeders emphasised fertility-related EPDs as well as Milk (**MILK**, additional pounds of calf weaned by an animal's progeny) and WW. Commercial operators preferred bulls with favourable calving ease (calving ease maternal [**CEM]** and calving ease direct [**CED]**; CEM, percentage unassisted births of first-calf daughters, and CED, calving ease of that animal's progeny), and docility (**DOC**, probability that an animal's offspring will score favourably on subjective temperament scores), followed by WW and MILK. The consequence of this selection pressure for greater WW and increased MILK EPDs has been larger calves at weaning, born of larger dams that had greater milk production. This trend toward growth and calfhood performance to yearling age has resulted in a larger average BW cowherd, and a heavier milking cow which may not be well adapted to the extensive production practices common in Western Canada. Even in a highly productive environment, high milking beef cows have lower pregnancy rates, and thus lower kg of calf weaned per cow exposed, than their lower milking counterparts (Edwards et al., 2017). Edwards et al. (2017) also found that WW were not different between high (> 10 kg milk d^{-1}), moderate (8-9 kg milk d^{-1}), and low (< 8 kg milk d^{-1}) milking dams, which highlights the notion that producers may not be selecting for traits that improve their profit margins or gross income.

2.8. Nutrition and reproduction: The state of the art

Extensive research has indicated that dietary energy and energy status of primiparous and multiparous cows influences future reproductive performance (Richards et al., 1986) and alters the growth of offspring (Marques et al., 2016). A cow's nutritional status has been identified as the main limiting factor controlling successful reproduction (Short and Adams, 1988), particularly her nutritional status relative to calving time (Selk et al., 1988, Houghton et al., 1989). In addition, the stage of the reproductive cycle of a cow changes the cow's nutritional requirements, further complicating the relationship between reproduction and nutrition (Swecker Jr., 2015). Over the course of a year, the nutritional requirements of beef cows fluctuate, and are usually lowest at weaning time and highest during the third trimester of pregnancy and early lactation (NASEM, 2016). Cows enter the most energetically demanding period between parturition and rebreeding, as high lactation demands, restoration of the uterus, and resumption of normal estrous all coincide, but requirements are lowest at mid-gestation, when the cow is either dry or nearly weaned her previous calf and fetal growth is slow (Swecker Jr., 2015).

Body condition score (**BCS**) has been identified as an adequate predictor of future reproductive performance in both heifers and cows. In a study including multiple breeds, cows with BCS of 6 and 7 (out of 9) at calving had greater pregnancy rates than those cows with BCS 4 and 5, 70 d after the end of the breeding season (DeRouen et al., 1994). Further, Osoro and Wright (1992) found that the calving interval among higher BCS cows was 11.2 d shorter than that of lower BCS cows. On a scale of BCS 1 - severely emaciated; to 9 – severely obese, (Wagner et al., 1988), most research suggests the maintenance of BCS above 4, but below 8, especially at calving. Arnett et al. (1971) reported that heifer calves fed to be severely obese (BCS 8.5 and higher) had increased incidence of dystocia, weaned fewer calves, had a shorter average reproductive life, and had depressed milk production compared to their acceptable-BCS twins. The authors also investigated the effects of short-term induced obesity during gestation on reproductive efficiency among 8-yr old cows but found no significant differences between normal and obese animals. Arnett et al. (1971) concluded that severe obesity during the developmental stages of a heifer's life was very detrimental to future reproductive performance and stayability. These results have guided the beef industry to maintain moderate (BCS 4-8) body condition. Proper cow BCS maintenance can be particularly challenging in Western Canada, as many cows calve prior to spring greening and pasture turn-out. The preferred calving period for many Alberta producers starts March 1 (Audit, 2001), and 70% of Western Canadian producers recorded beginning calving prior to April 1st in a survey completed in 2014 (Petherick et al., 2009). Thus, many cows enter the most nutritionally demanding period in the reproductive cycle, weeks or months before the grass begins to grow in mid-April to early May (Donkor et al., 2003). Ensuring that cows are at the appropriate BCS to support a normal return to estrus and to promote lactation for a young calf is essential, but particularly challenging in the Western Canadian range environment.

While the acceptable BCS window for efficient reproduction has been established for some time, the exact physiological impact of proper body composition is not yet fully understood (Hess et al., 2005). The effects of undernutrition hinder the release of gonadotropin releasing hormone (**GnRH**) from the hypothalamus, thereby limiting luteinizing hormone (**LH**) and follicle stimulating hormone (**FSH**) (Wettemann et al., 2003). The lessened concentrations of LH and FSH are insufficient to produce a dominant ovarian follicle large enough to make estradiol (Wettemann et al., 2003). The suppression of follicular waves results in lower circulating estradiol and promotes anestrous, to the extent that thin cows require notably longer periods to return to a normal estrous cycle after calving. When gestational nutrition is adequate and cows calve at an appropriate BCS, but postpartum nutrition is lacking, the cow is able to mobilize the energy stored as lipid reserves in her body to ensure a timely return to estrus (Wettemann et al., 2003), emphasising the importance of ensuring cows are at an acceptable BCS prior to calving.

Maintenance of adequate BCS is challenged by environmental and physiological factors. The physiological status of the cow, particularly age, can influence a cow's ability to maintain BCS. Among 454 multiparous crossbred beef cattle, Renquist et al. (2006) reported that cow age at calving was correlated with cow BCS at calving. Three-year-old cows consistently reported the lowest BCS, and 8-year-old cows the highest. Similar interactions between age and BCS were observed by Coleman et al. (2017) among cows of *B. taurus* and *B. indicus* types. Cattle might be fed under winter management conditions for as many as 200 days in central Alberta (McCartney et al., 2004). As cattle in Western Canada are provided some form of stored forage resource (hay, silage, swath grazing, and/or stockpiled pasture), nutrient quality, availability, and digestibility can vary considerably between pastures, forage species, and even bale-to-bale. In the use of low-nutrient feedstuffs such as wheat straw, supplementation is required to ensure adequate nitrogen is present in the diet (Wood et al., 2010). The primary goal of supplemental nutrition should be to maintain or improve BCS during winter gestation in an effort to shorten the post-partum anestrous period. However, regular, adequate supplementation can be challenging when weather or location of the cattle make providing a consistent feed supplement difficult or impossible.

Where supplementation is possible, however, feed medications such as monensin have been shown to improve the feed conversion of beef cows, with no negative impact on reproductive performance. Among Hereford cows fed hay for the winter in a dry lot setting, cows that received monensin treatments had decreased hay intake compared to cows not fed monensin, with no negative impact on reproductive performance (Turner et al., 1980). The authors estimated that supplying 200 mg of monensin per cow per day could save more than 280 kg of hay during the winter per cow, with no effect on cow ADG during the winter or on the performance of the progeny through weaning. In several studies, the feeding of ionophores generally reduced the amount of time a cow was anestrous (post-partum interval; **PPI**), especially when breeding lasted more than 95 d (Randel, 1990).

In addition to feed additives, common production practices on cow-calf operations include providing some form of mineral supplementation to ensure that all cattle receive adequate amounts of mineral. Delivery may be in the form of free-choice loose mineral, mineral injections (micro minerals), and slow-release ruminal boluses. The ingredients of mineral supplements may differ based on operation location, management style, and forage stage, though forages are usually low in Cu, Mn, Se, and Zn (Mundell et al., 2012). Pregnancy rates at 63 d post artificial insemination (AI) were greater in cows offered organic trace mineral (**TM**) compared to inorganic TM, though overall pregnancy rate did not differ (Stanton et al., 2000). Earlier pregnancies result in older, larger calves at weaning, and the authors concluded that supplementing with organic TM may improve profit via larger calves born earlier in the season. Similarly, Mundell et al. (2012) gave mature cows an injection of TM or saline (control) and found that pregnancies in response to AI were greater in TM supplemented cows. All cows in that study were provided free choice mineral, and the authors suggested that injected TM ensured that all cattle received the mineral they needed, not just the animals which regularly consume free-choice mineral. Call et al. (1978) found no differences in age at puberty, conception or calving percentages between heifers fed 66% and 172% of NRC (1976) recommended levels of phosphorous. Canadian producers should always ensure that mineral is available to cattle to promote normal physiological processes, and they should be aware of mineral deficiencies and conditions which can predicate mineral deficiencies in their area.

2.9. Genetic selection for improved reproductive traits

Increasingly, producers are utilizing residual feed intake (**RFI**) as a selection tool to reduce input costs and improve animal efficiency. Unlike feed conversion ratio (**FCR**), RFI is independent of animal output (maintenance, milk, ADG, etc.) and body size, and can therefore be used to select for efficient animals without a corresponding change (increase) in mature body size. However, changes in metabolism associated with RFI selection may have corresponding effects in metabolism-related areas, such as animal reproduction and fertility. Selection for RFI has had mixed effects on age at puberty, as Shaffer et al. (2011) found that low RFI heifers reached puberty 7.5 d later than high RFI heifers. However, no effect of RFI was found by Basarab et al. (2011) between high and low RFI heifers, though when RFI was adjusted for body fat, low RFI heifers were 13 d later maturing than high RFI heifers. Basarab et al. (2011) illustrated that low RFI heifers had lower pregnancy rates throughout of the breeding season, and ultimately fewer pregnancies overall. As a result, low RFI heifers also calved later than high RFI animals, with fewer calves born before d 28 of the calving season (Basarab et al., 2011). However, when RFI was adjusted to include back fat thickness (a measure of body composition) or back fat thickness and feeding behavior (a measure of feeding activity), no pregnancy differences between efficient (low RFI) and inefficient (high RFI) cows were observed. Thus, the authors recommended that back fat and/or feeding behavior be included in selection for low RFI cattle, to control any negative effects RFI may have on fertility and economic performance. Shaffer et al. (2011) found no difference among RFI classes, even though that study did not include back fat in the model, and they concluded that RFI was independent of fertility in beef heifers. At this time, it appears that selection for efficient animals should not have an impact on cow reproductive performance, especially when controlled for body composition.

2.9.1. Calf crop percentage

Fertility is a complex trait, defined many ways and through many dynamic relationships between body processes. As a result, it is not simple to create or implement genetic change in fertility. Fertility differs among biological cattle type, between breeds, and can even be different between herds using the same breeds (Cammack et al., 2009b). American and Canadian purebred breed associations have moved to a whole- or total-herd reporting model in an effort to encourage purebred breeders to record reproductive traits every year on every registered female; however, uptake of this method for gathering phenotypic information has been slow (Cammack et al., 2009b), as it is labour-intensive and requires excellent record keeping. Further, reproductive traits are frequently binary in nature, and some require accurate reporting over a long period of time (such as stayability). As a result of this large amount of unaccountable variation, heritabilities of reproductive traits are generally low compared to other performance traits (Veerkamp and Beerda, 2007). Counter to popular producer thought, these low heritability numbers do not mean that selection for reproductive traits is impossible (Cammack et al., 2009b); rather, that genetic progress from selection will be slow and more generations of careful selection will be required to reach producer goals. Both Veerkamp and Beerda (2007) and Cammack et al. (2009b) describe multiple reproductive measures and their heritability estimates in dairy cattle (Veerkamp and Beerda, 2007) and beef cattle (Cammack et al., 2009b), where estimates of heritabily for reproductive traits were low.

Beef female fertility has been measured in a multitude of ways, including age at puberty, age at first calving, stayability, longevity, and pregnancy rate, among others. However, as objective reproductive traits are rare (many rely on producer-supplied scales or binary codes), genetic correlation with other, objective, and easy-to-measure traits are useful to ensure selection maximises the calf crop percentage of herd. Berry and Evans (2014) estimated genetic correlations between many different reproductive and production traits, using the Irish national beef herd. Greater muscularity was generally negatively correlated with reproductive performance (Crowley et al., 2011; Berry and Evans, 2014). The positive genetic correlations (0.19) between body size and age at first calving reaffirm that larger cattle are also slower maturing (Berry and Evans, 2014). Genetic correlations between BCS (measured on a thin-to-fat scale) and reproductive performance indicated that genetically higher BCS cows had better reproductive performance (Berry and Evans, 2014). Suggestions for enhancing genetic selection of reproductive traits are discussed later in this review.

2.9.2. Calving interval & post-partum interval

Calving interval defines the period between consecutive parturition events. Cows are expected to calve no more than 365 d after their previous parturition event, and cows that have the shortest calving intervals are commonly interpreted to be the most fertile. However, in beef production systems that utilize a limited breeding period, Bourdon and Brinks (1983) and Marshall et al. (1990) determined calving interval to be a biased trait. Cows that calve earlier in the previous parity have longer subsequent calving intervals than cows that calve late in the season, a bias that is due directly to the effects of herd management. As a result, many studies observe that cows exhibit the longest calving interval between their first and second calving events (Bourdon and Brinks, 1983; MacGregor and Casey, 1999). Calving interval is not a broadly useful metric for evaluating the fertility of beef cows under common restricted breeding season management protocols. The large effects of environment and management on breeding interval were observed in a low heritability of 0.02 ± 0.004 reported by Berry and Evans (2014). Genetic change in the calving interval of beef cattle is possible, but would take a considerable amount of time and effort on the behalf of cattle producers and would not be as effective as altering management styles to ensure that cows could calve every 365 d.

Post-partum interval is defined as the period between a parturition event and the first subsequent estrus event; it is the period that includes uterine involution and preparation for another pregnancy. The length of the post-partum interval is of obvious importance to cattlemen, as a short period between calving and return to estrus increases the opportunities that a cow will have to become pregnant again. Cows with long anestrous periods would have fewer estrous cycles and estrus events during the breeding season if they only return to estrous cycles after bull exposure has started. Improvement in post-partum interval may be possible. Among a population of tropically adapted crossbred cattle and purebred Brahmans, Zhang et al. (2013) reported moderate to high heritabilities of 0.29 and 0.51, respectively. Further, accuracies for the trait within a validation population were moderate and indicated that selection for post-partum interval was possible. However, there is a strong connection between nutrition and post-partum interval, where cows that are in poor body condition or lacking micronutrients have longer post-partum intervals than those that are in adequate body condition and not nutrient-restricted.

2.9.3. Longevity

Longevity is defined as the length of time a female remains in a breeding herd, or occasionally the length of time between birth and disposal or death. In some analyses, stayability is used as a proxy for longevity, and defined as the probability that a cow has three (or more) calves given that she calves a first time. Longevity of a beef cow is a trait of interest for primary beef producers because having cows that remain productive for a longer time reduces the number of replacement heifers required per year (along with associated costs), reduces the number of young cows in the herd, and could reduce the number of cows required to produce a set number of calves (Núñez-Dominguez et al., 1991; Roberts et al., 2015). Herds with greater longevity tend to have an older average cow age, which could influence the average weaning weight of the calf crop, as mature cows typically produce heavier calves than cows in their first and second parity (Kress et al., 1990; Roberts et al., 2015; Mulliniks et al., 2019).

Selection for longevity from a genetic standpoint is challenging. As with many other reproductive traits in beef cattle, heritability estimates for longevity and related traits (stayability, etc.) are moderate (Tanida et al., 1988; Snelling et al., 1995; Jamrozik et al., 2013), though genetic progress in improving longevity has been slow (Roberts et al., 2015). Longevity and related traits are difficult to analyse due to the time required to collect data – a cow must live to the stated endpoint in order to produce data for analysis. Further, despite widespread use of stayability EPDs in purebred breed associations in North America, genetic trends for longevity-related traits illustrate low rates of improvement primarily due to the time required to report usable data (many breed associations use stayability 1|5, or the probability (%) that a cow has 5 calves or lives to 6 years of age). Traits such as longevity are prime examples of the importance of improving genetic prediction methods in beef cattle.

2.9.4. Lifetime productivity

Lifetime productivity is closely related to longevity and is defined as the sum of either actual or adjusted weaning weights for a dam (Basarab et al., 2018). As a result, there is considerable correlation between a cow's lifetime productivity and her longevity, as cows that remain in the herd for more parities have more calves and therefore more total lifetime productivity. In a study of 412 crossbred Angus cows, Basarab et al. (2018) reported that cows with increased levels of retained heterozygosity produced 142 kg more calf weight than cows with lower retained heterozygosity. Those same high-retained heterozygosity cows lived 204 days longer and 25.6% of them survived to parity 5 (6 years of age) compared to 16.9% of low heterozygosity cows surviving to the same age. As a result, cows with greater retained heterozygosity had more breeding and weaning opportunities, which translated to increased total pounds of calf produced per cow.

Again, as with longevity, heritability of lifetime productivity was reported at 0.15 (Martinez et al., 2004) and challenged by the ability of producers to maintain accurate weaning records for each cow over her productive life, and the time required to collect such data (Roberts et al., 2015).

2.10. Advancements in reproductive technology

As in other areas of beef cattle management, technology in beef reproduction has many applications. From the use of estrus synchronisation and fixed-time artificial insemination (TAI), through pregnancy diagnosis via ultrasound or blood test, to products such as Moocall (Moocall Ltd., Co. Dublin, Ireland) and other devices used to predict calving events (Saint-Dizier and Chastant-Maillard, 2015), technology has worked to improve on nature's design. Perhaps one of the clearest, and earliest, examples of technology in beef reproduction is the use of AI for breeding. Artificial insemination provides an economical and reliable means of collecting and distributing semen from superior sires (Foote, 2002), as well as improving the accuracy of the calving season and the ability to shorten the breeding and calving seasons, as with TAI. Semen was used fresh in the late 1890's and early 1900's in both Russia and Japan, limiting its use to local areas near the withdrawal site (Foote, 2002). With the innovation of extending semen and freezing with liquid nitrogen in the late 1940's and early 1950's, superior male germplasm could be transported around the world and used in cows anywhere (Foote, 2002). Thus, accessibility to superior genetics became simple and affordable, and AI technology is credited with being one of the most important biotechnologies ever applied to livestock production (Foote, 2002). Recently, Crosswhite et al. (2016) found that pregnancy rates were not different between ovulation-synchronised TAI cows exposed to bulls after AI, and cows that were only exposed to natural service. However, TAI cows calved earlier, and had larger calves at weaning than cows exposed to only natural breeding. Artificial insemination is an excellent tool for the economical importation of superior genetics to improve economically relevant traits in beef cattle.

In conjunction with the use of AI, estrous and ovulation synchronisation has also become well known. Estrus synchronisation can shorten the calving season and thereby improve calf uniformity, as well as facilitate the use of AI (as in the case of fixed-time artificial insemination). Estrus synchronisation under natural service can be as simple as a single administration of prostaglandin $F_{2\alpha}$, such as Estrumate (Merck Animal Health, Kirkland, QC, Canada) or Lutalyse (Zoetis, Parsippany, NJ, USA), which serves to promote a return to estrus earlier than normal. A single intramuscular dose can cause a majority of cows to come into estrus within days. However, this is not an effective treatment if a corpus luteum is not present at the time of administration. In situations where estrus occurrence must be more precisely managed for TAI, several multiple-step protocols have been established to ensure that all cows exposed to TAI are ovulating at the appropriate time. Lamb et al. (2010) reviewed multiple estrous synchronisation protocols for both multiparous cows and replacement heifers. Protocols varied in number of handling events and effectiveness, and heifers did not respond as positively to synchronisation as mature cows. However, protocols involving controlled internal drug release (**CIDR**) vaginal implants and a combination of prostaglandin and progesterone treatments provided reliable estrus for TAI (Lamb et al., 2010). Among heifers at 12 locations and administered 1 of 4 protocols, pregnancy rates were higher in heifers which were observed for estrus and bred following the am/pm rule (heifers in estrus in the morning were bred that evening, and vice versa) than in heifers bred via TAI using ovulation synchronisation (Lamb et al., 2006). Weaning rates between protocols were not observed.

Both TAI and estrus synchronisation have economic advantages over natural service alone. Calves from an AI protocol are generally born earlier than their natural service counterparts, and thus are heavier and more uniform when they are marketed

(Johnson and Jones, 2008; Rodgers et al., 2012). In addition, there are cost savings to producers covering at least a portion of their herd through AI, as fewer bulls are needed to breed the entire herd, reducing feed and labour costs (Johnson and Jones, 2008; Rodgers et al., 2012). Further, calves from AI sires are assumed to be genetically superior to calves from natural sires, as cost of excellent beef sires is usually too high for commercial producers. However, AI allows access to superior genetics, which may increase calf performance or value in the future (Johnson and Jones, 2008). This makes AI a very important tool in the improvement of reproductive traits in beef cattle, but one that is underused in the industry.

Once a female has been exposed to breeding, many producers want to verify that she is pregnant before carrying her through the winter on feed. Depending on the year and market conditions, however, it may make more financial sense to keep all cows for the winter and cull open females in the spring, or even rebreed and market those cows as bred fall-calving cows (Canfax, 2015). Regardless, it is a good practice to subject cows to pregnancy determination and cull open females to eliminate potentially infertile or sub-fertile genetics from the herd. Pregnancy determination may also allow prediction of calving date and permit different management groups based on expected calving date. Three common methods for pregnancy determination are currently in use: palpation per rectum of uterine contents, ultrasound, and blood testing for the presence of pregnancy-specific protein B (Bridges et al., 2008). Palpation per rectum of uterine contents is the oldest and most commonly used method for pregnancy diagnosis (Momont, 1990) and is especially accurate 45 d or more post-breeding, though experienced practitioners are often able to detect pregnancy after 35 d (Momont, 1990). Some concern about damage to the embryo has been raised in the past (Paisley et al., 1978), but Romano et al. (2007) found no effect of early (d 34-41) palpation per rectum on embryo loss in dairy cows. Palpation per rectum for pregnancy diagnosis can also offer calving date prediction based on calf size, placentome development, and other symptoms of pregnancy (Momont, 1990; Matthews and Morton, 2012), which is especially useful for predicting a calving date when the actual breeding date is unknown, as in the case of unlimited breeding seasons. In addition to palpation per rectum of the reproductive organs, transrectal ultrasound has been widely used. Pieterse et al. (1990) found that transrectal ultrasound was accurate for pregnancy detection in dairy cows (2-10 y of age) as early as 26 d post-breeding. However, ultrasound requires specialist training and is not generally available to producers outside of veterinary assistance, is only somewhat less time-consuming as palpation per rectum, and requires the use of expensive equipment. Finally, the most recent method to diagnose pregnancy is blood testing for pregnancy-associated glycoproteins (**PAGs**), particularly pregnancy-specific protein B (**PSPB**). BioPRYN (BioTracking Inc., Moscow, ID) testing for PSPB and DG29 (Conception Inc., Beaumont, QC) testing for PAG are both available to producers in Canada and offer sensitivity rates as high as 95% (Paré et al., 2008). In addition to simply providing pregnancy rates, testing methods behind BioPRYN and DG29 may also be able to verify embryonic viability by measuring PAGs, where cattle that undergo embryonic mortality expressed lower PAGs than cattle that maintained a pregnancy (Pohler et al., 2015). Limited genetic information is available concerning early embryonic death loss in beef cattle (Pohler et al., 2015; Taylor et al., 2016), but levels of hormones and glycoproteins may play an important role in identifying what drives early embryonic death loss in beef cattle (Pohler et al., 2013). While pregnancy testing itself may not improve weaning rates, the information it provides enables producers to make economically sound culling decisions and is a crucial part of yearly management.

Recently, the identification of haplotypes which cause embryonic death loss in dairy cattle led to the development of a genetic test for beef cattle. This genetic test, offered commercially by GeneSeek (Neogen, Lansing, MI, USA), has the potential to identify lethal gene combinations that may be implicated in embryonic death loss. By evaluating gene combinations which only occur in the sample population in the heterotic form, researchers may be able to identify lethal genes and lethal gene carriers and provide producers with a tool to manage their animal breeding practices accordingly (Taylor et al., 2016). This technology is available, but the causal genes associated with embryonic death loss have not been identified yet. Among several dairy breeds, as many as 8 genes have been identified and likely contribute to instances of embryonic death, and 3 more are implicated in reduced growth and higher mortality rates (Fritz et al., 2018). The observed decrease in fertility performance among the dairy breeds has probably resulted from their development out of a small number of founding animals, with some heavily used sires potentially contributing thousands of animals to the population (Georges et al., 2019). Subsequently, inbreeding rates are high in dairy cattle – 50% of the gene pool among dairy animals can be explained by 10-20 common ancestors (Fritz et al., 2013).

2.11. Challenges in improving reproductive efficiency

2.11.1. Technology adoption

As has been discussed, reproductive efficiency, by any metric, is dynamic, complex, and therefore difficult to manage on the extensive cow-calf operations of Western Canada. However, current and future technologies can ensure that cow-calf operations are improving their calf crop percentage, in addition to growth performance. Technology adoption appears to be one of the largest barriers to reproductive advancement; producers are not adopting some key technologies that could provide access to improved genetics, better breeding and calving season control, or even information on the nutritional status of their herd. The Alberta Cow-Calf Audit in 1997/1998 stated that only 49% of Alberta beef producers pregnancy determined their herd (Audit, 2001). In 2014, the number of cows and heifers that were pregnancy determined rose to 63% (Larson, 2015), but that still leaves 37% of Western Canadian producers unsure of their herd's pregnancy status for any given year. Additionally, even though it provides access to new or superior genetics, improve economic returns, and can reduce bull inventory, only 18% of Western Canadian producers were using AI technology on some or all of their herd, and estrus synchronisation was used in just 11.3% of herds (Larson, 2015). This contradicts the results of a national survey conducted by BEEF magazine in 2013, where producers identified AI technology as the second-most valuable innovations of the past 50 years (Ishmael, 2013). Even among large U.S. producers (a population associated with higher rates of technology adoption), a 2007-2008 USDA survey reported that AI was used in only 7.6% of all herds, and estrus synchronisation was used in 7.9% (USDA, 2009). Artificial insemination usage is higher in heifers than in mature cows (Ishmael, 2013; Larson, 2015), and highest in operations with more than 200 hd (USDA, 2009). However, the benefits of using AI are not being fully realised in the Western Canadian cow herd.

Additionally, not all producers are regularly monitoring animal BCS at any point during the year, despite its correlation with reproductive efficiency. In the Western Canadian Cow-Calf Survey conducted in 2014, 81% of producers who responded did not record BCS, and 78% did not weigh their cattle (Larson, 2015). Among American producers, 14.3% recorded BCS nationally, but 34% of producers with more than 200 hd recorded BCS (USDA, 2009). Body condition scoring is closely related to reproductive efficiency (Arnett et al., 1971; Selk et al., 1988; Short and Adams, 1988; Osoro and Wright, 1992), and a lack of monitoring may reflect a lack of producer understanding. However, it is also likely that producers that are not monitoring BCS have no concerns about the BCS of their animals and so do not feel it is necessary to monitor BCS. In the event of severe drought, it would be interesting to observe if BCS monitoring increased in Western Canada. American producers located in the drier Western and Central geographic regions of the U.S. reported numerically higher proportions of operations which monitored BCS (19 and 21% respectively; USDA, 2009) than producers in the wetter South Central and Eastern regions. This may reflect heightened drought awareness among producers in the Western United States, better understanding of management, and/or more supportive beef extension programs, as well as the fact that operations in the western half of the U.S. are, on average, nearly twice the size of

Eastern and South-Central operations (USDA, 2009). If reproductive efficiency is to be improved in the Western Canadian cowherd, greater emphasis should be placed on the adoption of existing management techniques and technology. The areas of reproductive management and appropriate nutritional maintenance are applicable, relatively simple to implement, and have track records of improving production.

2.11.2. Genetic selection

The genetic selection of superior animals is paramount to moving the beef industry forward in all forms of production, so long as management and nutrition can support improvement. The beef industry in Canada has been challenged regarding genetic improvement, with 28 recognised beef breeds represented in the country and a lack of reliable data for genetic improvement of reproductive traits (Berry et al., 2016). Data reported to purebred associations related to reproductive traits in beef cattle are often codes (binary yes/no pregnancy results, stayability, weaning and birthing data, for example), are subjective (measures of calving difficulty differ between producers), and frequently unreported due to time constraints, lack of initial data collection, or even confusion among producers as to the importance of maintaining records (Cammack et al., 2009b; Berry et al., 2016). This results in low accuracies and unreliable EPD values for important reproductive traits among purebred animals. In the commercial cow-calf industry, phenotype reporting for any trait, reproductive or otherwise, is negligible and often even sire of calves is not recorded or genomically verified (Berry et al., 2016). The improvement of genetic selection practices for beef reproductive traits is possible, especially when considering the genetic tools available to producers now. Sire verification, heterogeneity estimates, genomic prediction and genomically-enhanced EPDs (**GEPD**) are all becoming more accessible to beef producers and can be used to improve selection criteria for existing traits and correlated traits.

In Canada, producers have been encouraged to take advantage of additive and non-additive genetic effects through the processes of crossbreeding since the introduction of exotic cattle breeds in the late 1960's (Slen and Cameron, 1969). Prior to the availability of exotic genetics, crossbreeding had been widely investigated in Western Canada, even to the point of the importation of 4 purebred Brahman bulls to the Canada Department of Agriculture Experimental Substation at Manyberries, Alberta in 1950 for experimental crossbreeding on Shorthorn, Angus, and Hereford cows (Peters and Slen, 1967). Interestingly, those authors note the particular hardiness and thriftiness of the F_1 Brahman-British females, which outperformed the straight-bred Hereford dam measures of weaning weight, total lifetime productivity, and longevity despite the tropical adaptations of the Brahman genetics and the relatively severe winters experienced at the Manyberries Research Station. These results generally agree with the notable work of Larry Cundiff and others at the U.S. Meat Animal Research Centre (Clay Center, NE), who reported that crossbred Hereford × Angus, Shorthorn × Angus, and Shorthorn × Hereford cows (and their reciprocal crosses) outperformed their straight-bred counterparts in the percentage of the population that conceived at the first breeding, were pregnant at the end of the breeding season, retained a pregnancy to the fall, carried a calf to full term, calved a live calf, kept the calf alive past two weeks of age and weaned a live calf, weaned heavier calves, and weaned more pounds of calf per cow exposed (Cundiff et al., 1974a). Further, Cundiff et al. (1974b) found that crossbred dams birthed heavier calves and weaned heavier calves and reported that those calves went on to grade higher at slaughter than the calves born to purebred Angus, Shorthorn, or Hereford cows. They also reported greater milk production at 6 weeks post-calving and at weaning compared to straightbred counterparts. Those reports from the United States have been corroborated in Canada as well, with reports like Arthur et al. (1993) who found that the longevity of crossbred beef cows was greater than the longevity of purebred Hereford cows, under very strict culling protocols. The crossbred beef cows also weaned more calves with heavier average weaning weight than the Hereford cows. Taken together, the abundance of knowledge concerning crossbreeding and its effects on beef cow reproductive efficiency and productivity indicates that Canadian beef producers should be utilizing heterosis to a greater extent. Indeed, the commercial cow-calf herd in Canada today is primarily made up of crossbred females (WBDC, 2015). However, recent trends in beef marketing through breed-based value-added programs may be changing the amount of heterozygosity in the national herd. The National Beef Quality Audit, completed in 2016 by the National Cattlemen's Beef Association, revealed a trend toward the homogenization of the U.S. beef herd. The proportion of black-hided cattle coming to slaughter has increased, from 45.1 in 2000 to a high of 61 percent in 2011. In North America, one breed, Aberdeen Angus, is primarily responsible for black coat colour. Many breeds have crossed with Angus cattle, as they are highly maternal, naturally smooth polled, and produce excellent carcasses that are eligible for premium domestic and international markets. This focus on breeding black cattle that are eligible for the Certified Angus Beef marketing program may be starting to limit the heterogeneity of the commercial cow herd.

Genetic improvement of beef reproductive performance has relied on the accurate and timely reporting of relevant traits by producers. Unfortunately, the reproductive traits currently measured by breed associations are not necessarily accurate, due to subjectivity and the use of limiting binary codes for reporting, as many traits are not quantitative. However, it is possible to improve the genetic selection of reproductively efficient animals through correlated selection of indicator traits that are easier to record and have better heritability. Recent work in dairy animals has revealed predictive, easily measured traits with genetic correlations to reproduction. Anogenital distance is inversely related to the likelihood of pregnancy to the first AI in first and second parity dairy cows (Gobikrushanth et al., 2017), and dairy cows and heifers were both more likely to be pregnant after the first AI if they had serum insulin-like growth factor 1 higher than .31 and .85 ng / mL, respectively (Gobikrushanth et al., 2018). Both traits are easy to measure (neither require special equipment and can be accomplished in conjunction with normal stock handling events) and heritable with reported estimates of heritability of 0.46 ± 0.31 for circulating insulin-like growth factor 1; heritability was not reported for anogenital distance. Selection for them may improve the reproductive performance of dairy cattle. Exploration into novel indicators of reproductive performance should be a priority for the Canadian beef industry.

2.12. Conclusion

The Canadian beef industry has improved markedly in many areas over time. Genetic increases in animal efficiency and productivity, improvements in nutrition and management, and an emphasis on the quality and consistency of the product have resulted in fewer cattle producing more beef, using fewer resources, and contributing less to environmental impact. However, challenges still exist concerning the reproductive efficiency of the cow herd, which is hampered by considerable environmental influence and the lack of continuous data collected without producer bias. Methods to improve reproduction can be antagonistic to other production goals, and often reproductive efficiency is overlooked in favour of the low-hanging fruit presented in growth and quality traits. However, the beef industry cannot overlook the improvement of reproduction for much longer, lest it follow the example set by peers in the dairy industry. In the pursuit of increased milk production, which improved impressively through genetic selection, the fertility of the modern dairy cow is found wanting. Beef producers should use this as a cautionary tale and look to take proactive steps in the selection of beef replacement females.

Challenges associated with reproductive selection include the time required to collect data. In many instances, such as lifetime productivity and longevity, phenotypic records can only be solidified and reported for genetic analysis after a cow has lived out her productive life – more than 15 years in some instances. Further, the current methods of recording such data are often binary or coded and subjective. All of these factors are then mixed with a very large influence of environment, nutrition, and management, and result in very low heritabilities and result in very slow or no genetic improvement per generation.

Methods of improving reproduction in the Canadian cow herd could include using related traits, measured earlier in life, as a proxy for the actual trait in question. Given relationships between feed efficiency and feeding behaviour, or dry matter intake, cows could be selected based on the results of feed intake tests as replacement heifers and selected for reproductive efficiency by their genetic correlation. However, it is crucial that beef producers pay close attention to the correlated responses to such selection. As such, indices that include proxy measurements for genetic selection to improve reproduction should be developed and employed. Through careful examination of years of reproductive data, such indices could be developed and deployed to cattlemen. However, as has been observed with other novel selection traits, care must be taken by the academic community developing the indices to properly educate and emphasise the selection tools. Beef producers have been historically slow to adopt new selection tools or other intangible management techniques, and often fall into the habit of selection for economically relevant traits with more immediate results (i.e., weaning weight single-trait selection). Through proper development and deployment, any tool developed that improves producer’s ability to increase reproductive efficiency in the cow herd would benefit the producer economically by reducing input cost and improving outputs. In order to develop and deploy effective genetic selection tools to producers, certain knowledge gaps need to be addressed, which include identification of important indicator traits such as feed intake and feeding behaviour and their heritability, genetic correlations of the indicator traits with reproductive performance, and ensuring that such selection pressure does not negatively influence other areas of production.

3. SHORT COMMUNICATION: PHENOTYPIC AND GENETIC CORRELATIONS BETWEEN FEEDING BEHAVIOURS AND FEED EFFICIENCY IN CROSSBRED BEEF REPLACEMENT FEMALES

3.1. Abstract

Objectives were to identify the phenotypic and genetic relationships and heritability (**h²**) of feeding behaviours in replacement beef females. Between 2005 and 2017, heifers (N = 1394) were tested for feed intake using an electronic feed bunk system. Feeding behaviours (**FB**) were: **DUR**, min d^{-1}, **HD**, min d^{-1}, **FREQ**, events d^{-1}, **TTB**, min; **DMI**, kg d^{-1} and RFI_{FAT} were also reported. Heritability estimates for DUR, HD, FREQ, TTB, DMI, and RFI_{FAT} were 0.25 ± 0.05, 0.26 ± 0.06, 0.27 ± 0.05, 0.29 ± 0.06, 0.26 ± 0.05, and 0.40 ± 0.07, respectively. These are the first h^2 to be presented for these FB among developing replacement heifers on a high-forage diet.

Keywords: cattle, behaviour (feeding), correlation (genetic), heritability, heifer (replacement)

Abbreviations: FB, feeding behaviour; **DUR**, feeding duration; **HD**, head-down time; **FREQ**, feeding frequency; **TTB**, time-to-bunk; **DMI**, dry matter intake; RFI_{FAT}, residual feed intake adjusted for ultrasound back fat thickness

3.2. Introduction

Feeding behaviours (**FB**) measured during dry matter intake (**DMI**) test in cattle housed in feedlot environments has demonstrated moderate phenotypic and genetic correlations with animal growth and efficiency (Nkrumah et al., 2007; Chen et al., 2014). However, FB in developing crossbred replacement heifers in dry lot settings have not been reported. Given relationships that have been observed between FB and growth and efficiency traits, it is possible that FB could be useful in identifying replacement females with improved growth, efficiency, and reproduction, and so these relationships are of interest to the beef industry. The purpose of this short communication was to identify the phenotypic and genetic relationships between FB measured in developing replacement heifers.

3.3. Materials and methods

Nine hundred ninety-one heifers were maintained at the Agriculture and Agri-Food Canada Lacombe Research and Development Center (**LRDC**, Lacombe, AB, Canada), and 403 heifers were located at the University of Alberta's Roy Berg Kinsella Research Station (**KIN**, Kinsella, AB, Canada). All heifers were cared for according to guidelines of the Canadian Council on Animal Care (CCAC, 1993).

3.3.1. Description of animals and herd management

The replacement heifers were, on average, 62% Angus (**AN** sum of red and black), 15% Hereford (**HE**), 15% Charolais (**CH**), 6% Simmental (**SM**), 5% Limousin (**LM**) and 3% other breeds as determined by genomic analysis.

In both locations, heifer calves born between March and May each year remained with their dams until weaning at 6-7 mo of age. All calves were vaccinated with Bovi-Shield Gold FP5 VL5 (Pfizer Animal Health, Pfizer Canada Inc., Kirkland, QC, Canada) for infectious bovine rhinotracheitis, parainfluenza-3 virus, bovine viral diarrhea, and bovine respiratory syncytial virus; One Shot Ultra (Pfizer Animal Health) for *Pasteurella multocida*; and Ultrabac 7/Somnubac (Pfizer Animal Health) for *Haemophilus somnus* and clostridial diseases at 2–2.5 m of age. Six weeks before weaning, heifers received booster vaccinations and an Ivomec parasiticide (Merial, Baie-d'Urfe, QC, Canada). At weaning, LRDC heifers were fed a 90% barley silage and 10% steam-rolled barley grain diet (as-fed) over a 30-40 d adaptation period. The heifers were then performance tested for feed intake for at least 70 d. Nutrient composition of the test diet and days on test for LRDC-housed heifers were reported by Callum et al. (2018) for 2005 to 2013. Years 2014 and 2015 were similar; with total digestible nutrients = 62.4% and 66% and days on test 76 and 75 d, respectively at LRDC. Kinsella Research Ranch heifers were fed a silage-based diet between 50% and 70% barley silage with total digestible nutrients between 66% and 70% and were on-test an average of 80 d. Heifers remained on the diet and in confinement post-test until mid-May of each year, when they were placed on mixed-species cool-season pasture.

3.3.2. Feeding behaviour and feed intake

Feed intake and FB were collected on 1394 replacement heifers using the GrowSafe automated feed bunk systems (GrowSafe Systems Ltd., Calgary, AB, Canada) located at LRDC and KIN. Heifers were tested for feed intake post-weaning, between mid-February and April of each year for at least 70 d. All replacement heifers were fed in a dry lot setting, in pens that were fitted with 8 automated feed bunks per pen at both locations (4-6 animals per bunk). Feed intake (kg DM d^{-1}) and FB were collected continuously for the duration of the test period. Feeding behaviours collected were feeding duration (**DUR**; min d^{-1}), feeding frequency (**FREQ**; events d^{-1}), head down time (**HD**; min d^{-1}), and time-to-bunk (**TTB**; min; Jackson et al. (2016)). A single feeding event began when an animal's radio-frequency identification (RFID) tag was detected by the automated feed bunk antenna at a single feeding node and ended when a) the time between the last two readings was longer than 300 s (Schwartzkopf-Genswein et al., 2002), b) another animal's transponder tag was detected, or c) the same RFID tag was detected at another node. Feeding duration is defined as end time of a feeding event minus start time of that feeding event. Head down duration is similar but is the number of occasions an animal's transponder was picked up by the GrowSafe system, multiplied by the scan rate of the system (2 s). These traits were summed for daily totals, then averaged for each animal to provide average DUR, average HD, and average FREQ. Time-to-bunk is the average difference over the feed test between the first feed delivery event in a day and the first subsequent feeding event in that day. Of the 1394 heifers, 1205 had TTB available for analysis due to differences in early GrowSafe system recording settings.

3.3.3. Trait derivation and statistical analysis

Residual feed intake adjusted for off-test ultrasound back fat thickness (**$\mathrm{RFI}_{\mathrm{FAT}}$**) calculations are thoroughly reviewed in Basarab et al. (2011). Briefly, $\mathrm{RFI}_{\mathrm{FAT}}$ was computed as the difference between standardised DMI (kg DM d^{-1}) and expected feed intake per animal. Expected standardised DMI was found using a linear regression of standardised DMI on ADG (kg^{-1}), metabolic mid-test body weight ($\mathrm{kg}^{0.75}$) and end-of-test ultrasound back fat thickness (mm).

Phenotypic and genetic variances and covariances were estimated for each of the feeding behaviours using a bivariate animal model (ASReml 4.1; Gilmour et al. (2015)):

$$\begin{bmatrix} y_1 \\ y_2 \end{bmatrix} = \begin{bmatrix} X_1 & 0 \\ 0 & X_2 \end{bmatrix} \begin{bmatrix} b_1 \\ b_2 \end{bmatrix} + \begin{bmatrix} Z_1 & 0 \\ 0 & Z_2 \end{bmatrix} \begin{bmatrix} a_1 \\ a_2 \end{bmatrix} + \begin{bmatrix} W_1 & 0 \\ 0 & W_2 \end{bmatrix} \begin{bmatrix} c_1 \\ c_2 \end{bmatrix} + \begin{bmatrix} e_1 \\ e_2 \end{bmatrix}$$

In which y_1 and y_2 are vectors of phenotypic values for any 2 traits considered in the model, b_1 and b_2 are vectors of fixed effects for trait 1 and trait 2, respectively, a_1 and a_2 are vectors of random additive genetic effects, c_1 and c_2 are vectors of random contemporary effects, and X, Z, and W are known design matrices for fixed effects, random additive genetic effects, and random contemporary effects, respectively. e_1 and e_2 are vectors of random residual effects. The fixed effects for the FB traits were breed composition (percentage by genomic breed composition of Angus, Charolais, Hereford, Limousin, Simmental, Shorthorn, and(or) Beefbooster), and age at day 0 of the GrowSafe feed intake test. Heifers weaned and performance tested together in the same year were placed in a contemporary group. For these analyses, multivariate normal distributions were assumed for the random vectors $a, c,$ and e with means equal to 0, which led to $E(y) = Xb$. The variance – covariance matrix for the random effects is described below:

$$\begin{bmatrix} a_1 \\ a_2 \\ c_1 \\ c_2 \\ e_1 \\ e_2 \end{bmatrix} = \begin{bmatrix} A\sigma_{a_1}^2 & A\sigma_{a_1a_2} & 0 & 0 & 0 & 0 \\ A\sigma_{a_1a_2} & A\sigma_{a_2}^2 & 0 & 0 & 0 & 0 \\ 0 & 0 & I_{n_c}\sigma_{c_1}^2 & I_{n_c}\sigma_{c_1c_2} & 0 & 0 \\ 0 & 0 & I_{n_c}\sigma_{c_1c_2} & I_{n_c}\sigma_{c_2}^2 & 0 & 0 \\ 0 & 0 & 0 & 0 & I_{n_e}\sigma_{e_1}^2 & I_{n_e}\sigma_{e_1e_2} \\ 0 & 0 & 0 & 0 & I_{n_e}\sigma_{e_1e_2} & I_{n_e}\sigma_{e_2}^2 \end{bmatrix},$$

in which $\sigma_{a_1}^2$, $\sigma_{a_2}^2$, and $\sigma_{a_1a_2}$ refer to the additive genetic variance for trait 1, trait 2, and their genetic covariances, respectively; A is the additive genetic relationship matrix constructed from a 1 generation pedigree that included 1394 animals and their 117 sires; $\sigma_{c_1}^2$, $\sigma_{c_2}^2$, and $\sigma_{c_1c_2}$ are the variances and covariances of contemporary group effects; likewise $\sigma_{e_1}^2$, $\sigma_{e_2}^2$, and $\sigma_{e_1e_2}$ are the variances for traits 1 and 2 and covariances of residual errors, respectively; I_{n_c} and I_{n_e} are the identity matrices, where n_c is the number of random contemporary groups and n_e is the number of animals with phenotypic records (when TTB was considered in a bivariate analysis, the N of the analysis was 1205). All components were estimated by REML using ASReml 4.0 software.

Phenotypic variances (σ_p^2) were calculated in ASReml 4.0 by summing variances of additive (σ_a^2), contemporary group (σ_c^2), and residual effects (σ_e^2). Phenotypic covariances were derived as $\sigma_{p_1p_2} = \sigma_{a_1a_2} + \sigma_{c_1c_2} + \sigma_{e_1e_2}$. Phenotypic and genetic correlation coefficients were computed as $r_p = \sigma_{p_1p_2} / \left[\left(\sigma_{p_1}^2 \sigma_{p_1}^2 \right)^{1/2} \right]$ and $r_a =$

$\sigma_{a_1a_2}/\left[\left(\sigma^2_{a_1}\sigma^2_{a_1}\right)^{1/2}\right]$, respectively. For these analyses, heritability was estimated as: $h^2 = \sigma^2_a/\sigma^2_p$. Heritability estimates were averaged over all bivariate analyses of the trait.

3.4. Results and discussion

Table 3.1. Mean (SD), number of animals (N), range, and CV for feeding behaviour and efficiency traits in replacement heifers

Trait	Mean (SD)	N	Range	CV, %
Birth weight, kg	39.3 (4.7)	1394	23 to 58	11.89%
Wean weight, kg	244.3 (25.7)	1394	152 to 335	10.52%
Age at start of test, d	288 (38)	1394	202 to 383	13.25%
Duration, min	150.4 (35.6)	1394	33.6 to 285.6	23.70%
Frequency, events	89.9 (29.4)	1394	8.81 to 179.6	32.71%
Head down, min	93.0 (30.5)	1394	12.1 to 195.1	32.81%
Time to bunk, min	40.7 (24.8)	1205	1.5 to 156.0	60.91%
Dry matter intake, kg	7.87 (1.12)	1393	4.59 to 12.25	14.17%
RFI$_{\text{FAT}}$	-0.01 (0.43)	1391	-1.93 to 1.65	--

Summary statistics including mean, SD, and CV are presented in Table 3.1. Mean values for DUR, FREQ, and HD were considerably greater in this study than those reported by both Nkrumah et al. (2007) in a population of crossbred beef steers and Chen et al. (2014) in purebred Angus and Charolais steers of similar age. However, they are similar in magnitude to the behaviours reported by Callum et al. (2018) among commercial replacement heifers. Diet composition was notably different between the present study and the feedlot finishing diets used in both Nkrumah et al. (2007) and Chen et al. (2014) and likely has a role to play in the longer feeding times and greater feeding frequencies observed here. Average DMI observed in the present study was similar to DMI reported on high-forage diets in Durunna et al. (2011) and Callum et al.

(2019), but less than that reported by Nkrumah et al. (2007) and Durunna et al. (2011) on feedlot finishing diets. Durunna et al. (2011) concluded that differences in FB between grower and finisher diets could have been due to diet particle size, with the larger particle size of the grower diet necessitating greater chewing and sorting behaviours, adding to the time animals spent feeding. The diets provided for the heifers in this present study were very high in roughage (>50% silage, up to 90%) compared to the grower diet used by Durunna et al. (2011), which was 20% hay and 80% oats and supplement. The greater DUR, HD, and FREQ observed in this study were likely due to the large percentage of roughage in the diets and highlights the importance of analysing FB across cattle diets. Further differences in management, breed composition, and sex could also play a role in the observed differences between studies.

Estimates of heritability (h^2), phenotypic, and genetic correlations among FB are presented in Table 3.2. Heritability estimates for DUR, HD, FREQ, and TTB were 0.25 ± 0.05, 0.26 ± 0.06, 0.27 ± 0.05, and 0.29 ± 0.06, respectively. Estimates of h^2 for DMI and RFI_{FAT} were 0.26 ± 0.05, and 0.40 ± 0.07, respectively. Heritability estimates in this study for DUR and FREQ were similar to the estimates provided by Nkrumah et al. (2007). The estimate of h^2 for FREQ were lower than those reported by Nkrumah et al. (2007), Durunna et al. (2011), and Chen et al. (2014). Heritability estimated for RFI_{FAT} in the present study fell in the range reported by Crews (2005) in a review of the genetics of RFI. Durunna et al. (2011) found that h^2 for DUR and HD decreased when crossbred steers were switched from a grower diet (74% oats, 20% hay, 6% supplement) to a finisher diet (57% barley, 28% oats, 10% alfalfa pellets, and 5% supplement), which could be due to differences in the time steers needed to consume the different diets. However, the h^2 estimates reported in this study are more consistent with the values of steers on the grower diet, which had more roughage than the finisher diet and was more similar to the high-roughage, low-concentrate development diet fed to the heifers in the present study. To our knowledge, no estimate of h^2 exists in the literature for TTB.

Table 3.2. Heritability (diagonal), phenotypic (above diagonal +/-SE), and genetic (below diagonal +/- SE) genetic correlations between feeding behaviors

Trait[1]	DUR	HD	FREQ	TTB	DMI	RFI_{FAT}
DUR	0.25 ± 0.05	0.24 ± 0.05	0.10 ± 0.10	0.06 ± 0.09	0.26 ± 0.05	0.24 ± 0.03
HD	0.81 ± 0.05	0.26 ± 0.06	0.02 ± 0.07	-0.07 ± 0.06	0.21 ± 0.07	0.30 ± 0.03
FREQ	-0.33 ± 0.1	-0.12 ± 0.12	0.27 ± 0.05	-0.09 ± 0.08	-0.36 ± 0.08	0.20 ± 0.04
TTB	-0.51 ± 0.11	-0.22 ± 0.14	0.17 ± 0.11	0.29 ± 0.06	0.06 ± 0.08	-0.03 ± 0.03
DMI	0.41 ± 0.09	0.26 ± 0.11	-0.16 ± 0.1	-0.29 ± 0.12	0.26 ± 0.05	0.40 ± 0.04
RFI_{FAT}	0.05 ± 0.12	0.01 ± 0.15	0.25 ± 0.11	0.00 ± 0.13	0.64 ± 0.07	0.40 ± 0.07

[1] DUR = feeding duration, min d^{-1}; HD = head down time, min d^{-1}; FREQ = feeding frequency, events d^{-1}; TTB = time to bunk, min; DMI = dry matter intake, kg d^{-1}; RFI_{FAT} = residual feed intake adjusted for ultrasound backfat thickness.

Phenotypic correlations among FB are presented in Table 3.2. The strongest phenotypic and genetic correlations existed between DUR and HD, and DUR and DMI, which was consistent with the phenotypic and genetic correlations reported by Chen et al. (2014) among Angus and Charolais steers. As was expected, as DUR increased, so did HD. Duration and HD are similar traits, and both measure the average amount of time an animal spends at the feed bunk every day. Further, the positive phenotypic relationship between DUR and DMI is also expected, as animals that spent more time at the feed bunk had greater opportunities for feed intake than animals that spent less time at the bunk. Variation in the magnitude of phenotypic and corresponding genetic correlations among FB in this study was greater than that reported by Chen et al. (2014), but similar to the differences reported by Nkrumah et al. (2007). To our knowledge, this is the first paper to present phenotypic and genetic correlations between TTB and other FB.

Genetic correlations are presented below the diagonal of Table 3.2. The correlation between DUR and HD is consistent with that reported by Chen et al. (2014). The lack of correlation between DUR and FREQ and FREQ and HD were not consistent with values reported by Chen et al. (2014) among steers on finishing diets. However, the relationship between DUR and FREQ in the present study was similar to the genetic correlations observed by Nkrumah et al. (2007). Further, the correlations between DUR, HD, and FREQ with DMI were similar to those reported by Nkrumah et al. (2007) and Chen et al. (2014), but DUR and HD correlations with DMI differed from those reported by Durunna et al. (2011). These studies were conducted in crossbred or purebred Angus and Charolais steers fed low roughage finishing diets; the difference in sex and diet may account for some of the differences with the present study. These genetic correlations indicate moderate relationships exist between FB and dry matter intake, and that selection pressure applied to one feeding behaviour in a breeding program could impact other behaviours as well. Recent selection pressure emphasising feed efficiency by maintaining production levels at lower DMI (e.g., -RFI and -RFI_{FAT}) could impact these FB through the correlations observed in this study. Cattle producers utilising -RFI for animal selection may observe that cattle spend less time at the feed bunk overall but make more trips to the feed bunk and require more time to approach the feed bunk after feeding. Conversely, while data for FB and feed intake are generally gathered concurrently through electronic feed bunks, if producers were to begin selection for decreased DUR or HD, they should also see a decrease in DMI, but not necessarily an improvement in feed efficiency. Thus, all traits of interest must be viewed in the context of a multi-trait selection index with accurate genetic correlations and economic weightings for each trait as this would avoid selecting for animals with decreasing DUR, DMI, and animal productivity.

Time-to-bunk, the difference between a day's first feeding event and the first subsequent appearance of an animal's electronic transponder in the GrowSafe system, averaged by animal over the feeding period, showed no phenotypic relationship with DUR, HD, FREQ or DMI. However, TTB was moderately, negatively genetically correlated with DUR, HD and DMI (Table 3.2), indicating that as heifers had increased time spent at the bunk, they were more likely to approach the bunk sooner after the passing of the feed truck. Time-to-bunk is also moderately heritable, with comparable h^2 and SE to the other three FB presented. It is possible that TTB physically manifests more in the social hierarchy of animal interaction, with more dominant heifers approaching the bunk sooner after feed delivery than timid heifers. Olson et al. (2019) reported a tendency for heifers with more excitable temperaments to take longer to approach the feed bunk than calm heifers; it could be that animal temperament and willingness to approach the feedlot alley plays a role in TTB variation. Time-to-bunk may be a better indicator of animal temperament or social hierarchical standing than of animal performance.

3.5. Conclusion

Technology has increased the availability of feeding behaviour data for analysis. Feeding behaviour correlations among replacement heifers fed a high-roughage diet have similarities magnitude and direction to FB in beef steers on a finishing diet. Genetic correlations and h^2 values indicated that selection for FB is possible and that selection for one FB in replacement beef heifers could affect other FB. Additionally, increased selection for reduced DMI could alter the FB of subsequent generations. The impacts of selection for FB should be mitigated by inclusion in balanced economically weighted selection indices. This study was the first to analyse TTB in replacement heifers and added to the understanding of the relationship between TTB and other FB. To our knowledge, these are the first genetic correlations and h^2 to be presented for FB in crossbred beef replacement heifers on high roughage diets.

3.6. Acknowledgements

We gratefully acknowledge funding support from Genome Alberta, the Beef Cattle Research Council (BCRC), and Alberta Agriculture and Forestry (AAF) and in-kind contribution in animals, facilities and people received from Agriculture and Agri-Food Canada (AAFC), Lacombe Research and Development Centre and the Kinsella Research Station, with special thanks to Cletus Sehn and Vern Erickson and their staff for animal care and management.

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4. PHENOTYPIC AND GENETIC CORRELATIONS OF BEEF REPLACEMENT HEIFER FEEDING BEHAVIOR, FEED INTAKE, FEED EFFICIENCY WITH COW PERFORMANCE AND LIFETIME PRODUCTIVITY

4.1. Abstract

Objectives were to quantify the phenotypic (r_p) and genetic (r_g) correlations between early-life feeding behaviors, dry matter intake, and feed efficiency and measures of cow performance and lifetime productivity traits. Traits were measured on 1145 crossbred replacement beef heifers and then on cows over parities one to four. Feeding event duration (FD) was phenotypically correlated with cow pre-breeding body weight (PBBW; r_p 0.29 to 0.45), cow pre-breeding back fat thickness (PBBF; r_p 0.35 to 0.49), progeny weaning weight (WW; r_p 0.09 to 0.31), and progeny birth weight (BW; r_p -0.06 to 0.17). Feeding event frequency (FF) was phenotypically correlated with PBBF (r_p 0.16 to 0.30). Dry matter intake (DMI) was phenotypically correlated with PBWT (r_p 0.16 to 0.20), and PBBF (r_p -0.22 to -0.05). Feeding event duration was genetically correlated with PBWT (r_g 0.38 to 0.41). Feeding event frequency was genetically correlated with PBWT (r_g -0.43 to -0.39). Dry matter intake was genetically correlated with PBWT (r_g -0.27 to 0.14). Days in herd (DIH) was phenotypically correlated with FD and DMI (r_p = 0.12, 0.20, respectively). Lifetime productivity was phenotypically correlated with FD and FF (r_g = 0.25, 0.22, respectively). Calving interval was phenotypically correlated with FD and FF (r_p = -0.12, -0.14, respectively) and genetically correlated with FF (r_g = -0.41). Due to moderate positive correlations with cow weight, caution would be required in selection to prevent an increase in mature cow

size. Use of FF, FD, DMI, and a measure of feed efficiency such as residual feed intake adjusted for back fat (RFI_{FAT}) in a balanced selection index is recommended.

4.2. Introduction

For most of the history of cattle production in North America, the choice to retain or cull replacement heifers was made with few, if any, data-driven decisions. Phenotypes and knowledge of pedigrees may have driven some selection (Lush, 1928, 1961), but heifers were retained without knowing their genuine ability to produce offspring, despite that reproductive ability being a cow's only method of returning a profit for a producer (Osoro & Wright, 1992; Trenkle & Willham, 1977). Identification of quantitative traits in replacement heifers prior to selection for breeding is limited to detection of puberty – all other reproductive traits cannot be evaluated until a cow is pregnant, calves, and(or) weans a calf. Some traits, such as longevity, require a cow to live out her natural life or be otherwise culled from a herd to be recorded. Reproductive traits are notoriously difficult to measure with consistency, as often they are subjective (e.g., udder scores, dystocia) or binary (e.g., pregnancy) and can require years to collect, as is the case of cow longevity (Berry et al., 2014). As an indicator of the lack of genetic progress in reproductive traits, the calf crop percentage (calves weaned per 100 cows exposed to breeding) in Western Canada has not changed in the last 30 years and remains at 85% (WCCCS, 2017) despite improvements in reproductive technology, knowledge of nutritional influences on reproduction, and the advent of genetic analysis for trait improvement in that time. Identifying and utilizing early-life traits in beef replacement heifers with phenotypic and genetic correlations with reproductive traits could aid in the identification of females with greater reproductive potential.

Measuring individual animal feed utilization is becoming more common as a selection tool in beef cattle due to efforts to reduce feed cost and improve production efficiency per unit of feed intake. The technology to record individual animal feed intakes over a period time with automated methods is now more readily available to the producer. One of the benefits of individually recorded feed intakes is the simultaneous recording of corresponding feeding behavior traits. Some of these feeding behaviors have been moderately correlated with growth and carcass traits in beef cattle on feedlot diets (Durunna et al., 2011; Nkrumah et al., 2007), and could have relationships with other economically relevant traits in the breeding cow. The purpose of this study was to quantify the phenotypic (rp) and genetic (rg) correlations between feeding behaviors measured in beef replacement heifers and the future parity body weight and fatness traits, cow performance, and lifetime productivity of beef cows.

4.3. Materials and Methods

Heifers (n=1145) were maintained at the Agriculture and Agri-Food Canada Lacombe Research and Development Centre (**LRDC**, Lacombe, AB, Canada) or at the University of Alberta's Roy Berg Kinsella Research Station (**KIN**). All heifers were cared for according to the guidelines of the Canadian Council on Animal Care (CCAC, 1993). Means, SD, and number of animals available for analysis are presented in Table 4.1.

4.3.1. Description of animals and management

Breed composition was determined genomically. At LRDC, cows averaged 66% Red Angus and Aberdeen Angus, 20% Hereford, 9% Charolais, and the remaining 5% consisted of Maine-Anjou, Limousin, and Simmental [herd development is described by Basarab et al. (2018)]. At KIN, cows were again predominantly Angus (69%), 5% each Hereford and Charolais, and 21% other breeds (AOB), which were primarily Limousin and Simmental but included Galloway, Gelbvieh, Shorthorn, and small amounts of the dairy breeds Holstein, Brown Swiss, and Jersey [herd development is described by Goonewardene et al. (2003)]. Details of the management of the cattle at both locations were previously reported by Olson et al. (2020). Briefly, heifer calves were born between March and May of each year and remained with their dams until they were weaned at 6-7 months of age. All calves were administered a vaccination schedule for the prevention of common infectious diseases at 2-2.5 months of age, consisting of modified live viral strains of infectious bovine rhinotracheitis, bovine viral diarrhea, parainfluenza virus 3, and bovine respiratory syncytial virus (Bovi Shield Gold FP5 VL5; Zoetis Canada, Inc. Kirkland, QC, Canada), and bacterial diseases blackleg, malignant edema, infectious necrotic hepatitis, enterotoxaemia, and enteritis (One Shot Ultra; Zoetis Canada), with a booster for each vaccine administered 6 weeks prior to weaning. Calves were also treated for internal and external parasites with ivermectin (Ivomec, Merial, Baie-d'Urfe, QC, Canada) 6 weeks prior to weaning. Prior to the commencement of feed intake tests, each heifer was fitted with a half-duplex radio-frequency identification (RFID) tag (Allflex USA Inc., Dallas, TX, USA). Heifers were then performance tested for individual feed intake using GrowSafe automated feed bunk technology (GrowSafe Systems, Ltd., Calgary, AB, Canada) located at LRDC (2005-2017) and KIN (2012-2017). Heifers at each location were tested for feed intake for between 69-114 days (depending on year and location) in a dry lot setting, in pens fitted with 8 automated GrowSafe feed bunks at both locations (4-6 animals per bunk). Feed intake (kg DM d-1)

Table 4.1. Feeding behaviour, feed efficiency, and reproductive means, standard deviations, and N across parities and over lifetime[1]

	Parity									
	1		2		3		4		Lifetime	
Trait	Mean (SD)	N	Mean (SD)	N	Mean (SD)	N	Mean (SD)	N	Mean (SD)	N
FD, min d^{-1}	143.0 (39.7)	1145	142.9 (41.4)	738	144.6 (41.1)	566	144.7 (41.1)	426	142.9 (39.3)	1210
FF, events d^{-1}	90.6 (29.7)	1145	91.3 (29.7)	738	91.3 (29.7)	566	93.1 (29.7)	426	88.9 (30.3)	1210
DMI, kg d^{-1}	8.02 (1.08)	1133	8.09 (1.07)	732	8.17 (1.05)	561	8.15 (0.99)	422	8.06 (1.08)	1197
RFI_{FAT}, kg d^{-1}	-0.01 (0.44)	1114	-0.01 (0.44)	721	0 (0.43)	554	0.01 (0.42)	415	-0.01 (0.45)	1175
PBWT, kg	378 (54)	1133	484 (62)	732	551 (75)	560	583 (68)	421	--	--
PBBF, mm	4.92 (2.46)	995	4.06 (2.76)	711	4.67 (3.27)	543	3.8 (2.63)	415	--	--
Progeny BW, kg	36.2 (4.4)	845	40.0 (5.1)	618	40.7 (4.6)	479	41.4 (5.0)	380	--	--
Progeny WW, kg	233.3 (39.6)	740	233.2 (38.8)	571	238.6 (36.1)	457	240.3 (31.9)	364	--	--
DIH, d	--	--	--	--	--	--	--	--	939 (803)	1207
CI, d	--	--	--	--	--	--	--	--	373 (12)	572
LTP, kg	--	--	--	--	--	--	--	--	692 (525)	828

[1] FD = feeding duration; FF = feeding frequency; DMI = dry matter intake; RFI_{FAT} = residual feed intake adjusted for ultrasound backfat thickness; PBWT = cow pre-breeding weight; PBBF = cow pre-breeding back fat; BW = birth weight; WW = wean weight; DIH = days in herd; CI = calving interval; LTP = lifetime productivity.

and feeding event behavior traits were collected simultaneously and continuously for the duration of the test period. Test days per pen were omitted due to issues such as equipment malfunction, power outages, and(or) when the assigned feed disappearance was less than 95%. Heifers housed at LRDC were fed a 90% barley silage, 10% steam-rolled barley grain (as-fed) ration over a 30-40 d adaptation period. Nutrient composition of the diets fed at LRDC between 2005 and 2013 were reported by Callum et al. (2019). Total digestible nutrients for years 2014 to 2017 ranged from 62 to 64% and days on feed were between 72 and 114, and average daily gain at LRC across all years was 0.91 kg d^{-1}. At KIN, heifers were also adapted to a barley silage-based ration that consisted of between 50 and 70% barley silage, 6-40% whole oats, and 0-13% corn dried distillers' grains or canola meal depending on year and ingredient cost. Total digestible nutrients were between 66 and 70% at KIN, and heifers were on trial for 72-91 days. Average daily gain of heifers at KIN from 2012-2017 was 1.03 kg d^{-1}. Wood chips and wood shavings were used in the pens for bedding as needed at both locations.

Heifers were weighed at the beginning and end of the test on two consecutive days and at approximately 28-day intervals. At the end of each test period at both locations, ultrasound back fat thickness (mm) was recorded with an Aloka 500V diagnostic real-time ultrasound with a 17-cm, 3.5 MHz linear array transducer (Overseas Monitor Corporation Ltd., Richmond, BC, Canada). The ultrasound measurements were recorded by an Ultrasound Guidelines Council certified ultrasound technician using methods described by Brethour (1992).

Heifers remained in confinement after each test until mid-May, following which they were placed on mixed-species cool-season pastures until mid-October. From mid-October to the following April, cows were fed stored forages under winter conditions. At LRDC, cows were fed in two groups, 1) cows were fed a silage diet in dry lot conditions, or 2) cows swath grazed various annual cereals (triticale, barley, and (or) corn) from mid-October until February-March, or until weather dictated that the cows could no longer access the swaths due to ice and snow buildup. Cows from both groups were then moved to open-fronted barns for calving and fed barley silage until spring-grazing in May of each year. Between 2005 and 2014, only cows in their third or greater parity were wintered on swath grazing. From 2014 onward that restriction was removed, and cows in their first and second parity were swath grazed with the rest of the herd. At KIN, heifers were again fed in confinement until mid-May, and then turned out onto a mix of native and tame cool-season grass pastures. In late December, KIN cattle were transitioned to a winter diet of hay fed on extensive pasture until grazing was available the following May. At both locations, cows were provided free-choice salt, mineral, and water, and were provided with protection from the wind (slatted wind brakes at LRDC; bush at KIN) and bedded when wind chill dropped below -20 or as deemed necessary by management for animal health and well-being.

Breeding seasons for heifers and mature cows differed. Heifers were exposed to breeding for 45 days beginning in late May (LRDC) or June (KIN), and mature cows were exposed for 63 days beginning 2-3 weeks after the heifers were exposed at both locations. Cows per bull during the breeding seasons were approximately 20-25.

Approximately 85 days after exposure ended, cows were diagnosed for pregnancy via rectal palpation. Females were culled if not pregnant. The resulting calves were born between March and mid-May and remained at the side of their dam until October-November when they were weaned. Calves were weighed at birth and weaning, and 200-d weaning weight was calculated as follows: 200 d wean weight, kg = [(wean weight, kg – birth weight, kg)/age at weaning, days] × 200 + birth weight, kg.

Cows were also culled post-calving or post-weaning for: failure to wean a calf, poor temperament, poor performance, skeletal structural issues, and poor udder structure scores. Udder scoring was based on the Canadian Simmental Association system (Canadian Simmental Association Performance Program Handbook), where a score of 1 – 5 was assigned to teats and udder suspension separately. Scores of 1 were highly undesirable traits (large teats, or pendulous, unsuspended udder) and 5 were desirable (small, well-placed teats and a tight, well suspended udder structure; Canadian Simmental Association Performance Program Handbook). Dystocia score, presentation type (normal/abnormal) birth type (single, twin or triplet), and calf condition scores were assigned at calving. Dystocia was scored from 1-4, where 1 is an unassisted/unobserved calving, 2 is easy assist, 3 is hard pull and 4 is a caesarian section. Calf condition was scored from 1-6 and 10, where 1 was healthy and alive, 2 was died after weaning, 3 was died between 2 mo of age and weaning, 4 was died prior to 2 months of age, 5 was dead at birth or stillborn, 6 was aborted, and 10 was born alive and healthy, but grafted to another cow because the biological dam died, had twins or triplets, or had poor mothering ability. All scores, mortality dates and reasons, and cow cull dates and reasons were recorded by the farm managers at KIN and LRDC, who have remained the same throughout the relevant production cycles.

4.3.2. Heifer feeding behavior, feed intake and feed efficiency traits

Feeding behaviors of beef cattle are influenced by weather (Schwartzkopf-Genswein et al., 2003), animal temperament (Voisinet et al., 1997), health status (Jackson et al., 2016), and management practices such as feed allotment and bunk management (Schwartzkopf-Genswein et al., 2003). The full effects of feeding behaviours on the spectrum of economically relevant beef cattle production traits are not fully established. Traits like feeding event duration and feeding event frequency are indicative of the amount of time required to consume a diet, the amount of socializing and grooming that an animal does in the feed bunk.

Details on calculation of feeding behavior, feed intake and feed efficiency traits were previously reported by Olson et al. (2020). Briefly, feeding behaviors collected were feeding event duration (FD, min d-1), and feeding event frequency (FF; events d-1). A feeding event began when a heifer's RFID was detected by the GrowSafe antenna at a single feeding node and ended when a) the time between the last two reading was greater than 300 seconds, b) another animal's tag was read by the bunk, or c) the same tag was detected at another node. Based on these criteria, FD was defined as the difference between the end time of a feeding event and the start time of that event. Feeding event frequency was the average number of feeding events recorded each day. These traits were summed for daily totals averaged for each animal to provide average FD and FF.

Heifer average feed intake collected by the GrowSafe system was converted to total dry matter intake (DMI) and total ME consumption (MJ d^{-1}) was found from total DMI. Standardized DMI was calculated as total ME consumption divided by 10 (standardized to an energy density of 10 MJ ME kg^{-1} DM). Total standardized DMI was divided by the number of days on feed to provide an average standardized daily DMI. Feed efficiency was measured as a modified version of residual feed intake (Koch et al, 1963) using a linear regression of standardized DMI on average daily gain (kg d^{-1}), metabolic mid-test body weight ($kg^{0.75}$) and end-of-test ultrasound BF thickness (mm). Residual feed intake adjusted for off-test ultrasound BF thickness (RFI_{FAT}) was used as a measure of heifer feed efficiency. Calculation of RFI_{FAT} was thoroughly presented by Basarab et al. (2011) and was computed here as the difference between standardized DMI (kg DM d^{-1}) and expected feed intake per heifer.

4.3.3. Cow performance, and lifetime productivity traits

Parity traits included cow pre-breeding body weight and backfat thickness recorded once per year, and progeny birth weight and progeny 200 day weaning weight. Parity data was limited to parities 1-4, due to number of observation limitations of parities greater than 4. Cows at LRDC and KIN were weighed and measured for ultrasound BF thickness at pre-breeding (April-May) each year. A heifer was deemed to have survived to parity 1 if she had a calving record (dead or alive). She did not survive to parity 1 if she was culled for non-pregnancy, aborted a calf, or died before her first calving, and all subsequent parities were set to missing. A cow survived to parity 2 if she had a calving record for parity 2 and did not survive if culled post-weaning of the first calving due to failure to wean a calf, poor temperament, poor performance, poor skeletal structure, and(or) low udder score, and for non-pregnancy, aborted calf, and cow death loss before the second parity. All subsequent parities were set to missing. The same pattern was used to determine survival to the third and fourth parities. Days in the herd (**DIH**) was determined by the difference between a cow's first breeding date (standardised to May 25 at LRDC, and June 25 at KIN, of any given year) and a cow's recorded culling or death date. As a measure of total lifetime productivity, a cow's progeny wean weights were summed across all cow's recorded parities to provide a cumulative total 200 day wean weight (**LTP**, if a cow did not wean a calf in a given year, her wean weight was 0 kg). Average calving interval (**CI**) was calculated as the average of all recorded calving intervals for a cow, starting at parity 1 and continuing until the cow died or was culled. All phenotypic data were checked for normality in SAS 9.4 (SAS Institute, Cary, NC, USA) and phenotypic values that were outside of ± 3 standard deviations from the mean were removed. Log-transformations were performed on DIH and LTP to normalize their distributions for further analyses.

4.3.4. Statistical analysis

Phenotypic and genetic variances and covariances were estimated for pairs of the heifer feeding event behavior, feed intake, feed efficiency with cow performance for each parity, and lifetime productivity traits recorded using a bivariate animal model in ASReml 4.1 (Gilmour et al., 2015). Details for the animal model have been discussed by Durunna et al. (2011), Chen et al. (2014), and Olson et al. (2020). Briefly, the animal model has the general form:

$$\begin{bmatrix} y_1 \\ y_2 \end{bmatrix} = \begin{bmatrix} X_1 & 0 \\ 0 & X_2 \end{bmatrix}\begin{bmatrix} b_1 \\ b_2 \end{bmatrix} + \begin{bmatrix} Z_1 & 0 \\ 0 & Z_2 \end{bmatrix}\begin{bmatrix} a_1 \\ a_2 \end{bmatrix} + \begin{bmatrix} W_1 & 0 \\ 0 & W_2 \end{bmatrix}\begin{bmatrix} c_1 \\ c_2 \end{bmatrix} + \begin{bmatrix} e_1 \\ e_2 \end{bmatrix}$$

Where y_1 and y_2 are vectors of the phenotypic values for the traits under consideration; b_1 and b_2 are vectors of fixed effects for trait 1 and trait 2, respectively; a_1 and a_2 are vectors of random additive genetic effects, c_1 and c_2 are vectors of random contemporary effects, and X, Z, and W are known design matrices for fixed effects, random additive genetic effects, and random contemporary effects, respectively. e_1 and e_2 are vectors of random residual effects. The fixed effects for the models evaluating parity data were breed composition (percentage by genomic breed evaluation of AN, CH, HE, and "other" breeds), age at day 0 of the feed intake trial, and age at the date of measurement for cow pre-breeding weight and cow pre-breeding back fat and when appropriate, the weight of the calf from the previous parity (parities 2, 3, and 4, to account for impact of lactation). Fixed effects for lifetime data DIH, LTP, and CI were breed composition as above and age at day 0 of the feed intake trial. Contemporary groups were defined as a combination of calf birth year, feedlot test location (KIN or LRDC) and feedlot pen. Multivariate normal distributions were assumed for the random vectors $a, c,$ and e with means equal to 0, which led to $E(y) = Xb$. The variance – covariance matrix for the random effects is described below:

$$\begin{bmatrix} a_1 \\ a_2 \\ c_1 \\ c_2 \\ e_1 \\ e_2 \end{bmatrix} = \begin{bmatrix} A\sigma^2_{a_1} & A\sigma_{a_1a_2} & 0 & 0 & 0 & 0 \\ A\sigma_{a_1a_2} & A\sigma^2_{a_2} & 0 & 0 & 0 & 0 \\ 0 & 0 & I_{n_c}\sigma^2_{c_1} & I_{n_c}\sigma_{c_1c_2} & 0 & 0 \\ 0 & 0 & I_{n_c}\sigma_{c_1c_2} & I_{n_c}\sigma^2_{c_2} & 0 & 0 \\ 0 & 0 & 0 & 0 & I_{n_e}\sigma^2_{e_1} & I_{n_e}\sigma_{e_1e_2} \\ 0 & 0 & 0 & 0 & I_{n_e}\sigma_{e_1e_2} & I_{n_e}\sigma^2_{e_2} \end{bmatrix}$$

in which $\sigma^2_{a_1}$, $\sigma^2_{a_2}$, and $\sigma_{a_1a_2}$ refer to the additive genetic variance for trait 1, trait 2, and their genetic covariances, respectively; A is the additive genetic relationship matrix constructed from a one generation pedigree that included 1762 animals and their 116 sires; $\sigma^2_{c_1}$, $\sigma^2_{c_2}$, and $\sigma_{c_1c_2}$ are the variances and covariances of contemporary group effects; $\sigma^2_{e_1}$, $\sigma^2_{e_2}$, and $\sigma_{e_1e_2}$ are the variances for traits 1 and 2 and covariances of residual errors, respectively; I_{n_c} and I_{n_e} are the identity matrices, where n_c is the number of random contemporary groups and n_e is the number of animals with phenotypic records.

Phenotypic variances (σ^2_p) were calculated in ASReml 4.0 by summing variances of additive (σ^2_a), contemporary group (σ^2_c), and residual effects (σ^2_e). Phenotypic covariances were derived as $\sigma_{p_1p_2} = \sigma_{a_1a_2} + \sigma_{c_1c_2} + \sigma_{e_1e_2}$. Phenotypic and genetic correlation coefficients were computed as $r_p = \sigma_{p_1p_2}/\left[\left(\sigma^2_{p_1}\sigma^2_{p_1}\right)^{1/2}\right]$ and $r_g = \sigma_{a_1a_2}/\left[\left(\sigma^2_{a_1}\sigma^2_{a_1}\right)^{1/2}\right]$' respectively. For these analyses, heritability was estimated as: $h^2 = \sigma^2_a/\sigma^2_p$. Heritability estimates were averaged over all bivariate analyses of the trait.

4.4. Results and discussion

4.4.1. Heritability

Heritability (h^2) for feeding behaviors, dry matter intake, feed efficiency, parity traits and lifetime productivity traits are presented in Table 4.2. Feeding behavior h^2 across parities and in the analysis of lifetime productivity traits were low to moderate and consistent with Olson et al. (2020), from which a subset of animals in the present study were used. Heritability for FD was also similar to those presented by Durunna et al. (2011) in finishing steers fed a 20% roughage grower diet ($h^2 = 0.25 \pm 0.16$, diet = 2.6

Mcal kg^{-1}), but higher than the h^2 of those steers when fed a low-roughage barley-based finishing diet ($h^2 = 0.14 \pm 0.11$ and diet = 2.9 Mcal kg^{-1}). Feeding event frequency h^2 was lower than those values presented by Durunna et al. (2011) in both diets ($h^2 = 0.56 \pm 0.19$ and 0.59 ± 0.18, respectively). The discrepancy in the h^2 estimates may be reflective of differences in animal populations, sample sizes, and statistical models used.

Heritability for DMI were comparable to those reported in growing HE bull calves by Herd and Bishop (2000), though lower than reports in Canadian bulls by Schenkel et al. (2004) and mixed B. taurus – B. indicus bulls, heifers, and steers by Elzo et al. (2009). No reports of the h^2 of dry matter intake were found in the literature describing replacement heifers on high-roughage diets. Residual feed intake (adjusted for off test ultrasound back fat thickness) h^2 estimates were consistent with those reported in beef replacement heifers (Freetly et al., 2020; Mu et al., 2016).

Heritability of cow pre-breeding weight increased with cow age (Table 4.2), indicating that cow weights earlier in life are subject to greater environmental influence than those measured on older cows. Nephawe et al. (2004) reported h^2 of 0.52 for body weight and 0.16 for cow body condition score in crossbred cows 4 years of age and older, similar in magnitude to the h^2 reported in the present study for cow pre-breeding weight of parity 4 cows and for cow pre-breeding back fat, an objective measurement of cow condition. Direct h^2 estimates for progeny birth and wean weights were similar to those reported for Angus cattle (Trus and Wilton, 1988; Bennett and Gregory, 1996).

Table 4.2. Estimates of heritability (SE) of feeding behaviors, feed efficiency, and cow performance across 4 parities and lifetime productivity traits[1]

	Parity				
Trait	1	2	3	4	Lifetime
FD, min d^{-1}	0.26 (0.05)	0.26 (0.07)	0.28 (0.08)	0.32 (0.09)	0.27 (0.05)
FF, events d^{-1}	0.29 (0.06)	0.36 (0.08)	0.32 (0.08)	0.45 (0.11)	0.28 (0.05)
DMI, kg d^{-1}	0.24 (0.05)	0.23 (0.05)	0.30 (0.07)	0.28 (0.08)	0.24 (0.05)
RFI_{FAT}, kg d^{-1}	0.43 (0.08)	0.50 (0.11)	0.53 (0.12)	0.45 (0.15)	0.43 (0.08)
PBWT, kg	0.15 (0.04)	0.19 (0.05)	0.24 (0.09)	0.40 (0.15)	--
PBBF, mm	0.11 (0.03)	0.10 (0.03)	0.19 (0.07)	0.16 (0.09)	--
Progeny BW, kg	0.15 (0.08)	0.22 (0.10)	0.14 (0.12)	0.13 (0.13)	--
Progeny WW kg	0.24 (0.07)	0.25 (0.08)	0.12 (0.09)	0.31 (0.13)	--
DIH, d	--	--	--	--	0.04 (0.04)
LTP, kg	--	--	--	--	0.06 (0.03)
CI, d	--	--	--	--	0.22 (0.11)

[1]FD = feeding duration; FF = feeding frequency; DMI = dry matter intake; RFI_{FAT} = residual feed intake adjusted for ultrasound backfat thickness; PBWT = cow pre-breeding weight; PBBF = cow pre-breeding back fat; BW = birth weight; WW = wean weight; DIH = days in herd; CI = calving interval; LTP = lifetime productivity.

Similarly, progeny wean weight estimates of h^2 were in line with Angus cattle reported by Bennett and Gregory (1996) for parity 1, 2, and 4, but were lower for parity 3. The reason for the deviation in parity 3 is not clear; but does coincide with the parity where cows at LRDC were exposed to swath grazing for the first time, which may contribute to the variation in that parity. Range and mean of progeny wean weight in parity 3 were not different from other parities.

Heritability of reproductive traits is notably low due to the large influence of management practices and other environmental conditions on reproductive success (Cammack et al., 2009; Berry et al., 2014). Longevity, expressed in this study as DIH: the total number of days a heifer remained in the breeding herd following her first breeding (standardized to May 25 at LRDC and June 25 at KIN), is a crucial measure of animal profitability for beef producers. Heritability for DIH in the present study was low (0.04 ± 0.04), and similar to that found in British Simmental cows by Roughsedge et al. (2005) and to those reported by Snelling et al. (1995), who estimated h^2 of stayability for Angus cows that had 2, 5, 8, or 11 calves, given they became a dam, and found h^2 ranged from 0.07 (8 calves) to 0.19 (11 calves). The low h^2 confirms previous reports that improvement in longevity would be difficult from a genetic selection standpoint (Rogers et al., 2004). Improvements in cow longevity may be more readily achieved by pursuing a crossbreeding program to increase individual animal heterozygosity, which has been shown to increase longevity (Cundiff et al., 1992; Basarab et al., 2018).

Estimates of heritability for LTP in the present study were lower than those presented by Martinez et al. (2004) among Hereford cows, where h^2 was between 0.17

and 0.18 for summed, 200-d adjusted weaning weights, and by Arthur and Makarechian (1992), who reported an h^2 of 0.27 among crossbred cattle born between 1966 and 1975 at KIN. Differences could result from larger influence of non-additive effects of crossbreeding in the present study cows, or environmental factors. Log transformation of the LTP data was required for the analysis in the present study.

Heritability for calving interval was lower than that reported by Toelle and Robison (1985) in a population of Hereford cows, but much higher than most other reports of heritability. Generally, heritability of CI in beef cattle is considered to be less than 0.05 (Berry et al., 2014). Calving interval has been criticized as a selection tool for beef cattle, as cattle with “short” intervals are also those prone to late calving in the previous season. Thus, selection for young cows with short intervals would result in the inadvertent selection for later-calving and likely later maturing replacement heifers (Bourdon and Brinks, 1983).

4.4.2. Phenotypic correlations

To our knowledge, no evidence exists in the literature that illustrates relationships between feeding behavior of the dam as a young heifer and her progeny’s performance. Phenotypic correlations across parity are presented in Figs. 4.1 & 4.2; correlation coefficients and SE can be found in Table 4.4. As phenotypic correlations are the result of both genetic and environmental (co)variances, it is possible that the phenotypic correlations reported here are unique to the KIN and LRC environments. Caution is advised when considering these effects outside of these environments.

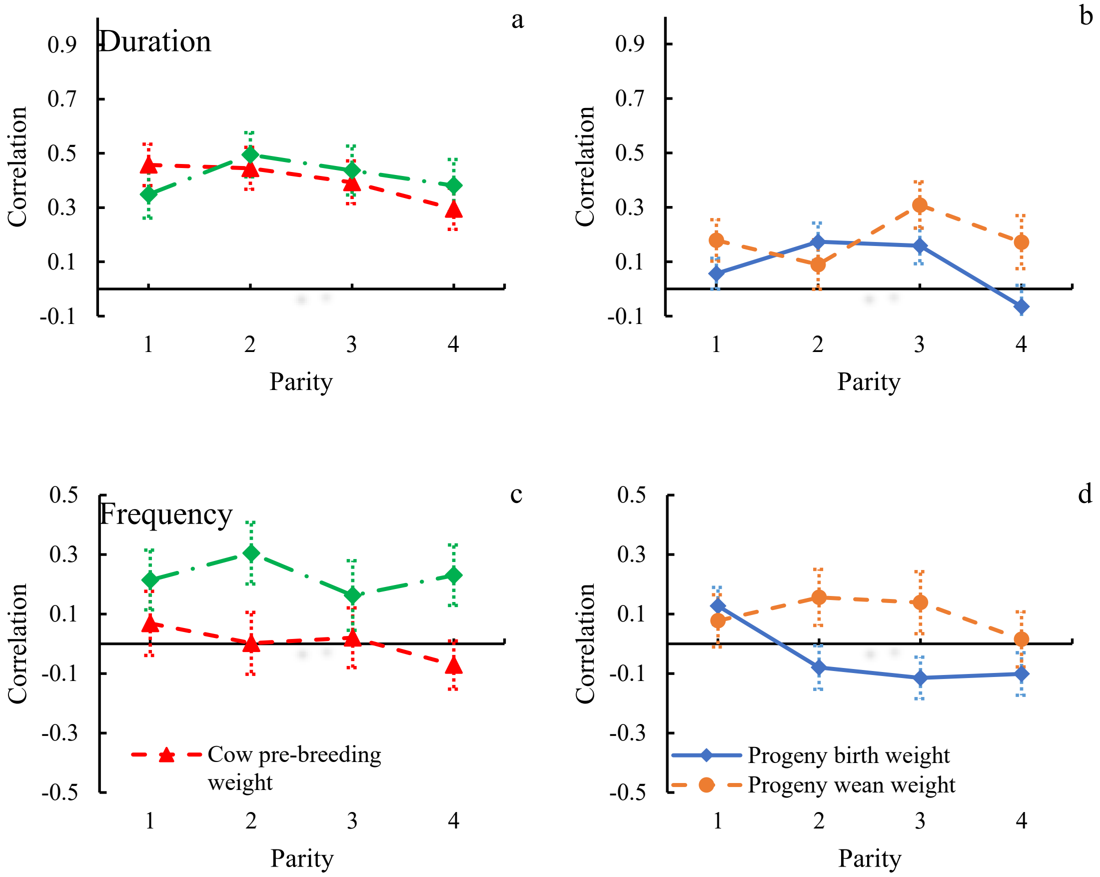

Figure 4.1. Phenotypic correlations across parities between feeding event duration, progeny birth and wean weight (a), and cow pre-breeding weight and back fat (b); and between feeding event frequency, progeny birth and wean weight (c), and cow pre-breeding weight and back fat (d).

Phenotypic correlations between FD and cow pre-breeding weight and back fat were moderate to strong (Fig. 4.1b) and illustrate the relationship between feed intake and body weight and fatness. Slight decreases in correlation strength over time are evident (Fig. 4.1b, 4.1c), and are likely due to the cumulative effects of environment. The phenotypic correlations showed that cows who spent more time eating as replacement heifers were more likely to carry more back fat through their 4th parity. The positive relationships between body fatness and fertility are well documented in the literature

(Dziuk & Bellows, 1983; Richards et al., 1986; Selk et al., 1988), though care should be taken to avoid overly heavy cows due to negative impacts of cow size and reproductive efficiency (Berry & Evans, 2014). No correlations existed between FF and cow pre-breeding weight, but FF showed low to moderate correlations with cow pre-breeding back fat across all 4 parities (Fig 4.1d). Replacement heifers with greater FF were more likely to maintain adequate body condition for reproduction through their life. Phenotypic correlations between heifer FD and their progeny birth weight and wean weight were low (Fig 4.1a), except in parity 3, where the correlation between FD and progeny wean weight was 0.31 ± 0.09, indicating that dams that eat for longer periods as replacement heifers under dry lot conditions could lead to heavier calves at weaning. Further studies, with greater n, would be required to discern the biological reasons for increased weaning weights from dams that eat for longer periods and to better elucidate the weak or variable responses observed. Genetic correlations of FF with progeny birth and wean weight were generally weak (Fig 4.1c) and were negative for progeny birth weight in parity 2-4. Cows that ate more frequently as replacement heifers could have calves that are slightly smaller at birth but larger at weaning than their contemporaries who ate less frequently. Generally, only small impacts on progeny birth weight or weaning weight would be expected if replacement heifers are identified for their feeding event duration, though the direction of the relationships between progeny growth and dam FD shown here are consistent with correlations reported in older growing cattle on feed (Nkrumah et al., 2007).

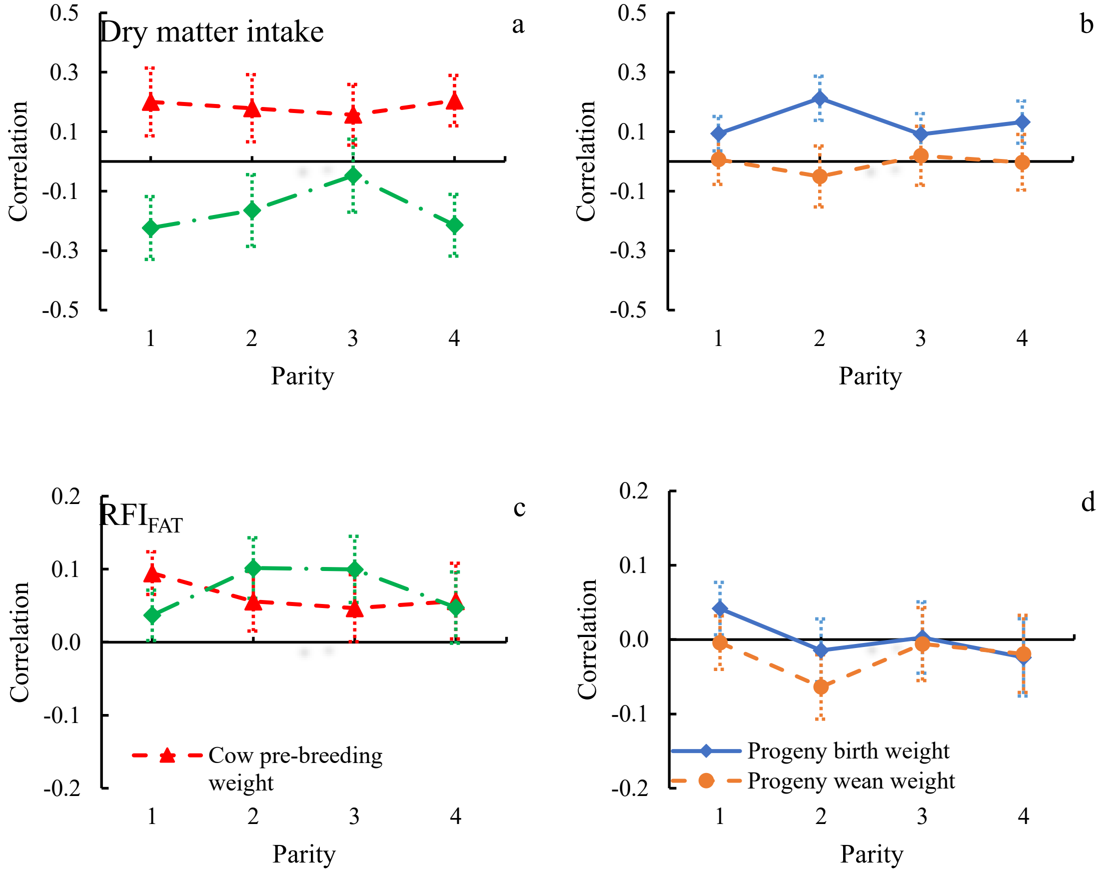

Figure 4.2. Phenotypic correlations across parities between dry matter intake, progeny birth and wean weight (a), and cow pre-breeding weight and back fat (b); and between residual feed intake (adjusted for back fat, RFI$_{FAT}$), progeny birth and wean weight (c), and cow pre-breeding weight and back fat (d).

Dry matter intake measured as a heifer was moderately, positively correlated with cow pre-breeding weight in parity 1-4 and showed a weak negative relationship with cow pre-breeding back fat across all 4 parities (Fig 4.2b). Generally, these correlations affirm that larger cows have greater DMI than smaller cows and agree with the findings of Walker et al. (2015). The relationship between DMI and cow pre-breeding back fat indicates that heifers that consumed more feed had less body fat than those that consumed less feed, though the relationship was generally weak, and correlations did not differ across parities. The cause of the negative relationship is not understood but could be related to the age of the cows in this study. Younger cows are usually leaner than older cows (Coleman et al., 2017; Renquist et al., 2006), and the preponderance of young cows in this study may have skewed the correlations between DMI and back fat thickness. Weak phenotypic correlations were observed between cow pre-breeding weight and back fat and RFI_{FAT} (Fig 4.2d). Residual feed intake adjusted for back fat thickness is independent of weight and body composition (Basarab et al., 2011) to remove the possibility of inadvertently selecting later maturing heifers or influencing cow body composition when considering feed efficiency in a breeding program. As such, a negligible relationship with body fatness was expected (Basarab et al., 2011). Dry matter intake exhibited a low-moderate positive phenotypic correlative relationship with progeny birth weight (Fig 4.2a), indicating that dams with greater DMI had heavier calves at birth. Few studies looked explicitly at DMI in the dam and effects on progeny birth weight. It is likely that much of the influence of DMI on birth weight is because larger cows have greater DMI than smaller cows (Walker et al., 2015), and larger cows have larger calves than smaller cows. The correlations between cow DMI and progeny wean weight did not follow the same pattern, however, and progeny wean weight showed little phenotypic relationship with dam DMI measured as a replacement heifer. Similarly, RFI_{FAT} exhibited negligible relationships with both cow progeny birth weight and wean weight, confirming the report of Lawrence et al. (2011), who reported no difference in progeny birth weight among crossbred beef heifers analysed for low, medium, and high RFI.

Feeding duration was correlated with DIH (0.12 ± 0.06), LTP (0.25 ± 0.08) and CI (-0.12 ± 0.05), indicating that heifers that spend more time at the feed bunk stay longer in the herd, produce more units of calf weaning weight, and have shorter calving intervals than those that spend less time at the feed bunk. Feeding frequency had no correlation with DIH (-0.04 ± 0.07), a moderate positive relationship with LTP (0.22 ± 0.10) and a negative relationship with CI (-0.14 ± 0.05), indicating that heifers that visited the feed bunk more often also produced more units of calf weaning weight during their lifetime, and had a shorter calving interval than heifers that did not visit the bunk as often. These are the first phenotypic correlations reported for cattle between feeding behavior and fertility measures and indicate that selection for heifers with increased FD and FF could be more productive over their lifetime.

4.4.3. Genetic correlations

Genetic correlations exhibited greater fluctuation between parities than the corresponding phenotypic correlations (Figs. 4.3 & 4.4); genetic correlation coefficients and SE are reported in Table 4.4. Breeding selection applied to increase FD would result in heavier cows that consume more feed, with no direct effect on longevity (Fig. 5a). However, increases in DIH may be observed indirectly, as genetic correlations between DMI, cow pre-breeding weight in the first parity, and DIH are moderate and positive. Similarly, little direct genetic effect on the improvement of LTP would be observed if FD were emphasised (Fig. 4.5b), though an increase in DMI and $\mathrm{RFI}_{\mathrm{FAT}}$ would

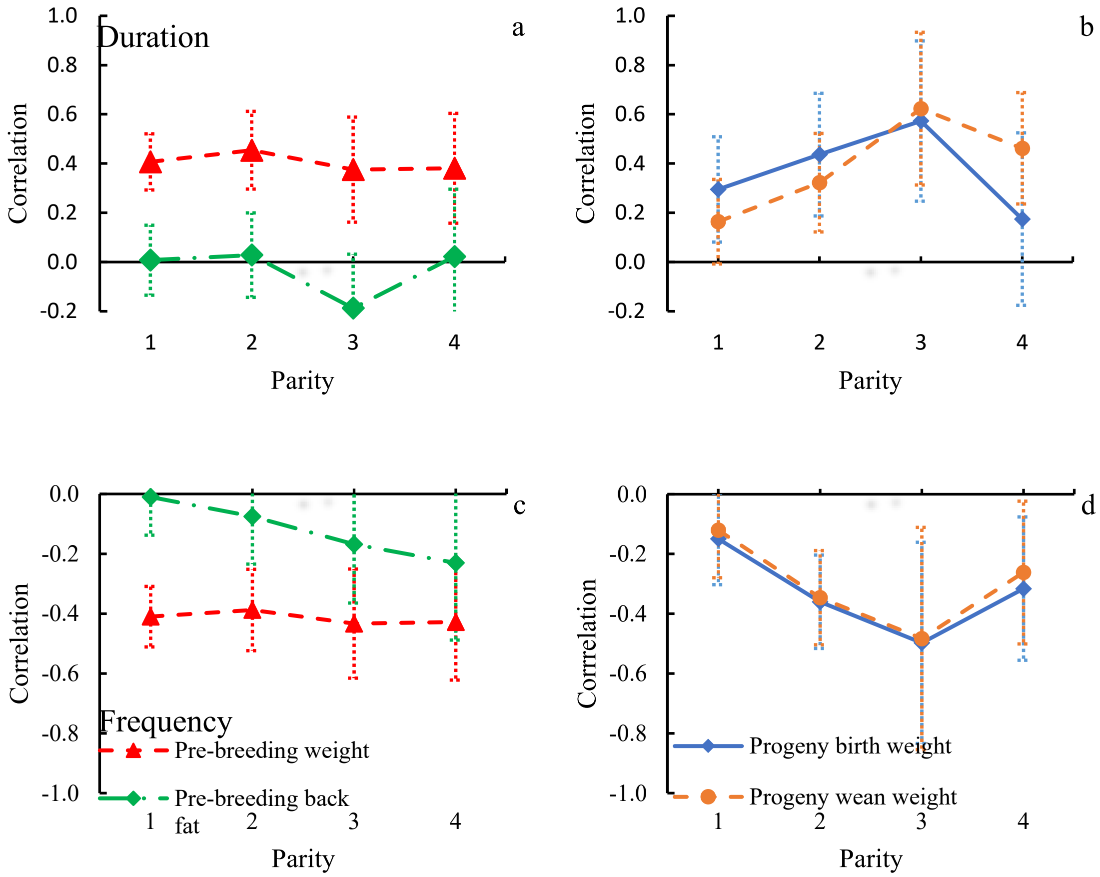

Figure 4.3. Genetic correlations across parities between feeding event duration, progeny birth and wean weight (a), and cow pre-breeding weight and back fat (b); and between feeding event frequency, progeny birth and wean weight (c), and cow pre-breeding weight and back fat (d).

likely be observed. These correlations reveal that selection for increased FD may not directly improve reproduction and longevity, but instead may lead to heavier cattle that consume more and have lessened feed efficiency (higher RFI_{FAT}). The positive correlations observed between heavier cows and improved longevity contradicts Berry and Evans (2014), where heavier cows had a negative genetic relationship with survival. The connection between heavier cows and improved DIH could be contributed, in part,

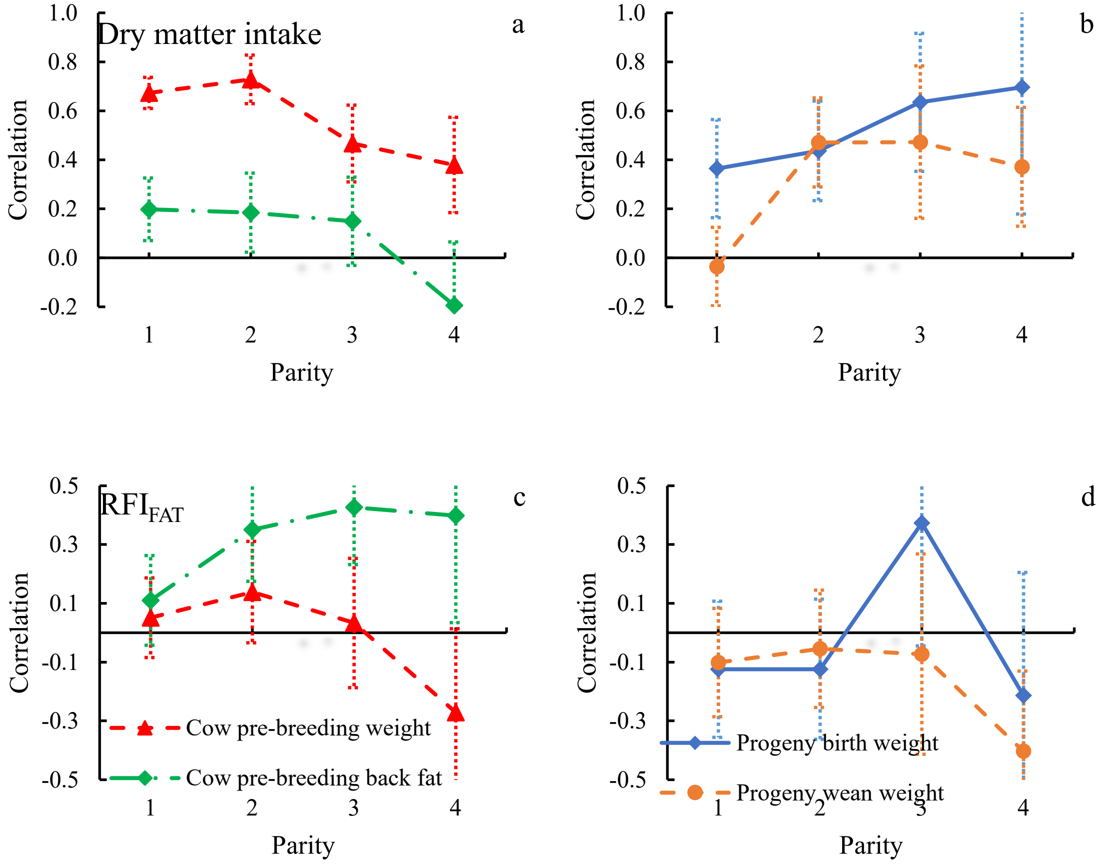

Figure 4.4. Genetic correlations across parities between dry matter intake, progeny birth and wean weight (a), and cow pre-breeding weight and back fat (b); and between residual feed intake (adjusted for back fat, RFI_{FAT}), progeny birth and wean weight (c), and cow pre-breeding weight and back fat (d).

to improved body fatness, where heavier animals at pre-breeding in the first parity are also carrying greater body condition. Cows carrying greater backfat (often measured in industry by body condition scoring) have reduced post-partum anestrous intervals (Osoro and Wright, 1992; Lalman et al., 1997), resulting in shorter calving intervals (Osoro and Wright, 1992) and healthier calves at birth (Bohnert et al., 2013). Further, Naazie et al. (1991) found that as heifer weight at first calving increased, instances of dystocia decreased; similar findings were reported in a review of dairy cattle dystocia (Mee, 2008), though dystocia was present in less than 1% of recorded KIN calving events and less than 5% of recorded LRDC calving events. Together, the influence of body fatness in heavier cows may increase DIH due to fewer opportunities for culling heavier open cows, and heavier cows that do not wean a calf due to calf death or

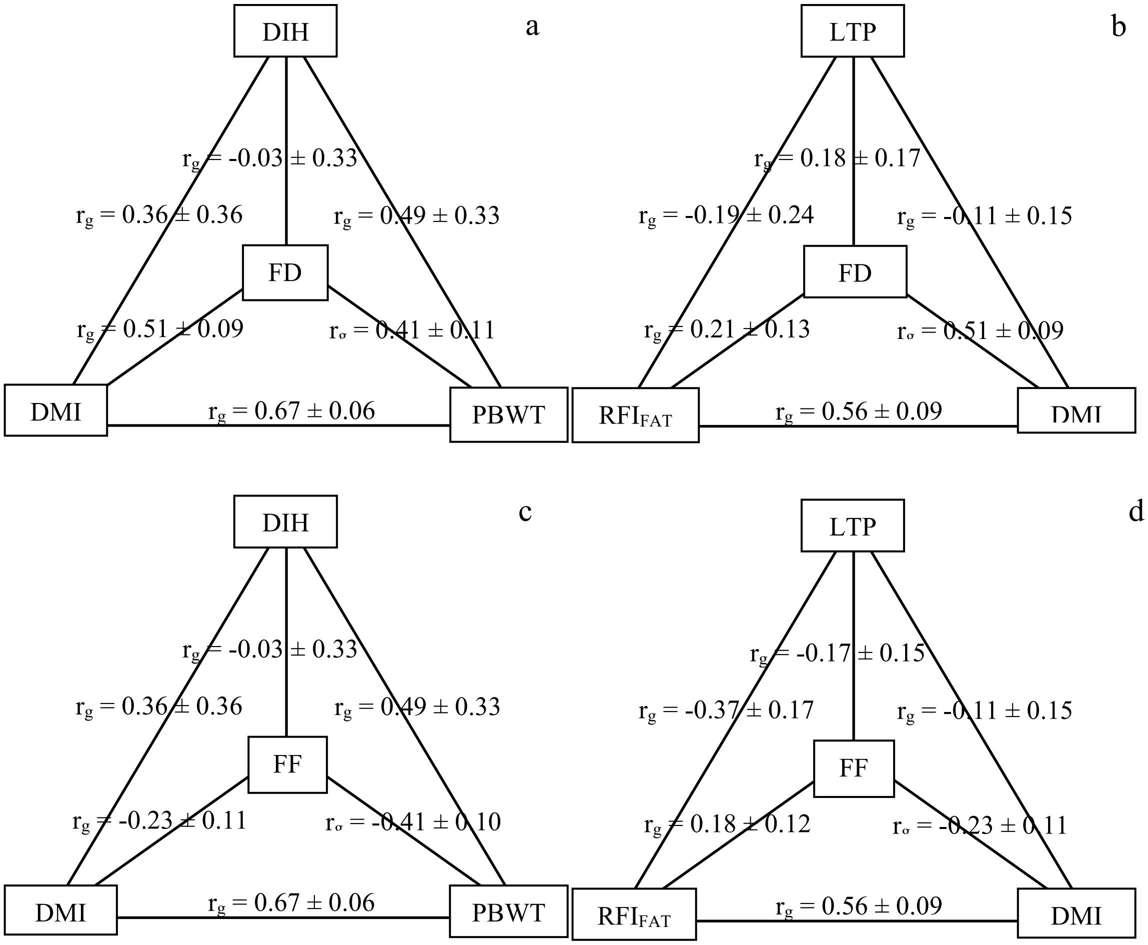

Figure 4.5. Genetic correlations between feeding event duration (FD) (a, b) and feeding event frequency (FF; c, d) on dry matter intake (DMI), parity 1 pre-breeding body weight (PBWT), residual feed intake (adjusted for back fat) (RFI_{FAT}), days in the herd (DIH), and lifetime productivity (LTP). NOTE In this figure PBWT refers specifically to first parity pre-breeding weight.

dystocia. Similarly, emphasis on selection for decreased FF would not directly improve DIH (Fig. 4.5c) and have little to no effect on LTP (Fig. 4.5d). However, pressure on decreasing FF would increase DMI, cow pre-breeding weight in the first parity, and decrease RFI_{FAT} (improve efficiency). In the present study, FD and FF were negatively genetically correlated ($r_g = -0.33 \pm 0.10$) and in agreement with genetic correlations reported by Nkrumah et al. (2007) and Olson et al. (2020), so concurrent selection for greater FD and fewer feeding events would not be contradictory. Ultimately, selection for the feeding behaviors FD and FF would have little correlated response directly with reproductive efficiency in crossbred beef cattle. However, through impacts on DMI, RFI_{FAT}, and first parity pre-breeding cow weight, selection using feeding behaviors could change the suitability of cows for an environment and thereby improve the efficiency of reproduction.

4.5. Conclusion

Feeding behaviors are recorded in replacement heifers when those heifers are tested for feed efficiency, a practice that is becoming more common as access to the required technology and infrastructure expands. Feeding behaviors of replacement heifers are heritable and have phenotypic and genetic correlations with her physical body weight and ability to carry body fat as well as her progeny calf birth and wean weights, important factors that influence her fertility. However, feeding behaviors are also implicated in increasing cow size, as is selection for increased DMI, and caution must be used to ensure that selection pressure applied to FD and FF in replacement heifers does not result in increased mature cow weight and maintenance cost. Therefore, it is recommended that FD and FF be considered for use in multi-trait selection indices that also control for cow mature size and feed efficiency, to insulate producers from unintended correlated responses. This was a small study, limited by the time required to collect relevant reproductive data. Further studies with greater sample size could solidify that feeding behaviors may perhaps be a useful tool to identify heifers that are likely to maintain adequate body weight and fatness for reproductive success and improve genetic rate of gain through early identification of replacement candidates.

4.6. Acknowledgements

The authors gratefully acknowledge in-kind contributions in animals and facilities received from Agriculture and Agri-Food Canada (AAFC) and Alberta Agriculture and Forestry (AAF). Technical support at the Lacombe Research and Development Centre and the Roy Berg Kinsella Research Station is also acknowledged, with special thanks to Cletus Sehn and Vernon Erickson and their staff for animal care and management

Table 4.3. Phenotypic correlations (SE) between parity cow production data, feeding behaviors, and feed efficiency measured post-weaning in replacement beef heifers.

Trait[1]	Duration	Head-down	Frequency	TTB	DMI	RFI_{FAT}
Parity 1						
Cow pre-breeding weight	0.46 (0.08)	0.34 (0.07)	0.07 (0.11)	-0.04 (0.08)	0.20 (0.11)	0.09 (0.03)
Cow pre-breeding backfat	0.35 (0.09)	0.24 (0.08)	0.21 (0.10)	-0.11 (0.08)	-0.22 (0.11)	0.04 (0.03)
Progeny birth weight	0.06 (0.06)	0.01 (0.05)	0.13 (0.06)	-0.02 (0.05)	0.09 (0.06)	0.04 (0.04)
Progeny wean weight	0.18 (0.08)	0.02 (0.06)	0.08 (0.09)	0.19 (0.06)	0.01 (0.08)	0.00 (0.04)
Parity 2						
Cow pre-breeding weight	0.44 (0.08)	0.26 (0.08)	0.00 (0.10)	0.12 (0.08)	0.18 (0.11)	0.06 (0.04)
Cow pre-breeding backfat	0.49 (0.08)	0.27 (0.09)	0.30 (0.10)	-0.03 (0.09)	-0.17 (0.12)	0.10 (0.04)
Progeny birth weight	0.17 (0.07)	0.05 (0.06)	-0.08 (0.07)	-0.01 (0.07)	0.21 (0.07)	-0.01 (0.04)
Progeny wean weight	0.09 (0.09)	0.03 (0.08)	0.16 (0.09)	0.02 (0.08)	-0.05 (0.10)	-0.06 (0.04)
Parity 3						
Cow pre-breeding weight	0.39 (0.08)	0.16 (0.08)	0.02 (0.10)	0.11 (0.08)	0.16 (0.10)	0.05 (0.05)
Cow pre-breeding backfat	0.44 (0.09)	0.15 (0.09)	0.16 (0.12)	0.04 (0.09)	-0.05 (0.12)	0.10 (0.05)
Progeny birth weight	0.31 (0.09)	0.13 (0.08)	-0.11 (0.07)	-0.01 (0.06)	0.09 (0.07)	0.00 (0.05)
Progeny wean weight	0.31 (0.09)	0.13 (0.08)	0.14 (0.10)	0.11 (0.07)	0.02 (0.10)	-0.01 (0.05)
Parity 4						
Cow pre-breeding weight	0.30 (0.08)	0.12 (0.07)	-0.07 (0.08)	-0.01 (0.07)	0.20 (0.08)	0.06 (0.05)
Cow pre-breeding backfat	0.38 (0.10)	0.10 (0.09)	0.23 (0.10)	-0.16 (0.08)	-0.21 (0.10)	0.05 (0.05)
Progeny birth weight	-0.06 (0.08)	-0.03 (0.07)	-0.1 (0.07)	-0.06 (0.07)	0.13 (0.07)	-0.02 (0.05)
Progeny wean weight	0.17 (0.10)	0.01 (0.09)	0.01 (0.09)	0.09 (0.08)	0.00 (0.09)	-0.02 (0.05)

[1] Duration = feeding duration, min d^{-1}; Head-down = head-down time, min d^{-1}; Frequency = feeding frequency, events d^{-1}; TTB = Time-to-bunk, min; DMI = dry matter intake, kg d^{-1}; RFI_{FAT} = residual feed intake adjusted for back fat thickness, kg d^{-1}. For a thorough description of all feeding behaviour traits, see Jackson et al. (2016).

Table 4.4. Genetic correlations (SE) between parity cow production data and feeding behavior as a heifer

Trait[1]	Duration	Head-down	Frequency	TTB	DMI	RFI_{FAT}
Parity 1						
Cow pre-breeding weight	0.41 (0.11)	0.31 (0.12)	-0.41 (0.10)	-0.21 (0.15)	0.67 (0.06)	0.05 (0.14)
Cow pre-breeding backfat	0.01 (0.14)	-0.07 (0.16)	-0.01 (0.13)	-0.3 (0.17)	0.2 (0.13)	0.11 (0.15)
Progeny birth weight	0.30 (0.21)	0.21 (0.23)	-0.15 (0.15)	-0.02 (0.26)	0.36 (0.20)	-0.12 (0.23)
Progeny wean weight	0.16 (0.17)	0.01 (0.19)	-0.12 (0.16)	-0.07 (0.21)	-0.04 (0.16)	-0.10 (0.18)
Parity 2						
Cow pre-breeding weight	0.45 (0.16)	0.23 (0.18)	-0.39 (0.14)	-0.06 (0.18)	0.73 (0.10)	0.14 (0.17)
Cow pre-breeding backfat	0.03 (0.17)	0.02 (0.20)	-0.08 (0.16)	-0.15 (0.19)	0.18 (0.16)	0.35 (0.18)
Progeny birth weight	0.44 (0.25)	0.09 (0.27)	-0.36 (0.16)	-0.41 (0.26)	0.44 (0.20)	-0.12 (0.24)
Progeny wean weight	0.32 (0.20)	0.19 (0.22)	-0.35 (0.16)	-0.23 (0.21)	0.47 (0.18)	-0.05 (0.20)
Parity 3						
Cow pre-breeding weight	0.38 (0.21)	0.11 (0.24)	-0.43 (0.18)	-0.07 (0.41)	0.47 (0.16)	0.03 (0.22)
Cow pre-breeding backfat	-0.19 (0.22)	-0.62 (0.29)	-0.17 (0.20)	0.17 (0.23)	0.15 (0.18)	0.43 (0.19)
Progeny birth weight	0.62 (0.31)	0.41 (0.34)	-0.5 (0.34)	-0.89 (0.43)	0.63 (0.28)	0.37 (0.42)
Progeny wean weight	0.62 (0.31)	0.41 (0.34)	-0.48 (0.37)	-0.17 (0.39)	0.47 (0.31)	-0.07 (0.34)
Parity 4						
Cow pre-breeding weight	0.38 (0.22)	0.29 (0.22)	-0.43 (0.19)	0.08 (0.27)	0.38 (0.19)	-0.27 (0.28)
Cow pre-breeding backfat	0.02 (0.27)	0.03 (0.28)	-0.23 (0.26)	-0.10 (0.33)	-0.19 (0.26)	0.40 (0.36)
Progeny birth weight	0.17 (0.35)	0.06 (0.39)	-0.32 (0.24)	0.51 (0.49)	0.70 (0.52)	-0.21 (0.42)
Progeny wean weight	0.46 (0.23)	0.28 (0.24)	-0.26 (0.24)	0.41 (0.30)	0.37 (0.24)	-0.40 (0.27)

[1] Duration = feeding duration, min d^{-1}; Head-down = head-down time, min d^{-1}; Frequency = feeding frequency, events d^{-1}; TTB = Time-to-bunk, min; DMI = dry matter intake, kg d^{-1}; RFI_{FAT} = residual feed intake adjusted for back fat thickness, kg d^{-1}. For a thorough description of all feeding behaviour traits, see Jackson et al. (2016).

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5. RELATIONSHIP BETWEEN COW REPRODUCTIVE EFFICIENCY AND WEIGHT GAIN OR LOSS DURING THE PRODUCTION CYCLE

5.1. Introduction

Cow body weight is related to fertility, especially when body condition score is considered. Cows that maintained stable body weights over time had earlier estrus, and therefore more chances to re-breed, than cows that lost weight (Dunn and Kaltenbach, 1980; Selk et al., 1988). Large decreases in body weight post-partum have been linked to reduced pregnancy rates (Rakestraw et al., 1986). Most studies analyzing reproductive performance of beef cows in relation to weight differences have been performed in the period between parturition and re-breeding or when cows were offered restricted diets to some extent. The present study examines the reproductive impact of differences between cow body weights at various time points and in normal Western Canadian management systems. The objective of this study was to determine the effects of weight loss or gain on culling for pregnancy, failure to calve, and (or) failure to wean a calf, and to determine the effects of differences between a model-predicted body weight and a real body weight at different time points across 5 parities on the same.

5.2. Materials and Methods

Cows ($n = 874$) were maintained at the Agriculture and Agri-Food Canada Lacombe Research and Development Centre (**LRDC**, Lacombe, AB, Canada) and at the University of Alberta's Roy Berg Kinsella Research Station (**KIN,** Kinsella, AB). All the cattle were cared for according to the guidelines of the Canadian Council on Animal Care (CCAC, 1993).

5.2.1. Description of cattle and management

All cows were followed over 5 parities and 2752 mating opportunities. Complete descriptions of cattle breed composition and management were reported in Olson et al. (2020). Briefly, the cattle housed at LRDC were predominately Red Angus (AR) and Aberdeen Angus (AN) crossed with Hereford (HE), Charolais (CH), Maine Anjou (MA), and Simmental (SM) [herd development was described by Basarab et al. (2018)]. Breeding bulls were purebred AN, RA, HE, CH, MA and more recently SM. At KIN, cows were the result of a beef-dairy crossbreeding program and are referred to as the Kinsella Composites (KC). They are predominately KC cows crossed with KC, AN, AR, CH, LM and HE bulls; the breeding program has been previously described completely by Goonewardene et al. (2003). Cow breed composition was determined genomically using Admixture software (Alexander et al., 2009) based on bovine 50K single nucleotide polymorphisms (SNP) genotypes (a full description of genotyping was presented in Basarab et al., 2018). Genomic breed composition was used to determine genomic retained heterozygosity (g**RHET**), which was calculated for each cow by: $RHET = 1 - \sum_{i=1}^{n} P_i^2$; where P_i is the fraction of each of the n contributing breeds.

Heifers were born between March and May of any given year at both locations and remained with their dams until mid-October, when they were weaned at 6-7 mo of age. All calves were administered a vaccination schedule for the prevention of common viral and bacterial diseases at 2-2.5 mo of age. After weaning, all heifers at both locations were fitted with a half-duplex radio-frequency identification tag (Allflex USA Inc., Dallas, TX, USA) and performance tested for individual feed intake using GrowSafe automated feed bunk technology (GrowSafe Systems Ltd., Calgary, AB, Canada). Depending on the year (2005-2019 at LRDC;

2012-2019 at KIN), heifers were tested for between 69 and 114 d in a dry lot setting. Each pen had eight GrowSafe bunks. Feed intake and feeding behaviour was collected continuously for the duration of each test. In all years except 2017, heifers at LRDC were supplied a 90-100% barley silage, 0-10% rolled barley grain ration (as fed basis), averaging 39.1% DM (SD=4.1%) and 9.77 MJ kg^{-1} DM (SD=0.41). In 2017, heifers were fed a 74% barley silage, 26% corn distillers' grain plus solids ration (cDDGS; as fed basis) containing 36.0% DM and 9.77 MJ kg^{-1} DM. Heifers at KIN were developed on high forage diets that varied from 55-78% barley silage, 6-40% whole oats, 4.5%-12% cDDGS, 0-13% canola meal and 4.7-5% protein supplement with Rumensin, as-fed, depending on year and commodity availability. Diet DM and energy content averaged 57.5% (SD=5.4) and 10.23 MJ kg^{-1} DM (SD=0.18), respectively. Wood chips and wood shavings were used to bed heifers in both locations on an as-needed basis for animal welfare and comfort. Straw bedding was used on 1-3 days in some tests when ambient temperature dropped below -20^{o} C.

After the end of each test, heifers remained in confinement until mid-May, after which they were placed on mixed-species cool-season pastures until mid-October. From mid-October to the following April-May, cattle at LRDC were fed in two groups: 1) cows were fed a barley silage diet in confinement; 2) cows grazed swaths of various annual cereals (barley, corn, and/or triticale, crude protein averaged 10.5% and 61% in-vitro true digestibility) from mid-October until February-March, or until weather dictated that the cows could not readily access the swaths due to ice or snow. Cows exposed to swath grazing utilized more than 70% of barley and corn and more than 80% of available Triticale swaths (Baron et al., 2006; Baron et al., 2014). In February-March, cows were moved to areas with open-front barns for calving and supplied a barley silage ration until mid-May. Between 2005 and 2014, only cows in their 3rd parity or greater were placed on swath grazing. Beginning in the fall of 2014, cows in their 1st and 2nd parity were also exposed to swath grazing. Cows were allocated to swath or confinement treatments to maintain a balance of breed type, body condition score, age, and weight. Cattle housed at KIN were transitioned from grazing extensive pasture to a winter diet of hay fed on extensive pasture until grazing was available in the following May. At both locations, cows were provided free-choice water, salt, and mineral. Cattle were bedded with straw when windchill values were below -20˚C or when deemed necessary for animal well-being by management.

Breeding seasons for heifers and mature cows differed. For 45 d beginning in May (LRDC) or June (KIN) heifers were exposed to breeding, and mature cows were exposed for 63 days beginning 2-3 weeks after the heifers. Bull:cow ratio was between 20:1 and 25:1 depending on the location and year. Approximately 85 d after the breeding season ended, cows were rectally palpated to diagnose pregnancy. The resulting calves were born between March and May of the following year, remained with their dams until weaning in mid-October at 6-7 months of age.

Cows at Kinsella in the Efficient herd were selected using molecular breeding values for efficiency that were predicted using phenotypic data of residual feed intake (adjusted for body composition), dry matter intake, average daily gain, and single nucleotide polymorphisms (SNPs). Molecular breeding values for residual feed intake were used in a selection index equation along with molecular breeding values direct and maternal weaning weights as described in Ekine-Dzivenu et al., (2018). Heifers that scored a high index value were selected as replacement heifers and entered the breeding herd. The control herd was selected using conventional phenotypic selection with no emphasis on residual feed intake.

5.2.2. Cow performance traits and culling

Cows were culled at pregnancy evaluation in the fall of each year if they were open. Cows were also culled post-calving for failure to calve, and post-weaning for failure to wean a calf. Additionally, cows were culled for poor udder structure (based on the scoring system designed by the Canadian Simmental Association), poor temperament, dystocia, poor skeletal design, and poor performance. All culling reasons, mortality causes, and associated dates were recorded by farm management, which remained the same from the beginning of data collection to present production cycles at LRDC and KIN.

Production cycle traits measured included body weight and ultrasound back fat thickness at pre-calving (February), pre-breeding (May), pregnancy diagnosis (October), and weaning (October) at LRDC and at pre-breeding (June), pregnancy diagnosis (October), and weaning (October) at KIN yearly. Parity data were limited to parities 1-5 due to n limitations in parities greater than 5. Parity was defined as the period from breeding to the weaning of the calf conceived; all points between those two events are referred to as being within parity “x” (see Fig. 5.1 for a visual of this concept). A heifer “survived” to parity 1 if she had a calving record (dead or alive). She did not survive to parity 1 if she was culled for non-pregnancy, aborted her calf, or died prior to the first calving event. A cow survived to parity 2 if she had a calving record for parity 2 and did not survive if culled postweaning of the first calving due to failure to wean a calf. The same pattern was used to determine survival to the third, fourth, and fifth parities. All phenotypic values were checked for normality using PROC UNIVARIATE in SAS 9.4 (SAS Institute, Cary, NC, USA) and values outside ±3 SD from the mean were removed from the analysis.

Values for the differences between two weight points were derived by subtracting the earlier weight from the later weight. The differences (average daily gain or loss) were standardised to the average number of days between weight events across location and parity:

$$standardized\ weight\ differences = \frac{(Weight2 - Weight1)}{Mean\ days\ between} \times mean\ days\ between$$

Differences were analyzed over several different periods each year, both within and across parities (Table 5.1). Winter, which was defined as the difference of dates in days between pregnancy diagnosis *i* and pre-breeding *j*, where *i* = preceding parity (beginning at parity 1) and *j* = subsequent parity. The summer variable was defined as the difference between pre-breeding *j* and weaning *i,* again where *i* = preceding parity and *j* = subsequent parity. A thorough visualization of the timing and overlap of the reproductive cycles of cows at LRDC and KIN can be found in Fig. 5.1.

Table 5.1. Variable descriptions

Item[1]	Description	Average length (d)
Within parity variables		
PB to PE	Pre-breeding to pregnancy evaluation (May/June - October)	150
PE to PC	Pregnancy evaluation to pre-calving (October - February)	130
PC to Wn	Pre-calving to weaning (February-October)	240
PB to PC	Pre-breeding to pre-calving (May/June - February)	135
PE to Wn	Pregnancy evaluation to weaning (October-October)	280
PB to Wn	Pre-breeding to weaning (May/June - October)	370
Across parity variables		
PEi to PBj	Pregnancy evaluation *i* to pre-breeding *j* (October - May/June)	130
PCi to PBj	Pre-calving *i* to pre-breeding *j* (February- May/June)	125
Summer	Pre-breeding *j* to weaning *i* (May/June - October)	130
Winter	Pregnancy evaluation *i* to pre-breeding *j* (October - May/June)	235

[1] i = preceding parity; j = subsequent parity.

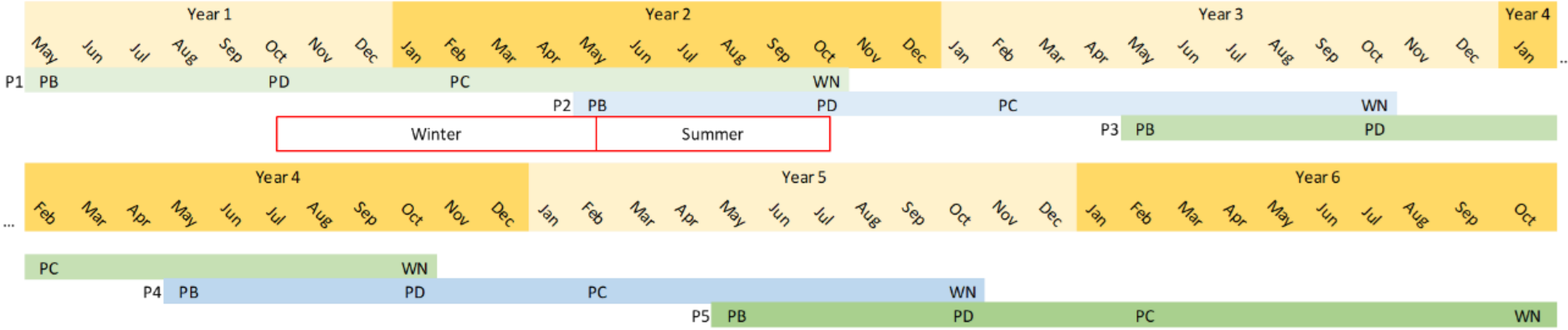

Figure 5.1. Reproductive cycles of beef cows at LRDC and KIN, beginning at pre-breeding in parity 1. P1 = Parity 1; P2 = Parity 2; P3 = Parity 3; P4 = Parity 4; P5 = Parity 5; PB = Pre-breeding; PD = Pregnancy Diagnosis; PC = Pre-calving; WN = Weaning; Winter = illustration of the winter period (repeats for each parity); Summer = illustration of the summer period (repeats for each parity).

5.2.3. Derivation of modeled and corrected weights

Direct measurement of individual conceptus weight in beef cattle is not possible. Modeled data were relied on to make inferences about the energy use, conceptus weight, and predicted weight at a given age. To estimate the weight of a calf at any point during gestation, a 283-d gestation length was assumed. Therefore, days pregnant (DP) was:

$$DP = 283 - (Birth\ date - considered\ date);$$

where birth date was equal to the birth date of the calf and the considered date was any day within 283 days prior to the birth date (for the purposes of this study, considered date was the date associated with a weight event at pregnancy diagnosis, pre-calving, or weaning). Days pregnant (DP) was calculated for every cow in every parity for weight events at pregnancy diagnosis, pre-calving, and weaning, and was not calculated for pre-breeding events, as it was assumed that all cows were not pregnant at that time.

Conceptus weight (**CW**) on a given date was estimated using days pregnant and calf birth weight, which was collected on calves within 24 hr of birth at both LRDC and KIN, and entered into this equation:

$$CW = CBW \times 0.01828 \times \left(e^{0.02 \times DP - 0.0000143 \times DP^2}\right)$$ [Eq. 19-69, NASEM (2016)],

where CW = conceptus weight (kg), CBW = calf birth weight (kg), DP = days pregnant, and *e* = natural log.

Conceptus-adjusted cow weights were derived from the following:

$$BW_{CA} = BW - CW;$$

where BW_{CA} = conceptus-adjusted cow body weight (kg), BW = cow body weight (kg), and CW = conceptus weight (kg). Cow age at any given date was found as the difference between the cow's birth date and the considered date and converted to months by dividing the difference by 365 and multiplying by 12.

A model was fit for each cow with a similar form to the target weight model used by Rotz et al. (2005), except that the asymptote is mature weight instead of mature weight plus birth weight. The model was fit with PROC NLIN (SAS Institute Inc., Cary, NC, USA).

$$model\, weight = Cow\ BW + (MW - Cow\ BW) \times \left(1 - e^{(-k \times age)}\right);$$

where model weight is the predicted weight (kg) for a cow at a given age (mo), cow BW = cow birth weight (kg), MW = mature weight (asymptote, kg), e = natural log, k = growth coefficient (common and age = age in months. An estimated weight was found for each cow at each weigh-point in each parity. A difference between the modeled weight and conceptus-corrected phenotypic weight was found for each weigh point to verify whether cows should be fed to an ideal body weight and composition.

5.2.4. Statistical analysis

Weight differences outside ±3 SD from the mean were removed (n = 166 across all variables and both locations) from the analysis. Weight and other continuous variables were normally distributed. Cows were excluded from analyses for the following conditions: fostered twin or twin that died; bred females sold for revenue. Parities past the fifth parity were also excluded due to lack of n. Cows that should have been culled but remained in the herd based on management decisions were excluded after their cull date.

A linear mixed model of SAS PROC MIXED (SAS Inc., Cary, NC, USA) was used to evaluate associations between culling with weight gain or loss phenotypes, with the form: $Y_{ijklmnop} = \mu + Cull_i + P_j + S_k + T_l + Sire_m + \beta_1 R_n + \beta_2 JDay_o + \beta_3 AN_p + e_{ijklmnop}$, where $Y_{ijklmnop}$ is the animal's phenotype; C_i is the culling status (culled for open, aborted and calf died before weaning); P_j is the parity (1-5); S_k is the breeding season (2005-2019 at LRDC; 2012-2019 at KIN); T_l is the winter treatment at LRDC (confined winter feeding vs. winter grazing at LRDC only) or the RFI selection group at KIN (Efficiency; Control); $Sire_m$ is the random effect of sire; β_1 is the partial regression coefficient of a cow's gRHET (R_n); β_2 is the partial regression coefficient of cow Julian birth date ($JDay_o$); β_3 is the partial regression coefficient of a cow's genomically determined percentage of AR plus AN (AN_p); and $e_{ijklmnop}$ is the residual error.

A similar model was fitted to evaluate the effects of culling across parities, with the form: $Y_{ijklmnopq} = \mu + Cull_i + P_j + S_k + T_l + Sire_m + \beta_1 R_n + \beta_2 JDay_o + \beta_3 AN_p + \beta_4 PCJday_q + e_{ijklmnopq}$, where $Y_{ijklmnopq}$ is the animal's phenotype; C_i is the culling status (culled or not culled); P_j is the parity (1-5); S_k is the season (15 seasons at LRDC; 8 seasons at KIN); T_l is the winter treatment at LRDC (2 treatments) or the RFI selection group at KIN (2 groups); $Sire_m$ is the random effect of sire; β_1 is the partial regression coefficient of a cow's gRHET; β_2 is the partial regression coefficient of cow

Julian birth date; β_3 is the partial regression coefficient of a cow's genomic AR plus AN breed composition; β_4 is the partial regression coefficient of the previous calving Julian date across parities($PCJday_q$); and $e_{ijklmnopq}$ is the residual error.

Kinsella cows fall into two biological types – a moderate British cross cow (crossbred AN, AR, and HE; **BRBR**), and a larger, later maturing Continental-British cross cow (AN, AR, HE, CH, and LM; **CNBR**). These types have indicated differing levels of environmental fitness in the KIN environment (J. Basarab, personal communication, April 2021), and as such, a model was developed that included biological type as a main effect, with the general form: $Y_{ijklmnopqr} = \mu + Cull_i + P_j + S_k + T_l + Sire_m + Biotype_n + \beta_1 R_o + \beta_2 JDay_p + \beta_3 AN_q + \beta_4 PCJday_r + e_{ijklmnopqr}$; where $Biotype_n$ is the animal's biological type classification (BRBR or CNBR). Cows were assigned to BRBR if the sum of AN, AR, and HE genomic breed compositions were greater than 0.6, and assigned CNBR if less than 0.6. The main effect of biological type was not significant at KIN, and the term was not included in the subsequent analysis.

To further examine the relationships between weight differences and culling likelihood, summer and winter weight difference variables were grouped by standard deviation into the following 5 categories: ≤ -2 SD; ≥ -2, ≤ -1 SD; ≥ -1, ≤ 0.0 SD; ≥ 0.0, ≤ 1 SD; ≥ 1, ≤ 2 SD, and ≥ 2 SD from the mean. These categorical variables were examined using χ^2 analyses [PROC FREQ; (SAS Inc., Cary, NC, USA)].

5.3. Results and discussion

5.3.1. Weight difference observations

Average culling for reproductive failure at LRDC across parities 1-5 was 4%; average culling for reproductive failure at KIN was 5%. Cows were culled for failure to become pregnant, failure to calve (diagnosed pregnant at pregnancy evaluation but did not calve), and failure to wean a calf (calf born dead or calf born alive but died before weaning). These values agree with both the 1997/1998 Alberta Cow-Calf Audit (Audit, 2001) and the 2014 Western Canadian Cow-Calf Survey (WBDC, 2015), which indicated that approximately 10% of breeding beef females in Western Canadian provinces were culled each year for reproductive failure, age, physical soundness, calf performance, temperament, economics, and other reasons. Approximately half of the cows culled every year were culled due to failure to become pregnant, failure to calve, or failure to wean a calf (WBDC, 2015). Average conceptus-corrected weight loss or gain across parities are presented in Table 5.2. Cattle housed at KIN were not weighed at pre-calving (PC), and so no data are available for differences between PC and other weight events. Conceptus-corrected weight differences were lowest for periods of time that spanned winter and early spring months, which agrees with Coleman et al. (2017), who found that body weights in multi-parous Angus, Brahman, and Romosinuano beef cows were lowest in March and April and increased rapidly in May and June, when cows in that study where exposed to actively growing Bahia grass pastures. In the present study, cows at LRDC and KIN were exposed to wintering conditions that caused some cows to lose weight, especially those at KIN, where supplemental hay, canola straw, pea straw,

Table 5.2. Average conceptus-corrected cow body weight loss or gain (kg) by location across parities 1-5 at LRDC and KIN

			Mean (SD)	
Variable	Description	Average length, d	LRDC (kg)	KIN (kg)
PB to PE	Pre-breeding to pregnancy evaluation (May/June - October)	150	64.4 (51.6)	66.2 (61.4)
PE to PC	Pregnancy evaluation to pre-calving (October - February)	130	-8.1 (80.8)	--
PC to Wn	Pre-calving to weaning (February-October)	240	35.1 (52.5)	--
PB to PC	Pre-breeding to pre-calving (May/June - February)	135	33.1 (30.2)	--
PE to Wn	Pregnancy evaluation to weaning (October-October)	280	36.6 (62.0)	42.9 (46.9)
PB to Wn	Pre-breeding to weaning (May/June - October)	370	56.6 (32.1)	102.8 (60.9)
PEi to PBj	Pregnancy evaluation *i* to prebreeding *j* (October - May/June)	130	1.7 (33.0)	3.5 (25.8)
PCi to PBj	Pre-calving *i* to pre-breeding *j* (February- May/June)	125	-9.8 (57.1)	--
Summer	Pre-breeding *j* to weaning *i* (May/June - October)	130	55.1 (48.8)	37.2 (45.7)
Winter	Pregnancy evaluation *i* to pre-breeding *j* (October - May/June)	235	3.0 (59.6)	7.0 (47.1)
Difference from modelled weight			30.18 (70.8)	98.2 (110.3)

availability) was fed on native range during the winter and early spring at a rate of 2.5% of body weight AF. The lowest average differences at LRDC are observed between pregnancy evaluation (October) and pre-calving (February), when some LRDC cows would have been exposed to swath grazing conditions, and from pre-calving$_i$ (February) to pre-breeding$_j$ (May), when cows entered their third trimester of pregnancy, underwent parturition, and began to lactate while consuming silage before being turned onto mixed cool-season grass pastures in May. Likewise, the greatest positive average weight difference observed at LRDC was over the summer periods, between pre-breeding (May) and pregnancy evaluation (October), which coincides with the annual growing season of cool-season pastures in Alberta (Baron et al., 2000). Similar observations are made at KIN, where the lowest positive average weight difference falls between pregnancy evaluation (October) and pre-breeding, (June), coinciding with the period where cows were provided conserved forage on open pasture.

5.3.2. Weight differences across parity

Conceptus-corrected body weight differences were greater in the Summer in cows that were culled for failure to become pregnant, failure to calve, and failure to wean a calf than in cows that successfully reproduced ($P < 0.001$; Table 5.3) but not over the Winter period at both KIN and LRDC. This result was not expected but should have been axiomatic – cows that were open, aborted a calf, or failed to wean a calf were exposed to the same summer environment at their respective locations as the cows that successfully calved and weaned a calf, but had considerably fewer energetic demands (shortened or absent pregnancy and lactation energy demands). As a result, the cows culled for.

Table 5.3. Change in conceptus-corrected cow body weight and backfat thickness, and linear effects of genomic retained heterozygosity (gRHET) and cow Julian birth date across parity at LRDC and KIN.[1]

Weight Change Period	Period length, d	N, Culled	N, Not culled	Culled, kg	Not Culled, kg	C	P	C × P	S	T	C × T	P × T	Cow RHET, kg/10% change	Cow birth date, kg/10-d	Previous Calving Date, kg/10-d
LRDC															
Summer	130	55	1473	69.2 ± 6.8	44.1 ± 2	<0.001	0.02	0.058	<0.001	0.969	0.063	0.017	-2.94 ± 0.99**	-0.68 ± 0.75	0.89 ± 0.86
Winter	235	60	1554	8.1 ± 8.9	-5.7 ± 2.7	0.119	0.15	0.134	<0.001	0.147	0.685	0.007	3.45 ± 1.32**	2.47 ± 1**	-4.22 ± 1.14***
KIN															
Summer	130	53	1071	68.7 ± 11.2	35.1 ± 4	0.002	0.207	0.211	<0.001	0.654	0.657	0.408	-5.86 ± 4.93	-0.3 ± 2.23	0.83 ± 1.8
Winter	235	56	1226	6.4 ± 9.9	5.8 ± 3.7	0.955	0.15	0.392	<0.001	0.282	0.521	0.166	3.75 ± 4.64	1.49 ± 2.07	3.24 ± 1.66†

[1] P = parity; C = cull reason; S = season; T = treatment; RHET = retained heterozygosity; * = P-value < 0.05; ** = P-value <0.01; *** = P-value <0.001;

infertility accreted greater back fat thickness over the summer period (Table 5.3) and gained more weight than those not culled for infertility. Osoro and Wright (1992) evaluated the effects of BCS and live weight on cow reproductive performance using crossbred British × Continental and British × Holstein cows. While not directly measuring culling rate, Osoro and Wright (1992) reported that there was no effect of live weight change from calving to the start of breeding or during the breeding season (9-10 weeks beginning in May) on cow reproductive performance. Further, in a review of the literature, Dunn and Kaltenbach (1980) concluded that cows in good body condition at calving do not suffer reproductively with either weight gain or weight loss. In the present study, cows at both locations were provided feed to target BCS of 4-5 (on a 9-point scale where 1 = emaciated and 9 = extremely obese) at calving, and yet cows that were culled over the Summer period from calving to weaning gained more weight than those that were not culled

Parity affected conceptus-corrected weight differences over Summer at LRDC but did not have an effect on Summer conceptus-corrected weight differences at KIN or Winter differences at either location. Differences over Summer at LRDC were greatest in parities 2 and 3 and were lower in parities 4 and 5 (Fig. 5.2). The definition of mature weight is contested, with British cattle (such as those in the present study) reported to reach maturity as early as 56 mo of age (Nadarajah et al., 1984), or as late as 84 mo (Choy et al., 2002). Cows housed at LRDC may not have reached maturity in parities 2 and 3 and would have been gaining body mass as part of their normal growth process,

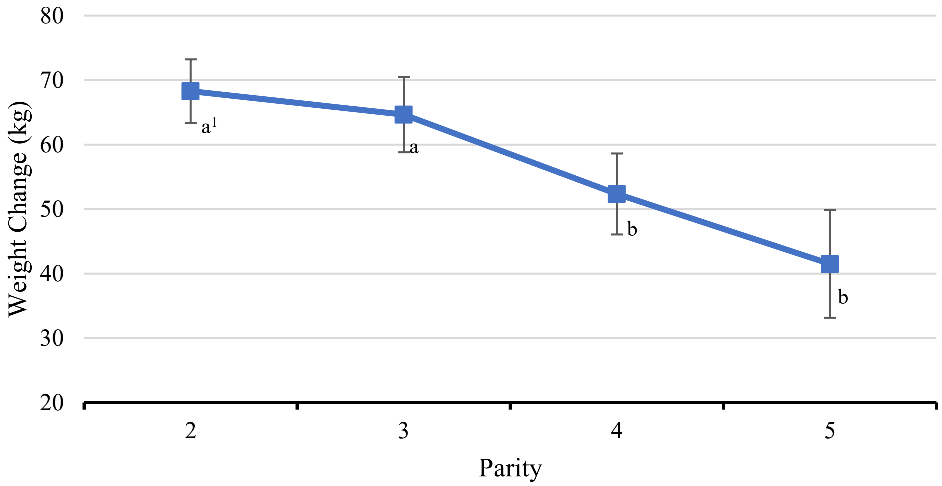

Figure 5.2. Least-square means of conceptus-corrected cow body weight differences (kg) over summer for cows housed at the Lacombe Research and Development Centre. [1]Means with different superscripts differ.

before stabilizing over parities 4 and 5. No study was found in the literature that described changes in weight over time related to age in cattle, but Renquist et al. (2006) reported that cows aged 3, 4, and 5 years old were always lighter in weight than cows age 6-10, but did not necessarily carry more backfat. Those results indicate that cows continue to increase in size as they reached 5 years old, not body fatness, which would help to explain the phenomenon observed at LRDC, where the largest weight gains are observed in younger cows. Weight changes over Summer at Kinsella were more variable and did not differ, which could be due to the effects of a somewhat harsher management environment more in keeping with the average environment of the Western Canadian cowherd. No differences were observed in either location over Winter, which may be due to increased energy demands for maintenance due to severe weather and lessened nutritional value of conserved forages compared to forages available over the summer.

Further, cows at KIN had an average gRHET of 0.51, and cows at LRDC had gRHET of 0.36, which may play a role in the ability of cows to withstand weight changes and could explain some of the differences observed in the Summer between KIN and LRDC. Crossbred cattle are believed to have greater environmental fitness; among AN, HE, and SH purebreds and crosses, Núñez-Dominguez et al. (1991) found that crossbred cows had consistently greater survivability than purebred cows when strict artificial culling for reproduction was imposed.

Season affected the amount of weight gained or lost by cows at both locations over Summer and Winter. Considerable variation in the data existed and values for Winter at both locations were lower than those for Summer, indicating that cows did not gain as much weight over the winter months. Webster et al. (1970) recorded weight gain and feed intake in young Hereford and crossbred beef females during a severe winter in central Alberta. Heifers in that study that were exposed to long-term cold without shelter had the poorest rate of gain but consumed more hay per unit of body weight than those heifers that were housed indoors at 20˚C. In a climate like that of Western Canada, where winters are long and cold and summers are short and hot, seasonal variation impacts on cow performance are outside the control of animal management.

5.3.2.1. Treatment effects at the Lacombe Research and Development Centre

Cows housed at LRDC were exposed to one of two winter feeding treatments. Cows were either provided conserved forage (barley silage) ad libitum in a dry lot setting from late October to mid-May, or they were provided swath grazing of various annual cereal crops (barley, triticale, and/or corn depending on the year) from late October until early

February and then fed conserved forage (barley silage) ad libitum until mid-May. Cows may have been removed from the swath grazing environment earlier than February if conditions were not conducive for animal well-being (ice or heavy snow that prevented swath access). Winter feeding treatment did not have any effect on culling for fertility, though a parity × treatment effect was observed for both Summer and Winter. Summer weight differences for cows that were fed silage in confinement were greatest in parity 2 and 3 and different from parities 4 and 5 (Fig. 5.3). Winter treatment × parity interactions indicated that weight differences were greatest in parity 2 for both treatments, but cows provided swath grazing in parity 4 lost the most weight during that time, with parities 3 and 5 being intermediate (Fig.5.3). Prior to 2014 at LRDC, cows in their first and second parities were wintered in confinement due to concerns about their ability to access the swaths beneath the snow and their ability to compete with older, heavier cows for swaths. This may be a factor in explaining why the cows in earlier parities have weight differences greater than those in later parities. Further, cow maturity likely also plays a role, with those cows in parities 2 and 3 accreting body mass as a part

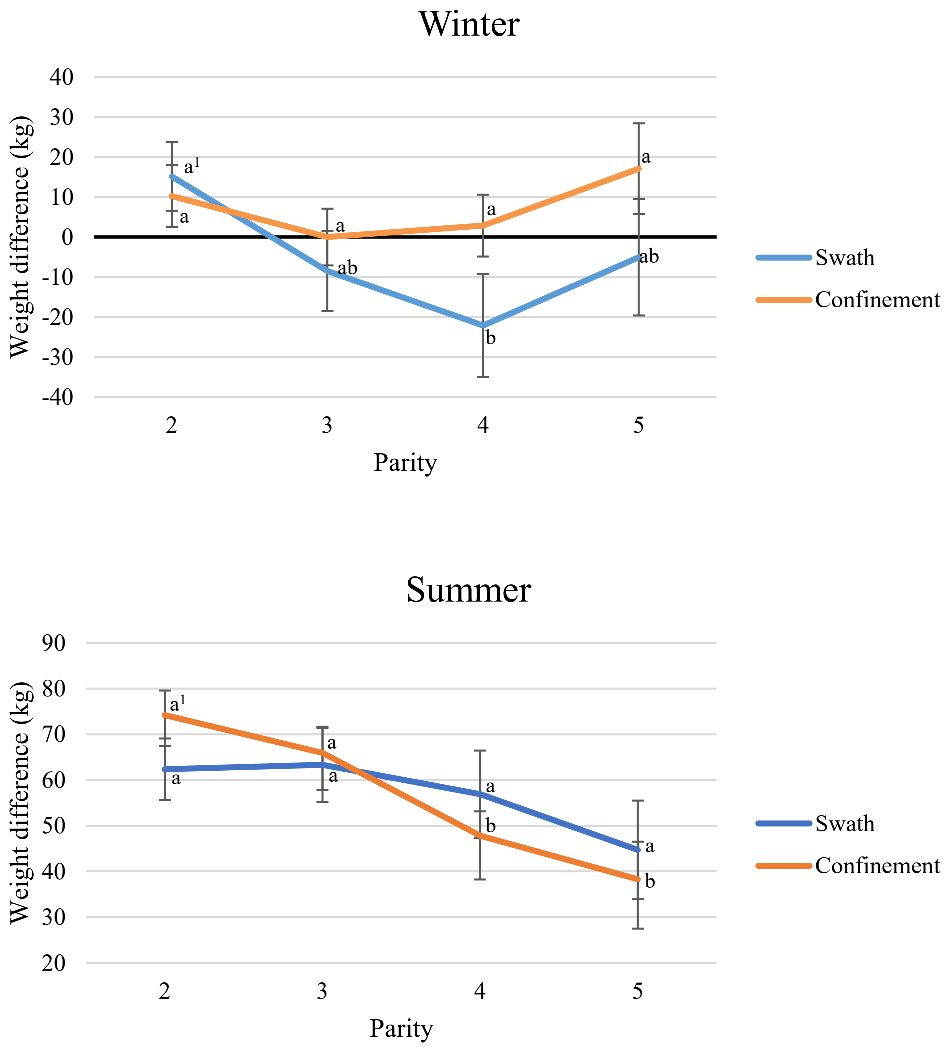

Figure 5.3. Interactions of winter treatment type and parity on the weight differences of cows (kg) housed at the Lacombe Research and Development Centre. Within treatment, points with different superscripts differ).

of maturation. The maturation process would be indicated by greater weight differences in parities 2 and 3 than parities 4 and 5. No interactions or effects of treatment were observed at KIN.

5.3.2.2. Linear effects of genomic retained heterozygosity, cow Julian birth date, and previous calf Julian birthdate

Genomic retained heterozygosity had significant linear effects on conceptus-corrected body weight differences in Winter and Summer at LRDC (Fig. 5.4), but no effect was observed at KIN. Lack of an effect at KIN may be due to the averaging of Continental-British crossbred cows (AN-LM and AN-CH) with British-British crossbreds (AN-HE). As the Continental-British crosses at KIN have been observed to be later maturing and typically carry less backfat, they are not as well adapted to the native prairie environment and have fewer days in herd, an important metric for estimating lifetime productivity (J. Basarab, personal communication, April 2021). In the present study, the effects of gRHET are averaged across the entire herd, and it is likely that the two breed type groups at KIN cancel each other out.

Genomic retained heterozygosity accounted for 5.3% and 5.0% of the variation in conceptus-corrected weight change in Winter and Summer, respectively. Cows with greater gRHET had greater conceptus corrected weight differences in the Winter than cows with lower gRHET ($P = 0.009$), and cows with greater gRHET had smaller weight differences in the Summer than cows with lower gRHET. The Winter results indicate that cows with greater gRHET were better able to withstand the season and the demands of gestation than cows with lower levels of gRHET, though the precise biological explanation for this phenomenon is not available from the dataset analysed. The summer results may indicate that cows with greater gRHET are producing larger calves, resulting in greater energy demands during the lactation period. Basarab et al., 2018 found that heifers with greater gRHET produced 35.7 kg more calf wean weight over 5 parities than cows with lower gRHET observations. Evidence that crossbred cattle are more resistant to disease was presented by Snowder et al.

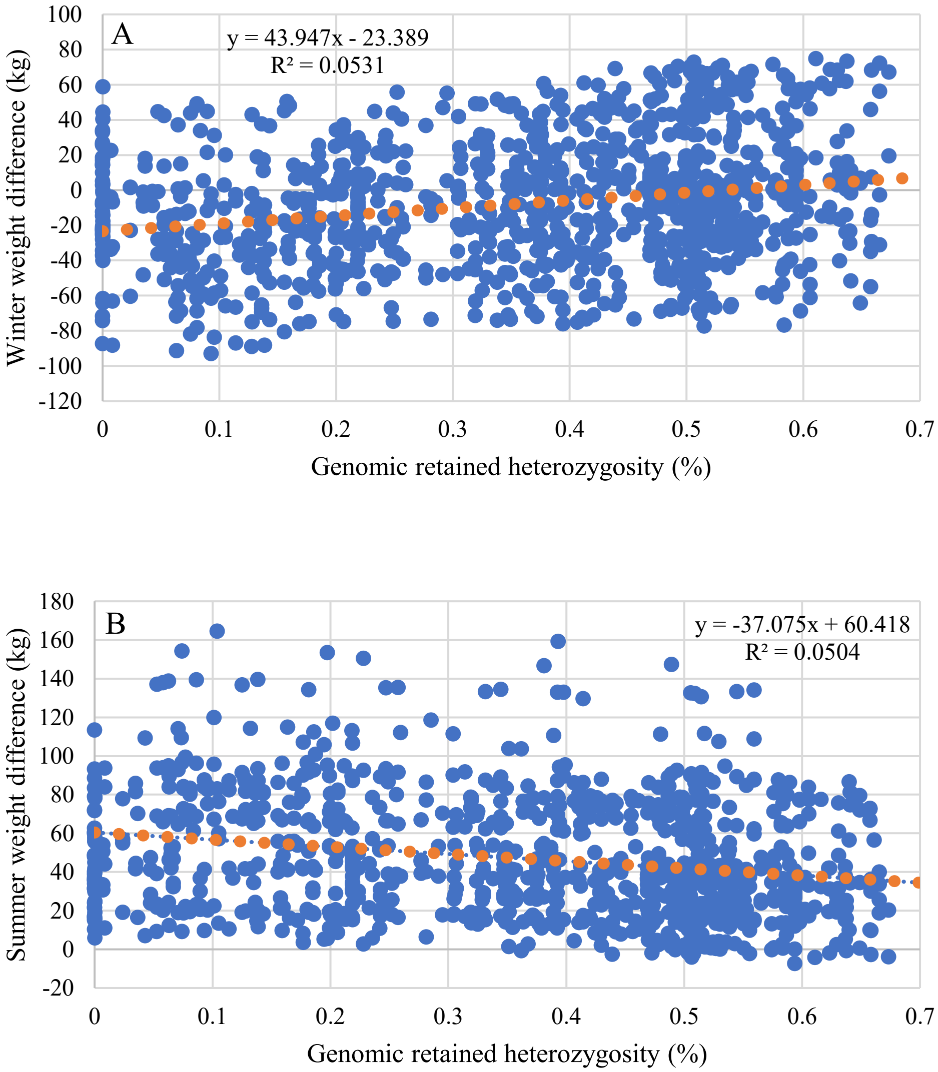

Figure 5.4. Effects of genomic retained heterozygosity on model-adjusted conceptus-corrected cow body weight differences in the Winter (A) and Summer (B) at the Lacombe Research and Development Centre.

(2005), who found that heterozygosity reduced susceptibility to bovine respiratory disease. It is possible that, in the present study, cows with greater gRHET were less susceptible to conditions affecting the health of the fetus, and so were able to maintain pregnancy and avoid culling for not pregnant, failure to calve, and failure to wean a calf. In a related population of cows, Basarab et al. (2018) reported that gRHET had a negative linear relationship with weight gain over summer grazing and the period from the beginning of a parity (pre-breeding) to the end (weaning), which agrees with the present results for Summer. This effect may be due to a greater rate of fat mobilization and accretion associated with reproductive activities. As a result, cows with greater gRHET may have experienced greater energy demands related to reproduction than cows with less gRHET, which may indicate that less intake energy was available for growth or fat deposition over the Winter. Further exploration into the biological reasons for greater cow resiliency in challenging winter range environments is necessary.

Genomic retained heterozygosity decreased Summer weight differences, so that cows with greater heterozygosity gained less weight over the summer period. However, when taken in consideration with the effects of gRHET on weight differences in the Winter, it appears that cows with greater gRHET lost less weight in the Winter and so had less weight to re-gain in the summer. These results are supported by Riley et al. (2016), who reported that full-blood Aberdeen Angus cows in a hot subtropical environment consistently lost more weight over lactation than either the Angus × Romosinuano or purebred Romosinuano cows, an indication that the Angus herd was not as environmentally fit as the crossbred or tropically adapted herd.

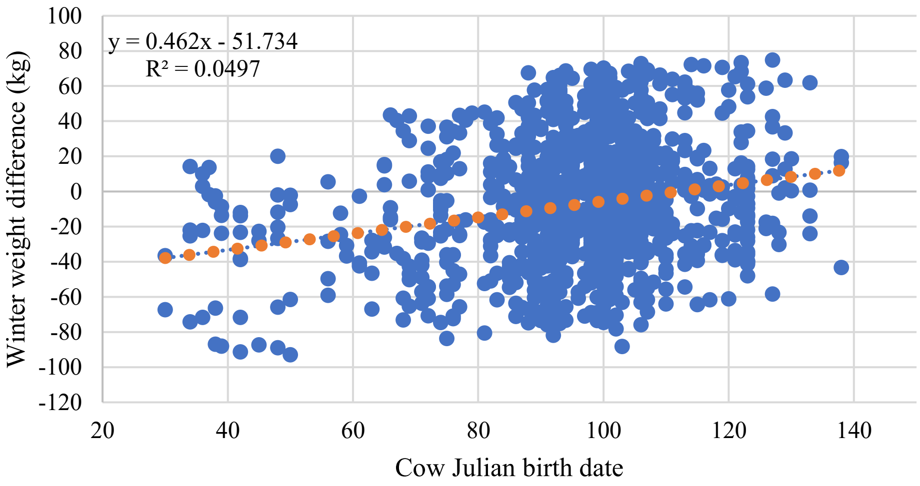

Figure 5.5. Effects of cow Julian birth date on model adjusted conceptus-corrected cow body weight differences in the Winter at the Lacombe Research and Development Centre.

Cow Julian birth date affected conceptus-corrected weight differences at LRDC such that cows born later in the calving season (with a greater Julian birth date value) lost less weight or even gained weight over the Winter compared to cows born earlier in the calving season (*P* = 0.014; Fig. 5.5.). It is not clear from the data why this trend occurs, nor is the phenomenon known in the literature specifically relating birth date and mature weight or body condition score differences over time. It is widely accepted that older calves, born earlier in the season, are heavier at weaning (Pell and Thayne, 1978; Butson et al., 1980; Ahunu and Makarechian, 1986). This trend may help to explain conceptus-corrected weight differences in parity 2 cows, which are likely still growing to maturity and thus older cows may not gain as much weight as younger cows born in the same year. We would expect, however, that the effect of birth date would lessen as cows mature and their weight stabilizes. The linear effect of cow Julian birth date was not observed in the Summer at LRDC, nor was it observed for either Summer or Winter conceptus-corrected weight differences at KIN, even though calving at KIN occurs later in the year at a more favourable time of year.

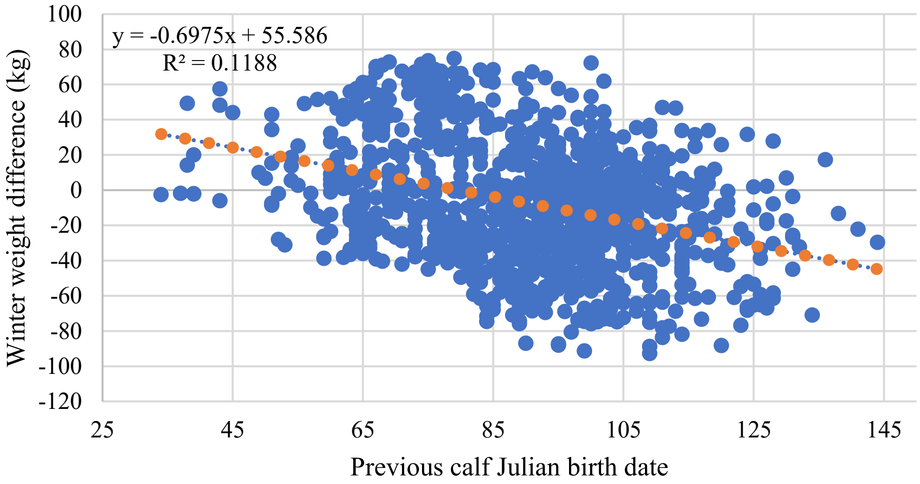

Figure 5.6. Effects of previous calf Julian birth date on adjusted conceptus-corrected cow body weight differences in the Winter at the Lacombe Research and Development Centre.

Previous calf Julian birth date was moderately negatively related to conceptus-corrected cow weight differences at LRDC in the Winter ($P < 0.001$; Fig. 5.6). Thus, as Julian birth date increased, the weight difference of the cow in the subsequent Winter period decreased and became negative (cows that calved later in the season lost weight). Contrarily, Drennan and Berry (2006) found that cows that calved prior to the 65th day of the year lost more weight over a winter period of 150 d in a confinement feeding environment. Those cows were heavier at the beginning of the winter period in that study; however, the weights recorded in those cows were not adjusted for conceptus weight. Therefore, cows that calved earlier in the season may have been heavier than cows that calved later due to the weight of the conceptus, and not necessarily the body weight of the cow. The greater weight loss observed in that study may also be due to the effects of calving and lactation, where cows that calve earlier in the season would have been lactating for a greater period of time, and therefore exposed to greater energy demands, than cows that calved later in the season. Some cows recorded by Drennan and Berry (2006) were pregnant at the end of the winter period, and some had already calved. In the present study, conceptus-corrected weights were compared, which should allow a better understanding of the changes of the cow herself, rather than the cow and the conceptus she is carrying and illustrates the importance of considering the weight of the conceptus when evaluating pregnant cows. Further, this provides evidence that cows that have later calving dates may struggle to regain weight during the summer due to a lactation curve that peaks when forage is decreasing in quality.

5.3.3. Differences between conceptus-corrected weight and predicted body weight

5.3.3.1. Body weight predictions

Body weight predictions at a given age were calculated using a modified Von Bertalanffy equation similar in form to that used by Rotz et al. (2005) to predict the target weights of beef heifers (Table 5.4). The only difference between the model used by Rotz et al. (2005) and the present study was that the asymptote in the present study was mature weight, not mature weight plus birth weight. The model varied in accuracy

Table 5.4. Predicted mature cow body weights at LRDC and KIN

	N	Mature body weight, kg	SD
KIN	499	650.19	78.04
LRDC	671	619.26	74.32

for each cow, with an average r^2 value of 0.49 at LRDC and 0.09 at KIN. Substantial differences at KIN were observed, primarily due to the lack of birth weight data in the majority of the cowherd born prior to 2012 and one less cow weight data point per year. It is important to note that the predicted weights in this study were considered to be 3 on a 9-point scale, in keeping with the estimates by Rotz et al. (2005). In the present study, cows housed at KIN had an average standardized BCS of 3.9, and cows housed at LRDC had a standardized BCS of 6.2. Predicted mature weights of beef cows on pasture could have considerable value as a monitoring tool for producers. Predicted weights are standardized to BCS 3, which is slightly below the recommended BCS of 4-8 for successful reproduction (Osoro and Wright, 1992). Therefore, if this or a similar prediction equation were to be applied to a mature breeding herd, cows that weigh less than their predicted weight could be more likely to fail reproductively than cows that are heavier than their predicted weight. As technology advances, remote sensing of individual cow body weights becomes more realistic and could result in producers being able to identify animals that are deviating substantially from their expected weight given their age. Further, given the current emphasis placed on the environmental impact of beef cows on pasture, having a reasonable estimate of the total weight of a cow herd could contribute to the body of knowledge surrounding energy demands and by-products of ruminal fermentation without the need to individually weight every cow.

5.3.3.2. Culling

Differences between predicted weight and conceptus-corrected weight were affected by culling at LRDC, but not KIN (*P* = 0.009 and 0.337, respectively, Table 5.5). The difference between the predicted weight and conceptus-corrected body weight was greater in cows that were culled than in cows that were not culled. These results are similar to the seasonal differences previously explored, and indicate that cows that were not pregnant, failed to calve, or failed to wean a calf were accreting greater body weight than cows that reproduced successfully. Further, these results may be applied on-farm through consistent remote measurements of cow weight. If a cow is consistently above or increasing the difference between a modelled weight and her conceptus-adjusted weight, producers may have the opportunity to identify animals that are non-pregnant, or in extremely extensive conditions, cows that have failed to calve or have lost their calf prior to weaning. As technology related to remote sensing and artificial intelligence increases in availability, the application of this notion will become more practical – with technology, cow weights may be estimated frequently and concerning trends could be reported to the producer.

Parity and season affected the difference between predicted and conceptus-adjusted weight (Table 5.5). Differences at LRDC increased over time ($P < 0.001$), with cows in parity 1 weighing 9.6 kg more than predicted and cows in parity 5 weighing 79.9 kg more than expected. Differences among parity at KIN were not as clear, and environment at KIN may have a greater impact on weight differences. Cows at KIN did not have different weight differences in the first 4 parities, but parities 1-4 were all heavier ($P < 0.05$) than cows in parity 5, which averaged 39.3 kg heavier than their predicted weights. Issues arise with the interpretation of the KIN data, as the r^2 of the

Table 5.5. Effects of culling, parity, season, treatment, RHET, and cow birth date and their interactions on the difference between conceptus-corrected cow body weight and modeled body weight at the same age.[1]

	Culled, kg	Not Culled, kg	C	P	C × P	S	T	C × T	P × T	Cow RHET, kg/10% change	Cow birth date, kg/10 d
Lacombe	44.9 ± 4.7	34 ± 3.4	0.009	<0.001	0.556	<0.001	0.031	0.056	<0.001	2.26 ± 1.46	-2.38 ± 1.07**
Kinsella	74.5 ± 12.9	86.5 ± 6.9	0.337	0.02	0.368	<0.001	0.063	0.922	0.610	1.23 ± 7.89	-7.63 ± 3.59*

[1] P = parity; C = cull reason; S = season; T = treatment; RHET = retained heterozygosity; * = P-value < 0.05; ** = P-value <0.01; *** = P-value <0.001;

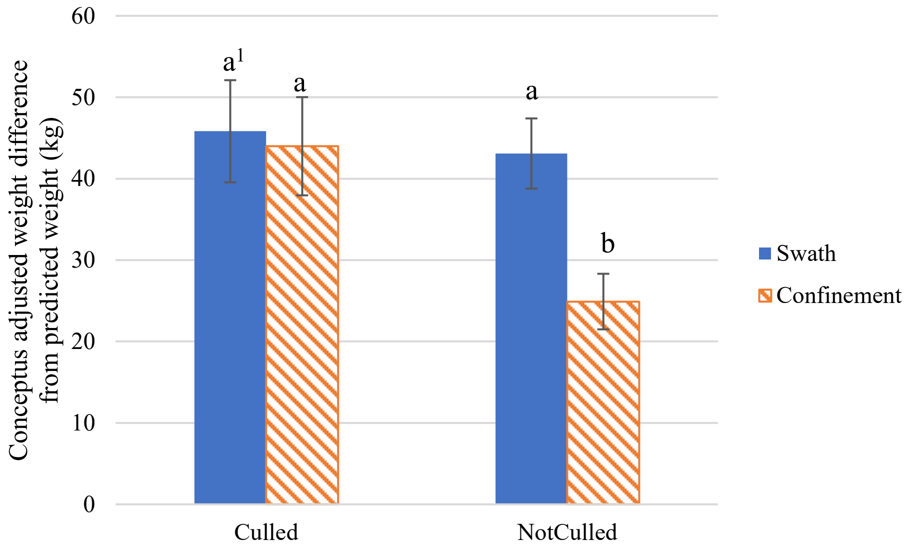

Figure 5.7. Interaction between culling status and treatment affecting difference between conceptus-adjusted cow body weight and predicted body weight in LRDC cows. ([1]Weight differences within culling status with different superscripts differ [$P < 0.05$])

relationship between the predicted and actual weights is quite low, and inconsistent trends are observed with little observable biological reason.

A tendency for interaction between culling for reproductive performance and treatment was observed ($P = 0.056$; Fig. 5.7) such that cows that were housed in confinement and culled were heavier than cows housed in confinement and not culled, but no difference existed between cows housed on swath grazing. Confinement-fed cows at LRDC included cows in parities 1-5 for all years, but cows exposed to swath grazing prior to 2014 were in parity 3-5, due to concerns about younger cows being able to access the swaths and compete with older cows for feed resources. For this data set, the average age of cows on swath grazing is older than the age of cows fed in confinement.

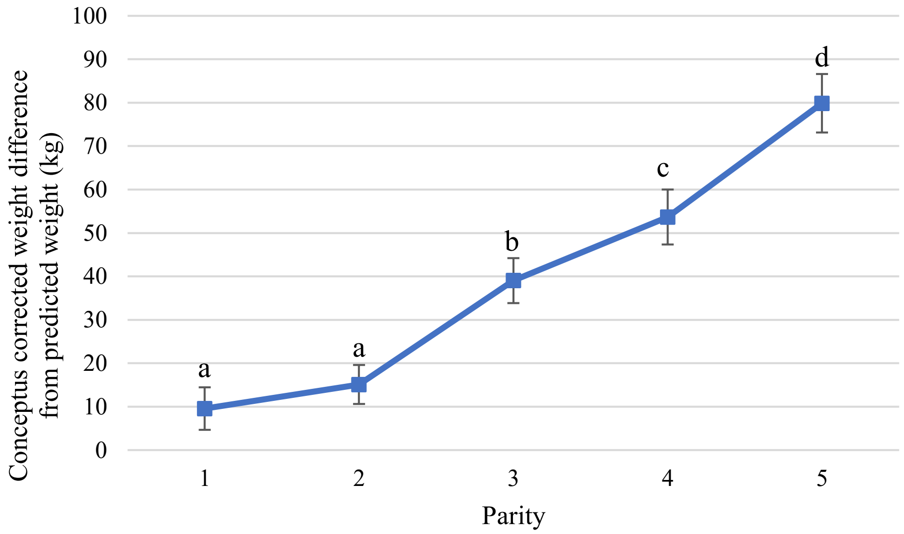

Figure 5.8. Difference of conceptus-corrected cow body weight relative to predicted body weight across parities 1-5 in cows housed at LRDC. ([1]Weight differences with different superscripts differ [$P < 0.05$])

As the cows in the present study accreted body mass in each parity (Fig. 5.8), the older cows in the swath grazing treatment are heavier, on average, than the cows in the confinement treatment. It is likely, therefore, that the tendency observed for this interaction is linked to the heavier average weight of the cows exposed to swath grazing and may not be due to the effects of winter treatment itself.

An interaction where treatment effects were different in different parities was observed for cows housed at LRDC ($P < 0.001$, Fig 5.9). Cows in parity 1 exposed to swath grazing had a greater difference between conceptus-corrected weight and predicted weight, where they were heavier than predicted, than cows exposed to swath

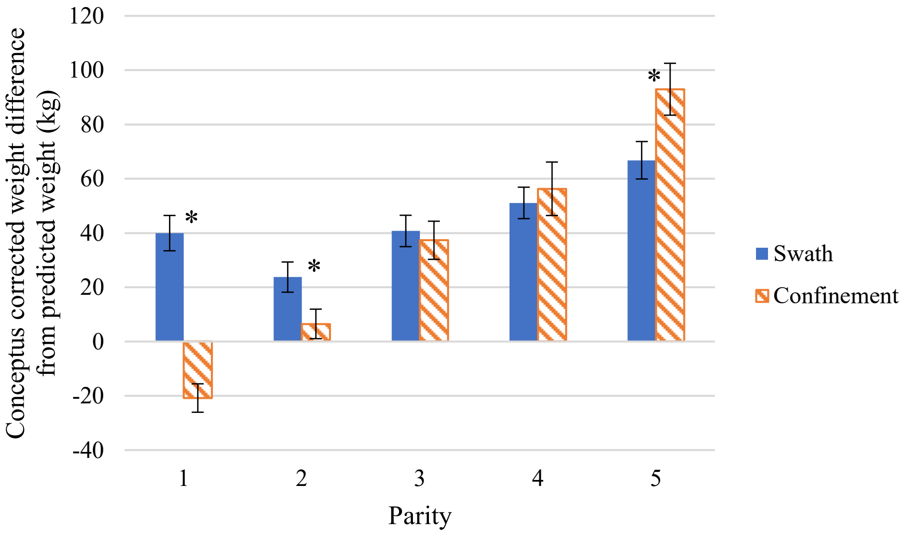

Figure 5.9. Interaction between treatment and parity affecting the difference between conceptus-corrected cow body weight and predicted body weight in cows housed at LRDC. (*Weight differences differ between winter treatment group within parity [$P < 0.05$]).

grazing. The confined-fed cows were also lighter than swath-grazed cows in parity 2, though both treatments had positive differences to their predicted weight. No differences between treatments were observed in parities 3 and 4, but confinement-fed cows had a greater weight difference in parity 5 than swath-grazed cows. Again, due to a change in management strategy in 2014, cows in parities 1 and 2 exposed to swath grazing were actually confinement-fed from 2005-2013, though the difference between confinement and swath grazing is not readily apparent in those age groups. It would have been expected that cows fed in confinement exhibited greater than predicted weight differences, not less than predicted, and cows exposed to the more environmentally exposed and therefore challenging swath grazing environment would have smaller differences between conceptus-corrected weights and predicted weights than those fed in confinement.

5.3.3.3. Linear effects of genomic retained heterozygosity and cow Julian birth date

Genomic retained heterozygosity did not affect the difference between conceptus-corrected weight and predicted weight in cows housed at both LRDC and KIN (Table 5.5). In contrast, larger body weights were reported in growing crossbred steers (Gregory et al., 1966b) and heifers (Gregory et al., 1966a) than in straight-bred AN, HE, or SH cattle. Cow Julian birth date was significant at both locations, though r^2 values were small (<2%) and did not account for sufficient variation observed in differences between predicted and conceptus-corrected weight to be useful. Cows born later in the season tended to have larger, positive differences between predicted and conceptus-corrected weights compared to cows born earlier in the season at both LRDC and KIN.

5.4. Conclusions

The use of conceptus-corrected body weights for mature cows under extensive management could be a useful indication of weight for estimation of energy needs or other management decisions. As body weights increase in some cows over time, producers may wish to re-evaluate previous pregnancy diagnoses, as there is a possibility that observed weight gain is due to loss of a calf in gestation. Doing so could prevent that cow from being held over through winter and early spring, a time when feed resources are expensive in Western Canada. Monitoring cow mature weights with regularity is not currently economically practical, however could become feasible as remote sensing technologies improve. Estimation of cow mature weight could provide producers and researchers a method to select cows for mature size prior to a heifer's first breeding and could therefore help to moderate large mature weights. Modelled weights for selection deserve closer investigation and testing. No realistic applications of comparisons between modelled weight and conceptus-corrected weights were observed in the present study.

6. ESTIMATION OF COW ENERGY INTAKE OVER TIME AND THE EFFECTS OF RESIDUAL FEED INTAKE AND WINTER-FEEDING ENVIRONMENT

6.1. Introduction

Feed costs for beef cow-calf operators constitute up to 70% of total annual production costs (Oginskyy and Boyda, 2018). The reduction of feed requirements has been a major theme of beef cattle research for decades (Koch et al., 1963; Archer et al., 1999; Herd et al., 2004; Terry et al., 2021), and considerable improvement in many definitions of animal efficiency have been made. However, estimation of individual animal energy intake from feed is rare in production settings for beef cows and has historically required removing cows from normal production environments. As a result, the effects of the selection for reduced feed requirements in the breeding cow herd have been difficult to ascertain in large-scale production settings, especially given the complexity of requiring frequent cow body weight, feed intake, calf performance and detailed breed composition records. Few datasets with the required resolution and meaningful number of observations are likely to exist, though we are aware of a large and elegant dataset which has greatly profited the industry at the US Meat Animal Research Center near Lincoln, NE. Nevertheless, a paucity of information is available on the total amount of energy demanded by a breeding cow over the entire course of her life. Therefore, the objectives of this study were to 1) estimate beef cow energy requirements over time on a data set containing detailed historic reproductive records, and 2) evaluate the effects of residual feed intake and winter-feeding environment on those estimates.

6.2. Materials and Methods

Crossbred replacement heifers and multiparous cows (n = 880) were maintained at the Agriculture and Agri-Food Canada Lacombe Research and Development Centre (**LRDC**, Lacombe, AB, Canada). All the animals used in this research were cared for according to the guidelines set forth in the Canadian Council on Animal Care handbook (CCAC, 1993), and the research procedures were reviewed and approved yearly by the LRDC animal care committee.

6.3. Description of cattle and management

The LRDC breeding herd has been developed and maintained to reflect the typical Western Canadian commercial beef cow; the herd is predominantly Aberdeen Angus (AN) × Hereford (HE) cows mated to purebred AN and black Simmental (SM) bulls, and Red Angus (AR) × AN cows mated to purebred red SM and AR bulls. The herd breeding program was described in detail by Basarab et al. (2018). Cow breed composition was determined from the Illumina Bovine 50k SNP panel and using Admixture Software (Alexander et al., 2009). Genomic breed composition (**gBC**) was used to estimate genomic retained heterozygosity (**gRHET**). Genomic retained heterozygosity was equal to one minus the sum of the squared fraction of each contributing breed observed in the gBC.

Cows calved between March and May in each year, and calves remained with their dam until weaning in mid-October at 6-7 mo of age. All calves were administered a standard vaccination schedule for the prevention of IBR, PI_3, BVD, BRSV, *haemophilus somnus*, *pasteurella multocida*, and clostridial diseases at 2-2.5 mo of age, and then given a booster vaccine and treated with pour-on parasiticide at 6 wk prior to weaning. Heifer calves were fitted with a half-duplex radio-frequency identification tag (Allflex USA Inc., Dallas, TX, USA), and post-weaning the heifers were performance tested for individual feed intake and growth using GrowSafe Feed Intake automated feed bunk technology (GrowSafe Systems Ltd., Calgary, AB, Canada). On average, heifers at LRDC remained on test for 89 (SD=16) d in a dry lot setting. Each dry pen was equipped with 8 feed bunk nodes, from which feed intake and feeding behaviour data were continuously collected for the duration of each test. Feed bunks were stocked at a rate of 4-5 heifers per feed bunk. Heifers tested all years except 2017 were offered a 90-100% as-fed barley silage, 0-10% as-fed rolled barley grain ration (39.1% dry matter, 9.77 MJ kg^{-1} DM on average). Heifers tested in 2017 were supplied a 74% barley silage, 26% corn dried distillers' grain plus solids (cDDGS) ration (36.0% DM, 9.77 MJ kg^{-1} DM). Wood chips or shavings were supplied as bedding as-needed, apart from 3 instances where straw was provided due to extreme cold (temperatures below -20^{o} C).

Following the feed intake tests, heifers remained in confinement until mid-May of each year, at which point they were placed on cool-season mixed tame grass pastures until mid-October. From mid-October to the following spring, cows at LRDC were placed in two groups. Replicates were balanced for cow age, weight and backfat thickness. Open cows were removed from the trial. Once a cow was placed into an experimental group (Swath or Confined), she remained in that group every winter. Cows were randomly assigned to each group every year as dictated by n. the Confined group were kept in dry lot pens where cows were fed a barley silage ration in confinement, or a swath-grazing environment where swaths of triticale, barley, and/or corn were provided until late February or March, unless weather conditions prevented cows from accessing the swaths due to excessive ice or snow accumulation. Prior to calving, cows were moved off the swath grazing to dry lot areas and provided a barley silage ration. The dry lot pens were equipped with open-fronted barns for calving, and the cows remained there until pasture turn-out in May. Cows in both environments were supplied with straw bedding as needed and when temperatures fell below -20^{o} C.

Replacement heifers were exposed to breeding for 45 d 2-3 weeks prior to the main herd, beginning in May. Cows were exposed in late May and June for 63 d, with a cow:bull ratio of 20:1 to 25:1 depending in the breeding group and year. Approximately 85 d after the breeding season had ended, cows were rectally palpated to diagnose pregnancy, and the resulting calves were born from March to May of the following year.

6.3.1. Performance traits

Production cycle traits were recorded at 3 time points during the year: pre-calving, at the time cows were moved into calving pens in late February; pre-breeding, when cows were sorted into breeding groups in late April and early May; and pregnancy evaluation, when cows were diagnosed for pregnancy in mid-October. At each of these points, cows had ultrasound body composition collected using an Aloka 500V real-time ultrasound machine with a 17 cm, 3.5 MHz linear array transducer (Overseas Monitor Corporation Ltd., Richmond, BC, Canada), along with any other relevant data or comments (pregnancy or cull status, etc.). Cows were not weighed at calving, and some years weaning occurred concurrently with pregnancy evaluation. Cows were culled at pregnancy evaluation each fall if they were open. Cows were also culled throughout the year for failure to calve despite a pregnant diagnosis, and post-weaning for failure to wean a calf. Cows were also culled for poor udder structure based on the Canadian Simmental Association udder and teat scoring system (Canadian Simmental Association, Calgary, AB), poor temperament, poor skeletal conformation, and poor performance. All culling reasons and mortality causes were recorded by the herd manager. A full description of udder, temperament, dystocia, and calf condition scores was provided by Olson et al. (2021).

Parity was defined as the period from pre-breeding to the weaning of the calf conceived – all events and associated data points related to the conception, gestation, birth, nursing, or weaning of that conception are part of the same parity. A heifer survived to parity 1 if she had a calving record (calf could either be born dead or alive) – a heifer did not survive to parity 1 if she was culled for non-pregnancy, aborted a calf, or died prior to the first calving event. A cow survived to parity 2 if she had a calving record for her second calf but did not survive if the cow was culled prior to giving birth to her second calf. The same pattern was used to determine survival to any parity.

Days in the herd (**DIH**) was determined by the difference between a cow's culling date and that cow's standardized first breeding date (May 25 of the year following birth year at LRDC). As a measure of total lifetime productivity (**LTP**), the cumulative 200-d weaning weights of a cow were summed to provide a total weight of calves weaned for each cow for her lifetime.

6.3.2. Estimation of lifetime energy intake

The direct measurement of individual cow energy requirements over a cow's lifetime is impractical, but these data are needed to make meaningful assessments of cow energy expenditure and energy efficiency. Energy demands can be estimated using models (NRC, 2001a; NASEM, 2016), but the assumptions and data resolution frequently available for beef cows in breeding herds limit the accuracy and precision of required energy estimates.

6.3.3. Derivation of modeled cow weights

Calf weight is an important fraction of the total body weight of a cow during gestation, and cows in regular breeding herds should spend more than 75% of their breeding years pregnant. To estimate the weight of a calf at a given point in gestation, days pregnant was needed (**DP**):

$$DP = 283 - (CfBD - considered\ date);$$

where $CfBD$ = birth date of the calf in question and the $considered\ date$ was any day within 283 prior to the birth of the calf (for the purposes of this study considered date was the date associated with pregnancy evaluation, pre-calving, or weaning, or estimated conception date). Days pregnant was derived for each cow at each relevant event; DP was not estimated for pre-breeding as it was assumed that cows were not pregnant at that time.

Conceptus weight (**CW**) on a given date was a function of days pregnant and calf birth weight (birth weights were collected within 24 hr of birth at LRCD):

$$CW = CfBW \times 0.01828 \times \left(e^{0.02 \times DP - 0.0000143 \times DP^2}\right)$$ [Eq. 19-69, NASEM (2016)],

where CW = conceptus weight (kg), $CfBW$ = calf birth weight for the calf in question (kg), DP = days pregnant (d), and e = natural log. Conceptus-adjusted cow weights were therefore a function of observed animal weight and CW, equal to:

$$BW_{CA} = BW - CW;$$

where BW_{CA} = conceptus-adjusted cow body weight (kg), BW = observed cow body weight (kg), and CW = conceptus weight as previously defined (kg).

Cow age was defined as the difference in months between a cow's birth date and the considered date. Cow weights were standardized to a body condition score (**BCS**) of 5 on a 9-point scale using the following equation derived from NASEM (2016) and Herd and Sprott (1986):

$$BW_5 = \frac{BW_{CA}}{1-0.0715\times(5-(2.2114+0.6092\,BF-0.0129\times BF^2))}; \text{ [Eq. 13-5,13-6, NASEM (2016)],}$$

where BW_5 = body weight at BCS 5 (kg), BW_{CA} = conceptus-adjusted cow body weight (kg), BF= ultrasound back fat thickness (mm).

A model was fit for each cow with a similar form to the target weight model used by Rotz et al. (2005), with the exception that the asymptote is mature weight instead of mature weight plus birth weight. The model was fit with the PROC NLIN function of SAS 9.4 (SAS Institute Inc., Cary, NC, USA) with the model:

$$BW_P = Cow\ BrW + (MW - Cow\ BrW) \times \left(1 - e^{(-k\times age)}\right);$$

where BW_P is the predicted weight (kg) for a cow at a given age (mo), $Cow\ BrW$ = cow birth weight standardized to BCS 3 (cow birth weight × 1.1421; kg), MW = mature weight (asymptote, kg), e= natural log, and k = growth coefficient calculated for each animal. An estimated weight was found for each cow at each weight point in each parity for each cow's lifetime. Estimates from this model for cow birth weight were assumed to be 3 on a 9-point scale. Cow weights were only used if they had a corresponding measure of ultrasound backfat for the prediction of BCS.

It was assumed that any observed difference between predicted body weight and conceptus-adjusted cow weight was due to deviations in BCS from BCS 5. Body condition score was assigned using the difference between modeled weights and the observed conceptus-corrected cow body weight using the following equation, which includes the weight adjustment factor equation from NASEM (2016):

$$BCS_P = 5 + \frac{(BW_{CA} - BW_P)}{(\frac{BW_P}{0.07105})};$$

where $BCSp$= predicted BCS, BW_{CA} = conceptus-adjusted cow weight (kg), and BW_P = predicted weight (kg) for a cow.

6.3.4. Cow maintenance and gain requirements

Cow maintenance requirements between two events was calculated using equations provided in NASEM (2016):

$$NE_m = (SBW^{0.75} \times 0.077 \times BE \times LE \times (0.8 + (BCS_P - 1) \times 0.05)) \times d;$$

where NE_m= net energy for maintenance (Mcal d^{-1}), $SBW^{0.75}$= average conceptus-corrected body weight (kg), BE = genomically-weighted breed effect (Table 6.1), LE = genomically-weighted lactation effect (Table 6.1), $BCS_P = \text{predicted BCS}$, and d= the number of days between events. Body fat and protein percentages were calculated to estimate total energy reserves (NASEM 2016):

$$TE = (9.4 \times \%BFat + 5.7 \times \%BProt) \times (0.851 \times BW_{CA});$$

Table 6.1. Breed effects for maintenance energy requirements and milk composition characteristics (adapted from NASEM (2016), Table 19.1).

Breed	Breed Effect	Lactation effect	Peak milk yield, kg/d	Milk fat, %	Milk protein, %	Milk solids non-fat, %
None	0	0	0	0	0	0
Angus	1	1.2	8	4	3.8	8.3
Charolais	1	1.2	9	4	3.8	8.3
Chianina	1	1.2	6	4	3.8	8.3
Devon	1	1	8	3.5	3.3	8.3
Galloway	1	1.2	8	4	3.8	8.3
Gelbvieh	1	1	11.5	4	3.8	8.3
Hereford	1	1	7	4	3.8	8.3
Holstein	1.2	1	43	3.5	3.3	8.3
Jersey	1.2	1	34	5.2	3.9	8.3
Limousin	1	1.2	9	4	3.8	8.3
Maine Anjou	1	1.2	9	4	3.8	8.3
Red Poll	1	1.2	10	4	3.8	8.3
Salers	1	1.2	9	4	3.8	8.3
Shorthorn	1	1.2	8.5	4	3.8	8.3
Simmental	1.2	1	12	4	3.8	8.3
Tarentaise	1	1.2	9	4	3.8	8.3

Where TE= total energy reserves (Mcal NE_m), $\%BFat$ = body fat percentage calculated from predicted BCS ((predicted BCS × 0.037683) ×100), $\%BProt$ = body protein percentage calculated from predicted BCS (0.20886-0.0066762×BCS) ×100, and BW_{CA} = conceptus-adjusted body weight (kg; NASEM 2016). Differences in total energy reserves were calculated between events and represented a gain or loss in total energy. Negative values were considered an energy input and converted to gain at 80% to reflect the inefficiency (20%) assumed to exist when tissue reserves are mobilized to meet energy requirements.

Conceptus energy was calculated for each event where a cow was presumed or confirmed pregnant. Conceptus weights were not calculated for pre-breeding events. Conceptus energy was equal to:

$$NE_P = \frac{CfBW \times 1.811 \times e^{(0.03233 \times DP \times 0.0000275 \times DP^2)}}{1000}\text{ ; [Eq. 13-35, NASEM (2016)],}$$

Where NE_P = net energy of the conceptus (NE$_\text{m}$), $CfBW$= birth weight of the gestating calf (kg), and DP = days pregnant based on an assumed 283 d pregnancy, as previously defined.

6.3.5. Derivation of calf energy requirements

Calf energy requirements were estimated using 7th edition of Nutrient Requirements for Dairy Cattle (NRC, 2001b) due to a paucity of data available for beef calves. The process outlined below was completed twice – once for the period from birth to 60 d of age, and once for the period from 60 d of age to weaning. Calf weights at 60 d of age were initially estimated with a relative equation:

$$WT_{60} = e^{\left(\log CfBW + \frac{\log(CfWW) - \log(CfBW)}{WNDT - BRDT} \times 60\right)};$$

Where WT_{60} = estimated weight at 60 d of age, $CfWW$ = calf weaning weight, $CfBW$ = calf birth weight, $WNDT$= calf weaning date, and $BRDT$= calf birth weight. However, that equation appeared to over-estimate calf gain in the first 60 d of life. Analysis of a related dataset (unpublished) with frequent weights of 30 calves from birth-weaning revealed that a linear model best explained the growth of calves from birth to 60 d of age (H. Block, personal communication). Therefore, a linear equation was fitted to estimate calf weight at 60 d of age:

$$WT_{60} = CfBW + \left(\frac{CfWW - CfBW}{WNDT - BRDT}\right) * 60.$$

Calf energy maintenance requirements from birth to 60 d of age and from 60 d of age to weaning were estimated by:

$$NE_m = 0.086 * \left(\frac{Initial+Final}{2}\right)^{0.75} \text{; [Page 215, NRC (2001)],}$$

And growth requirements from birth to 60 d of age and 60 d of age to weaning were similar and estimated by:

$$NE_m = 0.84 \times \left(\frac{Initial+Final}{2}\right)^{0.335} \times \left(\frac{Final-Initial}{60}\right)^{1.2} \times 0.69\text{; [Page 215, NRC (2001)}_{\text{b}}\text{],}$$

Where NE_m= calf net energy for maintenance (Mcal d^{-1}), $Initial$ = calf birth weight (kg) or estimated calf weight at 60 d of age, and $final$ = estimated calf weight at 60 d of age or observed weaning weight (kg). Based on these estimates, lactation energy requirement from birth to 60 d of age and 60 d of age to weaning were estimated by:

$$LE = \left(\left(60 \times \frac{NE_m}{0.86}\right) + \left(60 \times \frac{NE_g}{0.69}\right)\right) \div 0.96 \div 0.97\text{; [NASEM (2016)]}$$

Where LE= net energy for lactation provided by the cow (Mcal $\mathrm{NE_m}$), and $NE_m$and NE_g = net energy for maintenance ($\mathrm{NE_m}$) and net energy for growth ($\mathrm{NE_m}$) for birth to 60 d of age or 60 d of age to weaning, respectively. Milk energy

density was estimated from milk fat percentage and milk non-fat solids based on the breed estimates (Table 6.1) developed by Herd and Sprott (1986) and calculated for each cow, weighted by genomically-determined breed fractions. Milk energy density was therefore estimated by:

$$LE_C = 0.92 \times \%MF + 0.049 \times \%MNFS - 0.0569;$$

Where LE_C = milk energy density (Mcal $\mathrm{kg^{-1}}$ milk), $\%MF$ = milk fat percent weighted average for breed composition, and $\%MNFS$ = milk non-fat solids percent weighted average for breed composition. Peak yield was estimated from an equation adapted from the NASEM (2016):

$$PY = (\frac{LE}{LE_c}) \div -e^1 \times (60 \times e^{\left(\frac{-60}{60}\right)} + (60 \times (e^{\left(\frac{-60}{60}\right)-1})));$$

Where PY= peak milk yield (kg $\mathrm{d^{-1}}$), LE= net energy for lactation provided by the cow (Mcal $\mathrm{NE_m}$), LE_c = milk energy density (Mcal $\mathrm{kg^{-1}}$), and days in milk was set equal to 60 and time of peak yield was set to 60 d post-calving. It was assumed that lactation characteristics were based on an assumed milk peak yield at 60 d and all calf requirements from birth to 60 d of age were met by milk. Similarly, total milk yield was equal to:

$$TY = -PY \times e^1 \times ((WNDT - BRDT) \times e^{\left(\frac{-(WNDT-BRDT)}{60}\right)} + 60 \times (e^{\left(\frac{-(WNDT-BRDT)}{60}\right)} - 1);$$

Where TY = total milk yield (kg) from birth to weaning, PY = peak yield (kg d^{-1}), $(WNDT - BRDT)$= days in milk (d), and time of peak yield was assumed to be d 60 of lactation.

Milk energy from 60 d of age to weaning was allocated to maintenance and gain based on relative calf requirements for each, and the efficiency of milk energy for maintenance and gain. Not all the energy required for maintenance and growth in calves was accounted for by the preceding equations. It was assumed that the difference between the milk energy provided by the dam and the calculated requirements to accomplish the growth from birth to weaning weight was sourced from forage intake by the calves.

6.4. Statistical analysis

The relationship between RFI$_{\text{FAT}}$ values observed in weaned replacement heifers and in the same animals when mature cows was considered to estimate the effects of cow RFI$_{\text{FAT}}$ on feed intake. A model with the form:

$$Y_{ijklm} = \mu + HCon_i + CCon_j + CAGE_k + \beta_1 heifer\ RFI_{FAT_l} + Sire_m + \ e_{ijklm}$$

where Y_{ijklm}= cow RFI$_{\text{FAT}}$ phenotype, $HCon_i$ = main effect of the *i^th^* heifer contemporary group, $CCon_j$ = main effect of the j^{th} cow contemporary group, $CAGE_k$ = main effect of the k^{th} cow age in years on-test, β_1 = partial regression coefficient of cow RFI$_{\text{FAT}}$ on heifer RFI$_{\text{FAT}}$, $Sire_n$ = random effect of the n^{th} sire, and e_{ijklm}= random error of the ijk^{th} animal was used to estimate the relationship between heifer and cow RFI values and apply an adjustment to cow intake. Cow RFI was multiplied by the coefficient of heifer RFI$_{\text{FAT}}$.

Analyses were completed using the MIXED procedure of SAS 9.4. Data were analysed in 5 groups, in periods of approximately 365 d starting at a heifer's first pre-breeding event. The first period included data from pre-breeding, conception, pregnancy evaluation, pre-calving, and calving. All subsequent periods also included a weaning event. Heifers were not lactating during the first period and resulting estimates of NE_m are lower for that period than for the following 4 periods.

The MIXED model had the form:

$$Y_{ijklm} = \mu + RFI_i + T_j + S_k + RFIT_{ij} + \beta_1 AN_l + \beta_2 gRH_m + e_{ijklm};$$

Where Y_{ijklm}= is the cow energy intake phenotype (Mcal of NE_m), RFI_i= effect of the i^{th} heifer residual feed intake classification (High, Medium, or Low, classified at ± 0.5 SD from the mean), T_j = effect of the j^{th} winter feeding program (winter grazing of cereal grain swath or confinement feeding), S_k= effect of the k^{th} season (2005-2019), $RFIT_{ij}$ = two-way interaction term, β_1 = the partial regression coefficient of genomically-determined %AN, β_2 = the partial regression coefficient of gRHET (%), and e_{ijklm} = random error.

The same model was used to find the least-squared means estimates in dollars (Y_{ijklm} = cost of feed, \$). Cows in the confinement winter treatment group were assigned an average feed value of \$0.15 kg^{-1} DM, and cows in the swath treatment were given a value of \$0.12 kg^{-1} DM. Dry matter values for energy were from the NASEM (2016) estimates for barley silage. The base price of feed for the confinement-fed cows was estimated from the 5-year (2016-2020) Lethbridge feed barley price (\$ Bu^{-1}, Statistics Canada (2021)) and multiplied by 12.5 to find an estimated price for barley silage (\$ t^{-1}).

6.5. Results and Discussion

6.5.1. Modeled weights

Cow weights adjusted for conceptus weight (BW_{CA}), body condition score 5 (BW_5) and model-predicted weight are presented in Table 6.2. Cow body weight increased numerically in each year for each body weight type. These increases are normal and expected, given that mature body weight in beef cattle in a non-restricted environment is typically reached by age 5 yr (NASEM, 2016), which corresponds with Year 4 in Table 6.2. Cow BCS_p, a function of the comparison between conceptus-adjusted and predicted weights, remained numerically stable across all 5 years. Cows at LRDC are actively managed to maintain a BCS greater than 5 on a 9-point scale – if cows fall below BCS 4, they are removed from the general population and fed separately until they have regained an appropriate body composition. Therefore, the consistency of the BCS_p values across all 5 years was expected.

Table 6.2. N, age, and mean conceptus-adjusted, BCS-adjusted, and modeled weight and estimated BCS at pre-breeding.

	Year				
Item	1	2	3	4	5
N	880	517	421	318	230
Age, mo	13.0 ± 0.8	25.4 ± 0.6	37.3 ± 0.6	49.3 ± 0.6	61.2 ± 0.6
BW_{CA}, kg	410 ± 46	523 ± 57	595 ± 69	612 ± 67	648 ± 66
BW_5, kg	391 ± 39	507 ± 56	570 ± 63	608 ± 63	616 ± 58
BW_p, kg	385 ± 38	514 ± 48	572 ± 54	592 ± 55	602 ± 51
BCS_p	5.3 ± 0.6	4.8 ± 0.8	5.0 ± 0.8	5.4 ± 0.8	5.5 ± 1.0

Note: N = number of cows present at pre-breeding with body weight and back fat data; BW_{CA} = conceptus-adjusted body weight; BW_5 = body weight at body condition score 5 out of 9; BW_p = model-predicted body weight at BCS 5 out of 9; BCS_p = predicted body condition score comparing BW_{CA} and model-predicted weight.

6.5.2. Predicted energy intake

Measuring feed intake over short periods in beef cows is manageable with modern feed bunk monitoring systems. However, the dry lot environments required to gain accurate measures of feed intake and energy expenditure do not represent normal practices in the Western Canadian beef industry. Extensive pasture-based systems preclude the use of such equipment and add considerable difficulty to monitoring cow maintenance and growth requirements. However, it is possible to estimate energy intake based on animal performance over time using the requirement models published in NRC (2001a) and NASEM (2016). The ability for producers, or indeed researchers, to accurately estimate energy intake in grazing beef cows is hindered by the extensive husbandry practices common to Western North America, where cows are rarely handled in facilities equipped with scales. Further, model assumptions regarding cow growth and development rates and data resolution (frequency and accuracy of weight and body composition measurements) hamper the accuracy and precision of the existing models and the estimation of energy intake. Therefore, it is necessary and useful to the industry and to research to evaluate novel methods of energy intake estimation.

Least-squares means of energy estimates are presented in Table 6.3. Calf net energy for growth sourced from forage is not included in these estimates due to differences in units. A significant but biologically irrelevant interaction was observed between treatment and RFI_{FAT} class in year 2, but no interactions were observed in years 1, 3, 4, or 5. Season was significant in every year, likely due to environmental effects and the effects of changing cow populations every year, with cows entering and leaving the herd.

Residual feed intake adjusted for body composition (RFI$_{FAT}$) was a significant term in each year. Generally, inefficient cows (High RFI$_{FAT}$) consumed more than efficient (Low RFI$_{FAT}$) cows, except in year 5, where High and Low RFI$_{FAT}$ cows did not differ, but moderately efficient cows were estimated to have the greatest energy intake. The reason for this change in animal efficiency with age is not clear, however, it could be due to changes in the ratios of High:Medium:Low RFI$_{FAT}$. Residual feed intake adjusted for body composition classification was based on feed intake test results obtained when a cow was undergoing heifer development at 9-14 mo of age. As cows age and are culled for various reasons, the proportion of cows in each classification changes, and that yearly fluctuation in the population at LRDC may have influenced the

Table 6.3. Differences of least-squared means estimates of net energy for maintenance (Mcal NE$_m$) for fat-adjusted residual feed intake classification, winter treatment group, and season.[1]

	Year				
Item	1	2	3	4	5
N	880	517	421	318	230
RFI$_{FAT}$ Class					
P-value	***	***	***	***	***
High	3796^a	7389^a	7048^a	7144^a	6317^a
Medium	3501^b	6812^b	6752^a	6911^a	6932^b
Low	3392^b	6247^c	6048^b	6145^b	5930^a
Winter Treatment					
P-value	***	***	**	**	NS
Confined	3226	5748	6332	6451	6459
Swath	3899	7884	6900	7016	6328
T × RFI$_{FAT}$	NS	***	NS	NS	NS
Season	***	***	***	***	***

[1] * = P-value < 0.05; ** = P-value <0.01; *** = P-value <0.001; RFI$_{FAT}$ classes: High >= mean RFI$_{FAT}$ + 0.5 SD, Medium < mean RFI$_{FAT}$ +0.5 SD, > mean RFI$_{FAT}$ - 0.5 SD, and Low <= mean RFI$_{FAT}$ - 0.5 SD; T = winter treatment; Winter Treatment Confined = supplied barley silage in a dry lot setting, Swath = provided cereal swath grazing from weaning-March. NE$_g$ for calves attributed to calf forage is not included due to the inability to sum cow NE$_m$, calf NE$_m$ and calf NE$_g$.

results of year 5. Aside from year 5, Table 6.3 indicates that cows with Low RFI_{FAT} consistently consumed fewer Mcal of NE_m than cows with High RFI_{FAT}. As the feed efficiency values used in this study were subjected to correction for the composition of gain, differences in efficiencies are not due to differences between cows in the rate or amount of lipid or protein accretion during their feed intake test. This is furthered by the management of cows for a consistent minimum BCS greater than BCS 2. Variation in energy intake in the present population may be due to the heat increment of feeding, feed sorting or selection, energy associated with digestion, daily animal activity, and differences in the efficiency of individual thermoregulation, as postulated by Herd and Arthur (2009).

Practically, this outcome reinforced the assumption that selection of heifers with favourable RFI_{FAT} values would result in mature cows that consumed less energy over their life, at least until they turned 5 years of age. Table 6.4 expresses the savings producers may realize in over time and illustrates that those cows with lower RFI_{FAT} cost 14-17% less each year than cows with High RFI_{FAT}, again with the exception of year 5.

Relative to High RFI_{FAT} cows, the maintenance of Low RFI_{FAT} cows could potentially save beef cow-calf operators CAD \$404.15 from the beginning of a cow's breeding life to the weaning of her third calf. It is important to note that these values are based on an assumed average yearly diet similar in quality and dry matter to good-quality barley silage, and as such the price kg^{-1} DM was tied to a 5-year average bushel price for feed barley sourced from Lethbridge, Alberta (Canada, 2021). The authors encourage the application of different feedstuffs and price sensitivities as appropriate to ascertain the true value of lowered energy intake for individual cow-calf operations.

Table 6.4. Least squares means of $CAD estimates as affected by fat-adjusted residual feed intake classification, winter treatment group, and season.[3]

	Year				
Item	1	2	3	4	5
n	880	517	421	318	230
	RFI_{FAT} Class[1]				
P-value	***	***	***	***	*
High	$394.86^a	$852.96^a	$793.97^a	$792.97^a	$692.30^a
Medium	$342.97^b	$778.65^b	$733.20^b	$740.06^b	$736.90^b
Low	$347.60^b	$729.22^c	$676.03^c	$677.76^c	$666.53^a
	Winter Treatment[2]				
P-value	***	***	NS	NS	NS
Confined	$337.95	$688.51	$732.08	$732.21	$720.04
Swath	$385.67	$885.38	$736.72	$741.65	$677.11
T × RFI_{FAT}	NS	***	NS	NS	NS
Season	***	***	***	***	NS

[1,] * = P-value < 0.05; ** = P-value <0.01; *** = P-value <0.001; [1]RFI_{FAT} classes: High >= mean RFI_{FAT} + 0.5 SD, Medium < mean RFI_{FAT} +0.5 SD, > mean RFI_{FAT} - 0.5 SD, and Low <= mean RFI_{FAT} - 0.5 SD; [2]Treatment Confined = supplied barley silage in a dry lot setting, Swath = provided cereal swath grazing from weaning-March. [3]Yearly weighted average cost of feed for swath-treatment cows was set to $0.12 kg^{-1} DM, and confined was set to $0.15 kg^{-1} DM.

Cows at LRDC were managed in one of two winter feeding programs: conventional dry lot feeding, where barley silage was supplied daily to cows in feed bunks, or swath grazing, where a variety of cereal forages were swathed and electric fencing was used to control herd access to the swaths during the winter. Winter treatment influenced animal energy intake in years 1-3, such that cows in the Swath treatment had greater estimated energy intakes than cows maintained in confinement. The precise biological reasons for these differences are not axiomatic, however. Ultrasound BF measurements taken at pre-calving, when cows were removed from swath grazing were numerically lower than measurements from confined cows; similarly, Swath cows had numerically lower body weights compared to cows fed in confinement. This indicated that cows exposed to swath grazing during the winter lost body condition score and weight due to the treatment. That agrees with Baron et al. (2014) and Baron et al. (2016), where cows in confined winter-feeding environments at LRDC were heavier and had greater BCS at the end of the feeding period than cows exposed to swath grazed corn, triticale, and barley (Baron et al., 2014) or swath-grazed oats or stockpiled perennial forage (Baron et al., 2016), compared to a total mixed ration fed in confinement. It is possible that the additional Mcal of NE_m observed in the Swath cows was attributable to greater numerical gain in backfat observed in Swath cows between the end of the swath grazing period and weaning when cows were exposed to a barley silage or cool-season pasture diet (data not shown). While outside the intended scope of this study, such observations may call into question the published differences in cost of cow maintenance on swath-grazing and conventional confinement winter feeding programs. Baron et al. (2014) and Baron et al. (2016) reported that conventional confined winter feeding was more expensive than swath grazing barley, triticale, or oat cereals, however, those costs were only evaluated during the winter feeding period – the cost of cow maintenance during the late spring and summer was not included, and the present data illustrate that it may be more expensive to have cows lose body weight during the winter and then regain it during the subsequent seasons with a calf at side, at least in the first 2 years. To further investigate whether the lowered cost of swath grazing offset the cost of greater observed energy requirements in Swath cows compared to

Confined cows, two pricing structures were applied to an assumed average yearly diet similar to barley silage (NASEM, 2016). Confined cows were assumed to consume a diet priced at \$0.15 kg^{-1} DM, and Swath cows were assumed to consume a diet priced at \$0.12 kg^{-1} DM, which was calculated from an average (weighted for number of days exposed to swath grazing) of the 5-year average barley silage price and a swath grazing price of \$0.05 kg^{-1} DM (V. Baron, personal communication; Table 6.4). Maintenance costs for cows in years 1 and 2 were greater for Swath cows than for confinement cows, despite the differences in cost of feed, though no difference was observed for years 3-5. Alternative winter-feeding methods may need to be evaluated with data that includes the summer recovery period to determine if the weight and BCS lost by cows exposed to Swath grazing offsets or even overrides the cost savings of the winter-feeding program.

6.5.3. Effects of breed and genomic retained heterozygosity

Genomically determined breed composition played a role in maintenance energy in the present study. The percentage of Angus breeding had a positive effect on total estimated NE$_m$, such that each 10% increase in the percentage of Angus genetics resulted in 111 additional Mcal of NE$_m$ required or more (Table 6.5). There was no effect of the percentage of gRHET on estimated cow energy intake, indicating that increasing retained heterozygosity in the Western Canadian cow herd should not increase the energy demand of the herd.

Table 6.5. Linear effects of genomically-determined Angus breed composition and genomic retained heterozygosity on net energy for maintenance (NE$_m$)

	Year				
Item	1	2	3	4	5

%AN, Mcal/10% change[1]	111 ± 20*	159 ± 32*	240 ± 36*	223 ± 45*	358 ± 51*
Cow RHET, Mcal/10% change[2]	33 ± 28	7 ± 46	104 ± 50	-114 ± 62	101 ± 70

* = effect was significant (P-value < 0.05); [1]%AN = genomically determined percentage of Angus breeding; [2]gRHET = genomically determined percentage of retained heterozygosity

Schenkel et al. (2004) illustrated the differences in body composition between different breeds of Canadian beef cattle and reported that British-breed bulls had more subcutaneous and intramuscular fat and less muscle mass compared to continental breed bulls. Further, contrary to previous findings by Arango et al. (2002) that Angus cattle were smaller than all Continental breeds, new research by Zimmermann et al. (2021) from the US MARC herd indicated that Angus cattle are now larger than all other breeds reported, including Simmental, Limousin, and Charolais. Further, among Angus steer progeny from parents selected for and against RFI, Richardson et al. (2001) found that steers with low-RFI parents had less chemical fat than steers from high-RFI parents. As has previously been discussed, RFI_{FAT} classification here resulted in Low RFI_{FAT} cattle having lower estimated energy intake compared to High RFI_{FAT} cattle. Therefore, in the present study, the impact of the percentage of Angus genetics on the estimated NE_m values could be due to increased weight and body fatness in higher-percentage Angus cows, as both factors are primary drivers of the equations used to estimate NE_m requirements. Care should be taken to select cattle that fit an environment – Angus cattle are a leading breed in North America, but the modern Angus cow may not be ideally suited to all extensive operations where feed resources are expensive or scarce.

6.6. Conclusion

Prediction of energy intakes in beef cows is complex and relies on regular measurements of body weight and composition, calf performance, and measures of breed composition. Datasets that combine these traits with sufficient observations are not common, and the data presented likely represents the first instance of their use to predict annual or lifetime net energy intakes. Considerable work will be required to refine and adjust prediction equations to increase the reliability of these estimates. This dataset further reinforced the notion that the application of selection for decreased RFI_{FAT} would result in cows that are predicted to require less NE_m during their lives and could ultimately reduce feed requirements and costs for the national cowherd. Genomic retained heterozygosity may indeed be the "last free lunch" available to beef producers and utilizing crossbred genetics should not influence the energy demands of the cowherd, even though research has indicated considerable improvements in other economically relevant traits. Further, the percentage of Angus genetics positively influenced the estimated energy intakes of cows, which could aid producers in selecting cattle that best suit their production environment, potentially limiting cow failure due to environmental unfitness.

7. RESIDUAL FEED INTAKE MEASURED AS REPLACEMENT HEIFERS IS INDICATIVE OF RESIDUAL FEED INTAKE MEASURED AS MATURE COWS

7.1. Introduction

Feed costs represent the largest variable cost in beef cow-calf operations in Western Canada (Oginskyy and Boyda, 2020). Considerable effort has been made to understand the effects of selection for residual feed intake on feedlot (Nkrumah et al., 2004; Nkrumah et al., 2006; Nkrumah et al., 2007) and in beef cow reproductive performance (Basarab et al., 2007; Basarab et al., 2011; Callum et al., 2019). However, the application of RFI selection to the replacement heifer segment of the beef cow-calf sector has been hampered by a poor understanding of the relationship between RFI observed in post-weaning feed intake tests and its congruency with mature cow feed efficiency. Re-ranking and repeatability studies from various ages and classes of beef cattle taken together are largely inconclusive, though individually have shown that RFI observed in heifers should be similar in mature cows (Archer et al., 2002; Kelly et al.,2010; Durunna et al., 2011; Durunna et al., 2012; Manafiazar et al., 2015). Much of the problem in the application of RFI selection is the difference between consuming a diet in a controlled dry lot environment with feed supplied to feed bunks daily, compared to the normal extensive pasture system common for beef cow-calf operations in Western North America. This study does not compare dry lot RFI to pasture RFI; rather, we endeavoured to explore the linear relationship between RFI measured in heifers and then later as mature cows, with the hypothesis that heifers selected for RFI retain at least a portion of their efficiency throughout their reproductive life.

7.2. Materials and Methods

Cows (N=291) were maintained at the Agriculture and Agri-Food Canada Lacombe Research and Development Centre (LRDC, Lacombe, AB, Canada). All cattle used in this study were cared for according to the guidelines set forth in the Canadian Council for Animal Care handbook (CCAC, 1993), and all project standard operating procedure were reviewed and approved annually by the LRDC Animal Care Committee. All cows were tested post-weaning as replacement heifer candidates and were tested at least once more as mature breeding females.

7.2.1. Heifer feed intake tests

Table 7.1. Diet ingredient composition for diets fed to heifers and cows during feed intake tests at the Lacombe Research and Development Centre[1]

	Heifer Test Year				
Ingredient	2005-2015[3]	2016	2017	2018	2019-2020[3]
Barley Silage, %	79.3	100	79.3	52.6	100.0
Rolled barley grain, %	20.7	-	20.7	-	-
CDDGs, %	-	-	-	47.4	-
	Cow Test Year				
	2012	2013	2014		2016-2020[3]
Barley Silage, %	-	-	-		100.0
Forage Cube[2]					
Barley Straw, %	25.6	25.2	25.3		-
Alfalfa Hay, %	34.7	0.0	27.1		-
Grass Hay, %	38.7	73.8	46.7		-
Lime (binder), %	1.0	1.0	1.0		-

[1] Diet formulations are on a dry-matter basis. Dry matter presented in Table 7.2.

[2] Cows were provided an extruded forage-based cube made up of straw, alfalfa, and grass hay.

[3] Diet formulation was identical for grouped years.

Heifers were selected for replacement based on body weight and age (body weight > 208 kg) and placed in a dry lot pen and supplied a barley silage diet (Table 7.1) immediately post-weaning for 2-3 mo. Subsequently, heifers (average n = 77, minimum n = 20, maximum n = 114) were moved to pens equipped with 8-24 GrowSafe feed bunks (GrowSafe, Calgary, AB, Canada) such that there was an average of 4.6 heifers per node. Over the next 35-38 d, heifers were adapted to a high forage diet (Table 7.1) that was fed two times daily. The adjustment period was followed by a feed intake test that ranged in length from 72 d to 114 d. Heifers had free access to water, salt, and mineral plus vitamins in a granular premix throughout the feed intake test and thereafter. Pens were equipped with a concrete apron adjacent to the GrowSafe bunks and had an open-sided wooden roof shelter that prevented most precipitation from entering the feeding station. Pens were bedded with wood chips or shavings as required.

Heifers were weighed consecutively on day 1 and day 2 of the feed intake test, and consecutively on the final 2 days of the test. During the test, heifers were weighed at approximately 28 d intervals. Ultrasound body composition measurements were taken at the end of each test with an Aloka 500V diagnostic real-time ultrasound with a 17 cm 3.5 MHz linear array transducer (Overseas Monitor Corporation, Ltd., Richmond, BC, Canada) by a certified ultrasound technician. Ultrasound measurements of subcutaneous fat were taken over the longissimus dorsi at the location of the 13th rib, intramuscular fat was measured in the longissimus dorsi at the 13th rib, and ribeye size was measured as the area (cm^2) of the longissimus dorsi at the same location. The method for measuring feed intake (kg DM d^{-1}) was the same as described by Basarab et al. (2003); Basarab et al. (2007).

Feed samples were collected weekly and composited monthly. Samples were analyzed for DM, crude protein, neutral and acid detergent fibres, calcium, and phosphorus (Table 7.2). Dry matter was determined by drying the sample at 100˚C in a forced-air oven to a constant weight. Crude protein was 6.25×N, and NDF and ADF were determined by the procedure defined by Van Soest et al. (1991).

7.2.2. Cow feed intake tests

Cow feed intake tests were similar to the tests for heifers. At the end of the fall grazing season, a subset of mature cows (3-14 years of age) was randomly selected and placed into dry lot pens equipped with GrowSafe feed bunks during their second trimester of pregnancy. Cows were all fed together, and supplied a diet of barley silage, chopped barley straw, and a protein, mineral and vitamin supplement (32% CP, 1.5% CF) at 100% of the nutrient requirements recommended by the National Research Council [(NRC, 2001); Table 7.1]. Diet DM composition is presented in Table 7.2. Wood chips or shavings were provided as needed for animal health and comfort, and individual cow intake of the silage-straw diet was monitored by the GrowSafe feed bunks continuously.

Cow feed intake trials were conducted in the same manner as the heifer trials described above. Cows were re-tested at various ages. At the end of the feed intake tests, the cows were returned to the main herd in late February for calving.

7.2.3. Calculations

Table 7.2. Diet composition for heifers and cows during feed intake tests

	Replacement Heifer		Mature Cow	
Item[1]	Mean	SD	Mean	SD
Dry matter, %	38.4	4.1	56.0	25.1
ME, MJ kg^{-1} DM[2]	9.9	0.4	9.1	0.5
Crude protein, %	12.9	1.9	10.6	1.2
ADF, %	30.6	2.5	36.6	4.8
TDN, %	64.7	2.8	60.2	3.6

[1] Within year, diet samples were collected weekly, composited and analyzed monthly

[2] ((TDN, %/100) × 4.4 DE Mcal kg^{-1}) × 4.184 MJ ME $Mcal^{-1}$ DE × 0.82 MJ ME MJ^{-1} DE (NASEM, 2016).

Heifer on-test body weight, mid-point weight and average daily gain were calculated by a linear regression of the animal's observed body weight against days on test using PROC GLM, as in Basarab et al. (2003); Wang et al. (2006); Basarab et al. (2011). Mid-trial body weights were estimated for heifers and cows using the regression-predicted weight on d 0 and the regression-predicted average daily gain multiplied by half of the total days on test. Metabolic mid-trial body weight was estimated by raising the mid-trial body weight to the 0.75 power. Average daily feed intake within each test was converted to dry matter intake by multiplying average daily feed intake by the DM content of the diet. Total ME consumption of each animal was standardized to an energy density of 10 MJ ME kg^{-1} DM, resulting in a total standard DMI, which was further divided by the number of days on test each year to yield standardized daily DMI (SDMI). The SDMI value for each heifer in each contemporary group was regressed against ADG (kg d^{-1}), metabolic midweight (kg$^{0.75}$) and off-test backfat thickness using the PROC GLM function of SAS 9.4 (SAS Institute, Cary, NC, USA) using the following model:

$$Y_{ijk} = \beta_0 + \beta_1 ADG_i + \beta_2 MMWT_j + \beta_3 BFF_k + e_{ijk},$$

Where Y_{ijk}= SDMI for the *ijth* animal, β_0 = the regression intercept, β_1= partial regression efficient of SDMI on metabolic mid-weight, β_3 = partial regression coefficient of SDMI on off-test ultrasound back fat thickness, and e_{ijk}= random error term. Heifer residual feed intake, adjusted for backfat thickness (**RFI$_{\text{FAT}}$**), was computed for each animal as the deviation of SDMI from the expected feed intake ([**EFI**]; HRFI$_{\text{FAT}}$ = SDMI-EFI).

Cow RFI$_{\text{FAT}}$ was calculated in a similar way to heifer RFI$_{\text{FAT}}$ but was refined to reflect the difference between SDMI and expected feed intake requirements for body size and production (where cow production was growth and change to body fatness, as measured by cow weight and backfat thickness). Cow weights were corrected for the estimated weight of the conceptus at each weigh date, assuming a gestation of 283 d and using the birth date and birth weight of the subsequent calf to estimate the weight of the calf and associated tissue weight in-utero [Eq. 19-69 (NASEM, 2016)], as reported in Basarab et al. (2007). The model to estimate SDMI was:

$$Y_{ijk} = \beta_0 + \beta_1 ADG_i + \beta_2 MMWT_j + \beta_3 BFF_k + e_{ijk},$$

Where Y_{ijk} = cow SDMI for the *ijth* animal and all other terms are equivalent to the terms listed for heifer SDMI previously. The covariate $\beta_4 AGE_l$ was also included when a stepwise regression indicated that it was appropriate, where β_4 = partial regression coefficient of SMDI on cow Age in years.

Breed composition for the calculation of genomically-determined retained heterozygosity (**gRHET**) was determined by the process described by Basarab et al. (2018). Retained heterozygosity for each individual was calculated based on Dickerson (1973): $gRH = 1 - \sum_{i=1}^{n} P_i^2$, where P_i is the fraction of each of the *n* contributing breeds, where P_i is determined genomically.

7.2.4. Cow production cycle

Cows at the LRDC were followed from birth or herd introduction across each parity for as many parities as they are not culled or do not die. Data on animals were collected from birth (birth weight, date, dam and calf observations), weaning (weaning weight, date), through a feed intake test post weaning, and starting with a heifer's first pre-breeding event, weight and ultrasound body composition traits are measured at each subsequent pre-calving event, pre-breeding event, and pregnancy diagnosis for as long as the animal remains in the herd. The LRDC breeding herd has been developed and maintained to reflect the typical Western Canadian commercial beef cow; the herd is predominantly Aberdeen Angus (AN) × Hereford (HE), and Red Angus (AR) × AN × HE cows crossed to AN, AR, Charolais, and Maine-Anjou bulls from 2005 to 2015, and Simmental, AN and AR bulls from 2016 to 2020. A complete description of the herd development was reported by Basarab et al. (2018).

Cows calved between March and May in each year, and heifer calves remained at the side of their dam until weaning in mid-October at 6-7 mo of age. All calves were administered a standard vaccination schedule for the prevention of common viral and bacterial disease at 2-2.5 mo of age. Heifer calves were fitted with a half-duplex radio-frequency identification tag (Allflex USA Inc., Dallas, TX, USA), and post-weaning the heifers were performance tested for individual feed intake using GrowSafe automated feed bunk technology.

Following the feed intake tests, heifers were moved to tame-grass and legume mixed pastures and exposed to breeding at a ratio of 15:1 heifer to bull for a 45-d breeding season. Pregnancy was diagnosed in heifers 1 month following the removal of bulls by transrectal ultrasonography (Aloka SSD 500 with a 7.5 MHz linear-array transducer). From mid-October to the following spring, cows at LRDC were placed in two groups: a dry lot group where cows were fed a barley silage ration in confinement, or a swath-grazing environment where swaths of triticale, barley, and/or corn were provided until late February or March, unless weather conditions prevented cows from accessing the swaths due to excessive ice or snow accumulation. Prior to calving, cows were moved off the swath grazing to dry lot areas and provided a barley silage ration. The dry lot pens were equipped with open-fronted barns for calving, and the cows remained there until pasture turn-out in May. Cows in both environments were suppled with straw bedding as needed and when temperatures fell below -20^{o} C. Cows were exposed in late May and June for 63 d, with a cow:bull ratio of 20:1 to 25:1 depending in the breeding group and year. Approximately 85 d after the breeding season had ended, cows were rectally palpated to diagnose pregnancy, and the resulting calves were born in between March and May of the following year.

7.2.5. Statistical analysis

Results were analyzed with heifer and cow RFI$_{\mathrm{FAT}}$ values calculated within contemporary group. Data were analyzed using the PROC MIXED function of SAS 9.4 using a model with the form:

$$Y_{ijklm} = \mu + HCon_i + CCon_j + CAGE_k + \beta_1 heifer\ RFI_{FAT_l} + Sire_m + e_{ijklm}$$

Where Y_{ijklm}= cow RFI$_{\mathrm{FAT}}$ phenotype, $HCon_i$ = main effect of the *i^th^* heifer contemporary group, $CCon_j$ = main effect of the j^{th} cow contemporary group, $CAGE_k$ = main effect of the k^{th} cow age in years on-test, β_1 = partial regression coefficient of cow RFI$_{\mathrm{FAT}}$ on heifer RFI$_{\mathrm{FAT}}$, $Sire_m$ = random effect of the n^{th} sire, and e_{ijklm}= random error of the ijk^{th} animal. R-squared was determined as the difference between 1 and the sum of squares error for the above model divided by the sum of squares error for a model with the form $Y_i = e_i$, where Y_i = CRFI$_{\mathrm{FAT}}$ phenotype and e_i= random error term for the i^{th} animal.

7.3. Results and Discussion

Number of observations (N), age on and off test, weight on and off test, and within-contemporary group HRFI$_{\mathrm{FAT}}$ and CRFI$_{\mathrm{FAT}}$ statistics are presented in Table 7.3. Means and standard deviations for heifer and cow RFI$_{\mathrm{FAT}}$ are similar to those presented by Basarab et al. (2007), which were from heifers and cows tested prior to this data set and overlapping in 2005. Cow age on and off test was variable, as cows were tested at multiple ages and some cows were tested over consecutive years, leading to larger variation in cow age than in heifer age. Heifers weighed more at the end of the test, whereas cows were approximately the same (start and end weights were within 1 SD),

Table 7.3. Summary statistics of replacement heifer and breeding cow feed intake tests.

Item	N	Mean	SD	Min	Max
Replacement Heifer					
Age on test, mo	259	10.0	1.0	8.3	12.8
Age off test, mo	259	13.1	0.9	11.1	15.3
Weight on test, kg	254	328.3	39.7	231.3	436.4
Weight off test, kg	259	410.8	40.1	313.0	560.2
Back fat off test, mm	259	6.7	2.0	2.7	12.0
DMI, kg d^{-1}	259	7.75	1.27	4.99	11.91
RFI_{FAT}, kg DM d^{-1}	259	0.06	0.42	-1.10	0.91
Cow					
Age on test, mo	259	67.9	22.6	42.7	165.0
Age off test, mo	259	70.6	22.6	45.4	167.7
Weight on test, kg	237	694.6	66.3	518.8	868.6
Weight off test, kg	240	719.2	67.7	527.6	897.0
Back fat off test, mm	259	11.8	4.2	2.0	26.0
DMI, kg d^{-1}	259	10.90	2.15	3.18	17.05
RFI_{FAT}, kg DM d^{-1}	246	-0.01	1.12	-3.35	2.83

[1] RFI_{FAT} for heifers and for cows was calculated within contemporary group.

which was expected due to the stage of development of the growing replacement heifers, and cows were managed to maintain stable BCS.

7.3.1. Relationship between heifer and cow RFI_{FAT}

Linear mixed model effects are presented in Table 7.4. Previous work by Manafiazar et al. (2015) reported that heifers classified as high RFI_{FAT} post-weaning consumed 0.46 kg d^{-1} more grazed forage than low RFI_{FAT} heifers when on pasture 6 mo post-trial as pregnant heifers. Moreover, cows of differing ages that produced low RFI progeny in the same production environment as this study consumed less feed during a second-trimester feed intake trial, had resulting lower RFI values, and carried a greater amount of backfat throughout the production cycle compared to medium- and high-RFI progeny (Basarab

Table 7.4. Linear mixed model fixed effects.

Trait		Estimate	S.E.	P-value
Intercept		0.09701	1.2916	0.9405
Heifer RFI_{FAT}, kg d^{-1}		0.7295	0.1967	0.0003
Cow Age, yr				
	3	0.1042	0.6409	0.8711
	4	0.4522	0.5256	0.3908
	5	0.5132	0.4316	0.236
	6	0.182	0.3661	0.6197
	7+	0	.	.
Heifer contemporary group				
	13	0.1976	2.0095	0.9218
	14	-0.05513	1.7025	0.9742
	15	0.02061	1.6332	0.9899
	16	0.01611	1.5444	0.9917
	17	-0.671	1.5122	0.6578
	19	-0.2088	1.4355	0.8845
	44	-0.6563	1.4314	0.6472
	51	-1.3139	1.4076	0.3519
	93	-0.8521	1.2849	0.5081
	96	-1.2467	1.2707	0.3279
	97	1.308	1.4983	0.3839
	98	-0.8833	1.3521	0.5144
	99	-1.319	1.2302	0.2852
	100	-0.798	1.2192	0.5137
	102	-0.6791	1.6163	0.6749
	103	-0.2719	1.2796	0.832
	105	0.3304	1.2006	0.7835
	106	0	.	.
Cow contemporary group				
	1	-0.3655	1.0416	0.7261
	2	-0.5332	0.9369	0.57
	3	-0.4033	0.8342	0.6294
	4	-0.07308	0.6156	0.9056
	6	0.2849	0.5815	0.6248
	8	0.2294	0.4936	0.6427
	10	0.5073	0.3705	0.1727
	12	0.3081	0.3038	0.3121
	14	0	.	.

et al., 2007). Repeatability and re-ranking of RFI classifications observed in young beef cattle and then at more advanced ages have been reported with mixed results. Kelly et al. (2010) reported a repeatability estimate of 0.62 among finishing beef heifers and concluded that RFI measured in early phases of feedlot production was indicative of RFI measured in the finishing phase on a more energy-dense diet. However, Durunna et al. (2011) indicated that 54% of feedlot steers fed a grower diet reranked more than 0.5 SD when fed a finishing diet, indicating that RFI measured on higher-roughage feedlot diets may not reflect the RFI of the same animal on a finisher diet. Among heifers tested for feed intake at LRDC, Durunna et al. (2012) found that there was no difference in RFI between the first half of the feed intake test and the second half but reported that 24% of heifers re-ranked between the early and later halves of the feed intake test. Therefore, the potential for RFI re-ranking in young animals in the growth stages of development post-weaning have had mixed results which, taken as a whole, are somewhat inconclusive. Animals may re-rank due to diet density or level of forage inclusion in dry-lot environments (Kelly et al., 2010; Durunna et al., 2011) or due to the fundamental differences in environment between testing and general production for beef cows, that being dry lot bunk-fed diets compared to pasture (Manafiazar et al., 2015). Comparisons between RFI measured post-weaning and RFI measured as a mature cow are rare. Archer et al. (2002) did not report the significance level of their correlations, however a phenotypic correlation of $r_p = 0.40$ was reported between RFI measured post-weaning and RFI measured at 3 years old (non-lactating and non-gestating) in the same animals. Nieuwhof et al. (1992) reported a low phenotypic correlation ($r_p = 0.07$) between growing dairy heifers and those same heifers measured as lactating cows, but a genetic correlation between the two ages for RFI ($r_g = 0.58$) was observed, again with no significance levels reported. In the present study, a partial regression coefficient of 0. 66 ($P < 0.001$; Fig. 7.1) was observed between RFI_{FAT} measured as a heifer and RFI_{FAT} measured as a cow. This relationship indicates that for every 1 kg of DMI above or below expected intake in post-weaning heifers, the corresponding mature cow can be expected to consume 0.66 kg more or less DM than expected, respectively (Fig 7.1). This result indicates that selection applied to improve phenotypic RFI_{FAT} in replacement heifers should result in a reduction in cow DMI, which agreed with observations made by Archer et al. (2002); Basarab et al. (2007), and Manafiazar et al. (2015).

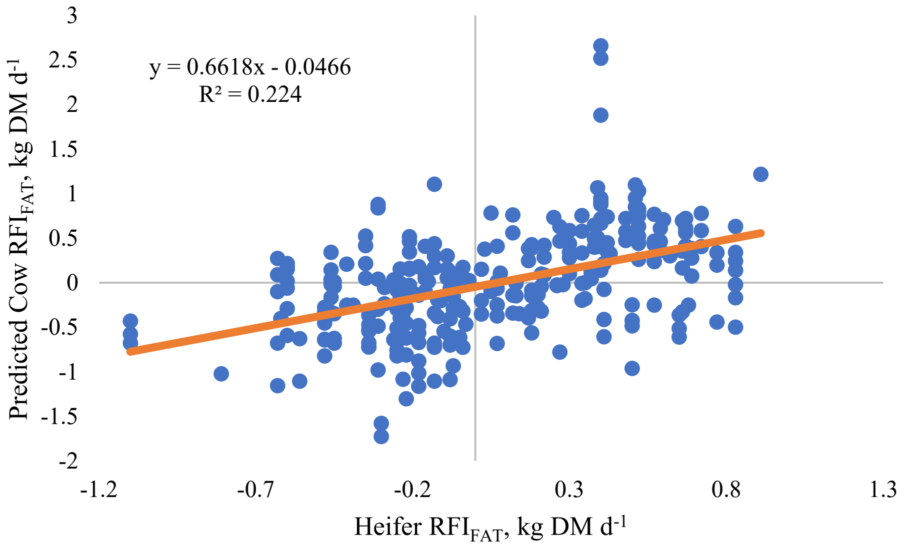

Figure 7.1. Relationship between cow RFI_{FAT} adjusted for model main effects and observed heifer RFI_{FAT}.

The precise biological reasons for the imperfect relationship between heifer and cow RFI_{FAT} are unclear. However, as can be observed in this study, cows had greater average off-test back fat than heifers, indicating that cows had a greater amount of body fatness than heifers (Table 7.3). It is understood that the efficiency of accretion of muscle tissue via protein synthesis is greater than the efficiency of the accretion of fat, and that in growing animals, protein synthesis exceeds the accretion of fat (Cantalapiedra-Hijar et al., 2018). However, in mature animals that have stopped growing, maintenance of existing protein tissue consumes a greater amount of energy than the maintenance of fat (Cantalapiedra-Hijar et al., 2018), and so it could be that the cattle in this study lost efficiency with age due to the differences in metabolic efficiency between growing and mature animals. Tixier-Boichard et al. (2002) proposed that differences in RFI observed between older and younger beef cattle and swine could be due to differences in body composition related to age.

7.4. Conclusion

Inconclusive results have historically limited the application of RFI selection in beef females. The present study indicates that selection for phenotypic RFI_{FAT} in replacement beef heifers should result in mature females that are also more feed efficient, the relationship is less than 1 to 1. The difference in efficiency between heifers and cows is difficult to narrow to precise biological causes but could be due to differences in metabolic efficiency driven by body composition change associated with maturity. Ultimately, phenotypic selection pressure for RFI among crossbred beef replacement heifers should improve cow RFI and reduce the cost of maintaining a cow herd.

8. GENERAL DISCUSSION AND FUTURE DIRECTION

8.1. General Discussion

Both reproductive efficiency and feed intake are crucial elements of beef production. With growing demand, heightened competition for commodity feedstuffs, and pressure from society to improve the perceived environmental impact of beef production, it is important that Western Canadian beef producers continue to improve herd efficiency. Therefore, this thesis was intended to evaluate methods of improving reproductive efficiency and feed efficiency using large historic data sets from two different production environments in north-central and central Alberta. Measures of feed intake (collected by electronic feed bunk technology), reproductive efficiency over multiple parities, and weight data collected at key intervals within each cycle comprised the bulk of the data available and represents one of the largest such datasets known to the authors at the time of writing.

In chapter 3, the phenotypic and genetic relationships between feeding behaviours were reported with estimates of heritability. This chapter represents a unique evaluation of these traits in post-weaning heifer calves consuming a high-forage diet in dry lot conditions, common to the methods used to develop replacement females in Western Canada. Feeding behaviour correlations (phenotypic and genetic) were consistent with reports in the literature from steers, bull, and heifers consuming concentrate diets in a feedlot environment, including previous work from this group. These feeding behaviour traits among post-weaning replacement heifers were novel and represented a valuable contribution to the industry's understanding of how feeding behaviours in different classes of beef cattle are related.

Chapter 4 represented an expansion of the feeding behaviour discussion and brought in additional data from the University of Alberta Roy Berg Kinsella Research Station. In addition, feeding behaviours were phenotypically and genetically correlated with greater dry matter intake and greater cow weights, but not correlated directly to measures of reproductive performance. Heifers that spent more time at the feed bunk and visited more frequently were generally larger, fatter mature cows in their 1st – 3rd parities. Further, cows that spent more time eating produced progeny with greater birth weights and weaning weights, though likely as a result of the larger cow body weights (larger cows produced larger calves). Ultimately, feeding behaviours are very closely related with measures of cow body weight and fatness, both of which lead to larger calves. However, care must be taken in the application of feeding behaviours as breeding selection tools in isolation from other traits like RFI, as doing so may result in larger cows that do not fit their environments. Further, feeding behaviours have been noted to be under environmental influence, and external factors such as weather and patterns in events like feeding time could influence these traits, as well as pen density and feed competition (Parsons et al., 2020). However, genetic control and variation in these feeding behaviours does exist, and so selection pressure could be employed in a selection index that includes traits to limit mature cow size and calf birth weights.

Chapter 5 investigated the usefulness of monitoring cow weight over time and comparing cow weights at specific ages to modelled ideal cow weights. As technology continues to advance in the area of remote monitoring of animal weights, it is conceivable that producers may be able to collect continuous daily weights (collected at feed or watering stations). Proper evaluation of such data over time may allow producers to identify cows with excessive gains or losses due to illness or reproductive malfunction, identify the cow, and remove her from the herd for treatment, re-breeding, or culling.

Chapter 6 provided detailed estimates of dry matter intake over time in cows under normal production environments and their relationship with breed composition, genomic retained heterozygosity, and winter grazing environments. Ultimately, we suggested that the estimation of dry matter intake over time in beef cows is possible using a combination of equations from the well-established NASEM (2016) and growth curves that required birth weight and date information. These equations will need considerable further refinement, especially relative to the growth and development of calves pre-weaning, where estimates of energy requirements were unreliable due to a lack of research in that area. This work represents the first step in refining prediction equations for calf and cow energy requirements and is useful in illustrating that selection for efficient heifer replacements should reduce the total feed intake for an animal over its lifetime in the cow herd.

Finally, chapter 7 presented a relationship between RFI_{FAT} measured in replacement heifers and RFI_{FAT} measured in mature cows. The reranking of RFI in animals that are in different stages of growth is fairly well established, though this was one of the first studies known to propose a relationship between the two traits in the same animals on high-forage diets. The work concluded that selection for residual feed intake in replacement beef heifers should result in cows that are also more feed efficient

Taken together, these results provide a framework that may allow beef producers to select heifers with a greater propensity for reproductive success based on factors observed prior to their first parity. Beef replacement heifer selection is not an exact science and often involves knowledge of prior generations or relatives' performance, and subjective phenotypic bias toward heifers of certain size, colour, and conformation. The introduction of tools to aid producers in making sound, profitable replacement heifer decisions should help improve selection pressure and could therefore advance the rate of genetic progress in relevant traits. However, this thesis did not report any direct relationships between early-life measures of feed intake traits and reproductive efficiency, though relationships between traits like feeding duration and body weight, and body weight and reproductive ability indicate that further investigation is warranted. Further, this work provided evidence that the increasing use of technology in agriculture is applicable to the beef operation. Remote monitoring of cattle through cameras with the ability to estimate daily weights on animals may allow producers to identify cows that are gaining too much weight and therefore may be under further suspicion of having lost a pregnancy or a calf. Finally, the relationship between feed efficiency measured in beef replacement heifers and then again in mature cows was presented with reassuring results; namely, that selection pressure applied to phenotypic residual feed intake in beef replacement heifers should result in a mature cow herd with decreasing RFI and increasing feed efficiency.

8.2. Limitations and future work

Overall, this work was limited by the number of observations available. Genetic analysis of traits has historically required many thousands of individuals and their accurate pedigree; this study was limited to under 2000 animals at most. Accurate pedigrees were not available for all animals. Further, due to the normal issues associated with handling livestock, not all data points were available for all animals, which required either the estimation of the data from prior and subsequent observations (as in weight) or the removal of the entire record from the dataset. Added to that, n was inversely related to parity, and advanced parities often did not contain sufficient observations to make analysis accurate or worthwhile. Continuing to keep records on large research herds in different environments is invaluable, and work like that done by the teams in Lacombe and Kinsella should be prioritized by future research.

Further, this work was complicated by the cyclical nature of beef reproductive data. Cow reproductive cycles are measured here from breeding to weaning, which are events separated by roughly 18 mo. However, each individual event is separated from the subsequent event by roughly 12 mo (cows are usually exposed to breeding every spring, calve every winter, and wean a calf every fall). That aspect confounded dates, time frames, and limited the application of statistical software. A thorough understanding of the beef reproductive cycle and common beef management techniques will be required for future work in this area, and such work should not be attempted by those unfamiliar with beef cattle. Unfortunately, the nature of the data cannot be changed, though it may be possible to streamline the analysis of the data through the use of machine learning as that technology develops, though again, a complete understanding of beef cow-calf operations would be required.

Cows at the Lacombe research centre were managed under two separate winter-feeding environments, which lead to some difficulty in interpreting the results of analysis. As the number of observations in each winter-feeding program continues to grow every year, it may be useful to fully separate the two herds and make data available for analysis where there is not an effect of swath grazing or confinement feeding. Swath grazing, in particular, is not a well-established practice and the full effects of maintaining cows on swath grazing for their entire lives is not very well understood and could have confused the interpretation of the analyses in this thesis. As was observed in Chapter 6, the effects of swath grazing on back fat gain and loss in beef cows is not well understood, and it very well may be that cows exposed to swath grazing require considerably more energy to recover during the spring and summer.

Finally, this thesis was not able to consider the underlying biological effects that lead to the observations presented, as the dataset used did not include measures of hormones, metabolites, or analyses of the rumen microbiome. Future work should endeavour to explain the phenotypic observations observed with biological processes that underlie those relationships, which may be extensive given the complexities of biological systems.

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