University of Alberta

INVESTIGATION OF RESIDUAL FEED INTAKE IN DAIRY COWS

by

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DEDICATION

This work is dedicated to my parents, Mr. Moharramali Manafiazar and Mrs. Nazi Shban, for their love, sacrifice and tolerance. It is also dedicated to my most beloved spouse, Mrs. Fatemeh Baghbaninaghadehi, for her support in every single moment of my life.

ABSTRACT

This thesis research was aimed to develop a residual feed intake (**RFI**) prediction equation in dairy cattle while accounting for the animals' multifunctional lactation non-linear energy requirements profiles. The possibility of shortening RFI test period and finding indicator traits for RFI selection were also investigated. A total of 281 first-lactation dairy cows at the Dairy Research and Technology Center of the University of Alberta from June 2007 through October 2012 were used. Individual daily feed intakes, repeated measurements of monthly body weight, and body condition scores of these animals were recorded from 5 to 305 days in milk. Milk production and milk composition data were extracted from the Dairy Herd Improvement Program, and their first type classification data was retrieved from the Canadian Dairy Network. To reduce the test period in a lactation, the acquired data from whole lactation (5 to 305 DIM) was subdivided equally into three shortened periods, early, mid, and late stage of lactation. RFI prediction equations were developed for the whole and each of the shortened periods. Each animal, based on its predicted RFI value, was assigned to high (RFI > 0.5 SD) medium (RFI = ± 0.5 SD) or low (RFI < 0.5 SD) RFI classes within each of the test period. Compared with the whole lactation, numbers of the animals' remaining in the same RFI class within any of the shortened test periods were determined to study the consistency of RFI prediction. Moreover, genetic and phenotypic correlations between the selected conformation traits and RFI were estimated to investigate the possibility to use

these conformation traits as indicator traits for RFI selection. The results showed that RFI could be predicted in whole, early, mid and late lactation with R-square of 0.68, 0.47, 0.49, and 0.79, respectively. Compared with the whole lactation, most of the animals (65.5%) remained in the same RFI classes in mid stage, so mid RFI prediction could be considered as the best representative of whole RFI in compare with early and late periods. Moreover, combinations of eight conformation traits could be used as indicator traits for RFI selection, since they had high genetic correlation with whole lactation RFI.

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LIST OF ABBREVIATIONS

ABCS: Average of body condition score

ABW: Average of body weight

ADG: Average daily gain

AEI: Actual energy intake

AFC: Age at first calving

AFC: Age at first calving

AN: Angularity

ANTE: Ante-dependence structure

AR (1): Autoregressive structure

BCS: Body condition score

BD: Body depth

BF: Bessel functions

BIC: Bayesian information criterion

BW: Body weight

CDN: Canadian dairy network

CF: Covariance function

CS: Cubic splines

CW: Chest width

DE: Digestible energy

DF: Degree of freedom

DHI: Dairy herd improvement

DIM: Days in milk

DMI: Dry matter intake

DRTC: Dairy research and technology center

DS: Dairy strength

EBW: Empty body weight

EBWC: Empty body weight change

EEI: Expected energy intake

F: Fixed effect

FCM: Fat corrected milk

FCR: Feed conversion ratio

FL: Feet and legs

GE: Gross energy

GEE: Gross energy efficiency

GHG: Green house gas

HF: Height at front

IGF-I: Insulin growth factor I

L: Linear

LAEI: Lactation actual energy intake

LDMI: Lactation dry matter intake

LECM: Lactation energy corrected milk

LFCM: Lactation 3.5% fat corrected milk

LFCR: Lactation feed conversion ratio

LGEE: Lactation gross energy efficiency

LP: Legendre polynomial

LRT: Log likelihood ratio test

LTE: Life time efficiency

MBW: Metabolic body weight

ME: Metabolizable energy

MPER: Milk production energy requirement

MS: Mammary system

MYC: Milk yield and components

NDF: Natural detergent fiber

NE: Net energy

NEB: Negative energy balance

NL: Non linear

NP: Not provided

OC: Overall conformation

PE: Permanent environment

PW: Pin width

R: Random effect

RAH: Rear attachment height

RAW: Rear attachment width

RFI: Residual feed intake

RFIg: Genetic residual feed intake

r_g: Genetic correlation

RMS: Residual mean square

r_p: Phenotypic correlations

RRM: Random regression model

RU: Rump

SD: Standard deviation

SF: Sinusoidal

ST: Stature

THI: Temperature and humidity index

TMR: Total mixed rations

UD: Udder depth

UN: Unstructured

UT: Udder texture

CHAPTER 1. GENERAL INTRODUCTION

1.1. INTRODUCTION

Global milk production is expected to increase by 80% from 2000 to 2050, to offset milk demands of the growing human population (Steinfeld et al., 2006). The increased production costs are tightly linked to feed costs, since these account for nearly 80% of the total variable cost of milk production (Connor et al., 2012). As production and the human population are growing, environmental concerns of greenhouse gas (**GHG**) production and carbon footprint by industries are increasing over time. The agriculture sector accounts for 9% of the total GHG production in Canada (Environment Canada, 2013) of which beef and dairy cattle have the greatest contributions through their enteric fermentation and methane emissions (Connor et al., 2012). Hence, to regulate GHG emitters, the “cap and trade” emission trading system was established for carbon offsets (Alberta Environment., 2007). Also, protocols for estimating carbon offsets related to dairy production are being developed (Haugen-Kozyra, 2010). Therefore, the demands for milk production should be undertaken in a cost effective and environmentally sustainable approach, which is achievable by the genetic selection for superior animals in energy efficiency (Berry and Crowley, 2013).

The feed conversion ratio (**FCR**) and gross energy efficiency (**GEE**) are traditional measures of feed/energy efficiency in dairy cattle. The FCR is the ratio of input (feed intake) to output (milk production) (Crews, 2005), and GEE is defined as the energy in milk relative to the total energy intake (Veerkamp and Emmans, 1995). Although historically FCR and GEE are the most common measures of feed efficiency, animal selection based on these measures does not necessarily improve feed efficiency because of drawbacks associated with increased body weight and maintenance requirements (Crews, 2005). Moreover, energy intake has different partial efficiencies for maintenance, lactation, and body tissue gain/loss, but neither FCR and GEE takes this concept into account (Veerkamp and Emmans, 1995). To address the problems related to FCR and GEE, an alternative measure of feed efficiency, residual feed intake (**RFI**), was developed by Koch et al. (1963) for beef cattle. RFI is defined as feed intake adjusted for body size and production level such as average daily gain. Efficient animals, which have low RFI values, consume less feed without compromising the production level (Koch et al., 1963). Issues and problems related to individual RFI in beef cattle have been extensively studied during the growth period (Archer et al., 1999; Crews, 2005; Nkrumah et al., 2007; Durunna et al., 2012). Results have shown that a viable option for improving feed efficiency is to genetically select of efficient animals for lower RFI. Under environmentally sustainable conditions, genetic selection can reduce production costs without compromising the production level under environmentally sustainable conditions (Connor et al., 2012). Research suggests that 10 to 12% of feed intake, 25 to 30% of GHG emissions, and 15 to 17% of nutrient losses could be decreased by genetically selection for RFI in beef cattle (Alberta Agriculture, Food and Rural

Development, 2006). As a result, RFI research in dairy cattle is being promoted (Coleman et al., 2010; Vallimont et al., 2011; Connor et al., 2012) to study the similar opportunities of feed efficiency improvement, same as those available for beef cattle. However, defining RFI in dairy cattle is not as easy as it is for beef cattle during the linear phase of growth because dairy cattle undergo lactation cycles and have multifunctional non-linear energy requirements profiles within a lactation period. In a lactation cycle, dairy animals lose their body reserves to support milk production in early lactation since the peak of feed intake occurs lag behind the peak of milk production. After the peak of feed intake, animals start to regain their body reserves prepare for the next lactation. It is well established that the energy expenditures for milk production and body gain/loss have non-linear profiles during lactation. Therefore, the multiple energy requirements and their non-linear profiles must be considered in the RFI definition for dairy cattle. As far as we aware, the proposed RFI models in dairy were developed mainly by using a linear regression to model the energy expenditures profile either during the short test (Van Arendonk et al., 1991) or the whole lactation period (Svendsen et al., 1993; Zamani et al., 2008). Other research (Coleman et al., 2010; Vallimont et al., 2011), which used non-linear regression to model the energy expenditures' profile, had a limited number of actual feed intake records for each animal (maximum of 10 observations) during almost 300 days in milk. Overall, the RFI obtained from the aforementioned studies may not be very accurate, which means that RFI in dairy cattle requires further investigation (Zamani et al., 2008).

Individual feed intake and body weight records are the main limitations of feed efficiency research in dairy cattle, mainly due to difficulties in measuring and costs associated with labor and equipment. The dairy cattle herd at the University of Alberta’s Dairy Research and Technology Center is one of the few populations in the world where in which the individual feed intake data has been recorded since 1999. Moreover, repeated measurements of individual monthly body weight and body condition scores of these cows have been recorded since 2007.Monthly milk yield and milk composition data are also available through the Dairy Herd Improvement program. This dataset provides an opportunity to address feed efficiency, particularly RFI related questions for improving feed efficiency in dairy cattle. The genetic improvement of feed efficiency could have significant effects on the economics of the dairy industry not only in Canada but also throughout the world by reducing feed consumption and GHG emissions. Therefore, in the first study of this project, a prediction equation was developed to estimate individual lactation RFI over-305 days in first lactation dairy cows while accounting for multifunctional non-linear energy expenditures.

To conduct a feed efficiency research in dairy cattle, it is necessary to obtain an accurate feed intake for each individual animal. This is very expensive and time consuming to measure. It is the major obstacle that limits feed efficiency studies in dairy. Therefore, it would be beneficial to shorten RFI test period within a lactation cycle in a way that measures efficiency in the reduced period still captures animal’s lactation feed efficiency performance. By shortening the test period, the individual feed intake record period and the feed test costs could be reduced, and the RFI test made applicable. Two research teams, the first using grazing dairy cows (Lopez-Villalobos et al., 2008; Prendiville et al., 2009) and the second (Connor et al., 2012) using limited numbers of indoor animals (n=32) examined the possibility of reducing the lactation RFI test period. Their results suggested that the RFI measurements after 100 DIM may provide a better indicator of lactation RFI (Connor et al., 2012). However, these studies did not use actual daily feed intake nor did they examine the genetic basis of RFIs and RFI component traits in different test periods, which are necessary in a breeding program. In the second study of this thesis, the RFI was predicted at different stages of lactation and genetic correlations among RFIs and RFI component traits in different test periods were examined to study the possibility of shortening the RFI test period within a lactation period.

In a dairy breeding program, individual feed intake is the major prohibiting factor for limiting the direct selection for RFI in the industry-wide genetic improvement application. Therefore, genetic improvement for RFI through indirect selection on indicator traits would be desirable in a dairy breeding program to improve RFI. The ideal indicator traits should be easily, routinely, and inexpensively measured traits which have moderate to high genetic correlations with RFI. The conformation traits which are being routinely recorded in the dairy industry (Canadian Dairy Network, 2006) may be beneficial as indicator traits for RFI. Therefore, in the third study of this thesis , genetic correlations among conformation and efficiency traits, especially RFI, were investigated to test potential conformation traits as indicator traits for RFI selection. Moreover, the correlations among intake, production, and RFI were examined, to shed light on further consequences of selection for RFI on intake and production traits.

1.2. RESEARCH HYPOTHESES

The following research hypotheses were tested in this thesis:

a) Whether phenotypic RFI is predictable while accounting for non-linear lactation profile of its component traits and multifunctional requirements in dairy cows, which can be used to accurately predict RFI in dairy cattle.

b) Whether there are genetic correlations among RFIs in different stages of lactation and whole lactation RFI in first lactation dairy cows, and whether those correlations can be used to shorten the feed intake measurement period and reduce test costs.

c) Whether there are phenotypic and genetic correlations among RFI, production, and feed intake traits and whether those correlations can be used to predict the indirect effect of long-term selection for RFI on the performance of other traits.

d) Whether there are phenotypic and genetic correlations among feed efficiency traits, especially RFI, and conformation traits, which conformation traits can be used as indicator traits for indirect selection for RFI in a dairy breeding program.

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CHAPTER 2. LITERATURE REVIEW

2.1. INTRODUCTION

The purpose of this chapter is to review the most common measures of energy efficiency and the factors that affect energy efficiency in dairy cattle. Since there are very few reports on direct selection for energy efficiency in dairy cattle, the associations between energy efficiency with other traits such as reproduction in other species are discussed. Because random regression technique has been applied in the statistical part of this research project, the concepts and principles of this technique is also concisely described.

2.2. REVIEW ON ENERGY EFFICIENCY[1]

2.2.1. Energy Efficiency Traits

Researchers have proposed many energy efficiency measures such as feed conversion ratio (**FCR**), gross energy efficiency (**GEE**), residual feed intake (**RFI**) (Koch et al., 1963; Archer et al., 1999; Crews, 2005), life time efficiency (**LTE**) (Vandehaar, 1998; Vandehaar and St-Pierre, 2006), and residual milk production (Coleman et al., 2010). The characteristics of the widely used

[1] A version of this section has been published as a book chapter. Manfiazar et al. 2012. Milk Production - An Up-to-Date Overview of Animal Nutrition, Management and Health. Chapter 6. PP 211- 138. ISBN: 978-953-51-0765-1

efficiency measures are reviewed in this section, and their advantages and disadvantages are discussed.

FCR and GEE are the most common measures of feed efficiency. FCR is the ratio of input (e.g. feed) to output (e.g. milk production), while GEE is defined as the energy in the milk divided by the total energy intake (Veerkamp and Emmans, 1995) and these approaches lead to only limited insight into the efficiency of the entire production system (Crews, 2005). The problems related to GEE and FCR, which have been discussed in numerous studies (Korver et al., 1991; Veerkamp and Emmans, 1995; Crews, 2005), are mainly categorized into three groups. Firstly, GEE and FCR do not distinguish partial energy efficiencies of feed intake for maintenance, lactation, pregnancy, and body tissue gain/loss (Veerkamp and Emmans, 1995). Secondly, FCR and GEE are well-known to be phenotypically and genetically correlated with measures of growth, production, and mature size. Therefore, animal selection based on these measures may increase maintenance requirements. Finally, changes in GEE and FCR could be the result of changes in either intake (numerator), yield (denominator) or both (Gunsett, 1984; Veerkamp and Emmans, 1995), and selection direction cannot be predicted very well. Then, selection for improvement of FCR (i.e. decreased FCR) and GEE (i.e. increased GEE) would result in increased growth rate, mature size, and consequently mature maintenance requirements in an unbalanced selection index (Korver et al., 1991). It can be concluded that improving FCR and GEE do not necessarily improve net feed efficiency, because of the drawbacks associated with increased maintenance requirements (Van der Werf, 2004; Crews, 2005).

Lifetime efficiency (LTE), another measure of energy efficiency, is defined as “the capture of feed energy in milk, conceptus, and body tissue divided by gross energy intake during the life of cow, starting at birth” (Vandehaar, 1998; Vandehaar and St-Pierre, 2006). This index attempts to summarize an animal’s entire life efficiency and is a good criterion to set up a long term vision. In order to compare the LTE in dairy cows, total milk production should be standardized for all factors such as housing, feeding, age at first calving and calving intervals. The LTE depends mostly on the precalving and intercalving intervals. The precalving interval is defined as a period between the birth and first parturition, and intercalving intervals are the intervals between the successive calvings (King, 2006). Overall, LTE is mostly affected by precalving and intercalving intervals; its calculation requires a great quantity of information and is only applicable for the entire life.

To overcome the problems associated with FCR, GEE, and LTE, an alternative measure can be expressed as residual feed intake (RFI). RFI is a measure of feed utilization corrected for live weight and production level (Koch et al., 1963; Korver et al., 1991; Luiting et al.,1992). The concept of RFI can be described as the difference between the actual and predicted feed intake based on the requirements for body weight maintenance and level of productions (Koch et al., 1963) as shown schematically in Figure 2.1. Energy intake is partitioned into portions required for body maintenance and production, and the left-over portion is called RFI. RFI is related to the true metabolic efficiency of an animal and is comparable across individuals (Crews, 2005). Variation in RFI probably reflects underlying biological efficiency after adjustment for energy deposition (Crews, 2005; Herd and Arthur, 2009). In a population, the mean of RFI index over all the individuals is zero, and approximately half of all the individuals have RFI values below or above the mean. The efficient animals have low RFI values; it implies that they consume less feed without compromising their production level (Crews, 2005). Finally, RFI is a good indicator of feed efficiency, which can be calculated at any stage or animals' entire economic life time.

2.2.2. Factors Affecting Energy Efficiency in Dairy Cattle

Several factors affect the energy efficiency in dairy cattle from which the effects of dry matter intake (**DMI**), production level, body weight, body tissue changes, age at first calving (**AFC**), and environmental factors (Vandehaar, 1998; Linn, 2006) have been well documented. The relationship between each of these factors and energy efficiency are concisely reviewed in this section.

2.2.2.1. Dry Matter Intake and Production

Dry matter intake (DMI) and production are direct components of the most energy efficiency traits. DMI establishes the amounts of nutrients that are required for an animal's maintenance and production level. Inadequate intakes of nutrient negatively affect production, efficient nutrient utilization, and the health status of the animal. On the other hand, supplying nutrients in excess amounts increases feed costs and can result in the excretion of nutrients into the environment (NRC, 2001; Collier et al., 2006). Therefore, providing a balanced diet, quality and quantity-wise, is necessary to optimise the energy efficiency and performance of an animal. In a dairy cow, the average DMI amount has been reported 22.7 kg/d ranging between 19.8 to 26 kg/d (Ordway et al., 2009; Vallimont et al., 2010), with heritability estimation ranging from 0.16 to 0.48. Thus, there is phenotypic and genetic variation for DMI among animals. DMI affects energy efficiency through energy transformation mechanisms from gross to net energy. The energy transformation mechanisms involve digestion, fermentation, and metabolic processes. Gross energy is the existing form of energy in feedstuffs, and it is converted to net energy by an animal in several steps (Figure 2.2). In each step, some amounts of energy losses in different forms and remaining part is termed differently (digestible, metabolizable, and net energy). Gross energy (**GE**) is the amount of released energy in heat combustion. Some amount of this energy is indigestible and ultimately appears in feces; the remaining part is called digestible energy (**DE**). Some part of DE is lost due to gas production (mainly methane) and urinary energy (mainly urea) during the fermentation process. The remaining DE after deduction for gas and urinary production is called metabolizable energy (**ME**). Finally, converting the ME to net energy (**NE**) requires metabolic reactions, and produces heat which is termed heat increment (NRC, 2001; Vandehaar and St-Pierre, 2006). NE is the energy directly used to support maintenance functions, milk production, conceptus growth, and body tissue gain (NRC, 2001). Overall, the accessible amount of NE from GE depends on the amount of losses in digestion, fermentation, and metabolic processes. Practically, the amount of these losses is affected by several factors including the DMI levels and the dietary fibre level (NRC, 2001). Some studies have been conducted to determine the relationship between these factors and the amount of nutrient losses in different steps of the energy transformation mechanisms (Moe, 1981; Van Soest et al., 1992). Altogether, the results show that the relationship between efficiency and each of these factors is not linear, and there is an optimum point between them. For example, Vandehaar (1998) has reviewed the literature to show the relationship between the DMI level and DE. He documented that when a dairy cow consumes DMI for its maintenance requirements, almost 80% of GE is captured in the form of DE; there is also a reduction in the digestibility level as the DMI level increases (Vandehaar, 1998). Overall, NRC (2001) suggests that digestibility is depressed linearly at 4% per multiple of the maintenance intake. It assumes that the optimum point of GEE occurs when DMI is consumed at the level of 3 times the maintenance requirements. Finally, due to the DMI level, the portion of losses in different steps of energy transformation shifts and it affects energy efficiency. At the higher levels of DMI the proportion of losses into feces increases, while the proportion of losses in the form of heat increment is greater at lower levels of DMI intake (Vandehaar and St-Pierre, 2006).

In addition, it has been shown that there is an optimum point of dietary fibre levels (especially natural detergent fibre; **NDF**) in terms of converting GE to DE, and it occurs at the levels of 25 to 30% of the diet. Higher levels of NDF beyond this range fill the rumen and decrease energy intake, whereas the lower levels may cause various health problems (Eastridge, 2006; Vandehaar and St-Pierre, 2006).

During the past 21years, the average milk production of Canadian Holstein cows has increased about 107 kg/cow/year. The average rate of this increase was 1.35% between 1991 and 2011 (DHI, 2012), and it is likely to continue this increasing trend. In addition, milk yield heritability was reported as 0.30 (Lee et al., 1992; VanRaden et al., 2009) ranging from 0.16 to 0.50 (Veerkamp, 1998). This means that there is still room to increase milk production by exploiting genetic selection. It is demonstrated that selecting dairy cows for milk yield automatically improves FCR and GEE (Veerkamp and Emmans, 1995), since the genetic correlation between these measures and milk production in dairy cattle ranges from 0.88 to 0.95 (Pitchford, 2004). For example, FCR value (4% FCM/DM) has improved from 0.91 in 1991 to 1.20 in 2006 (Eastridge, 2006). However, Korver (1991) concluded that the improved GEE and FCR mostly reflect the dilution of maintenance but not feed efficiency improvement. Dilution of maintenance means that as cows consume more, a relatively small fraction of energy is used for their maintenance, while a larger portion is captured in milk. Although production is a fundamental component of energy efficiency, the relationship between the marginal benefit of increased production and efficiency is not linear for all the time. To set a vision for the future, Vandehaar (1998) modelled the optimum point of the milk yield. He proposed that above 15000 kg/yr, the marginal increase in efficiency approaches zero. Therefore, the current positive correlation between the milk production and energy efficiency may change in the future, when average milk production surpasses 15000 kg/yr/cow (Vandehaar, 1998).

DMI and milk yield are tightly linked together since their genetic correlation was reported to be 0.5 (Vallimont et al., 2010), ranging from 0.46 to 0.84 (Veerkamp, 1998). Consequently, selection decision that changes the milk yield also would change DMI (Veerkamp and Emmans, 1995). However, with increased milk production per animal, there is a limit to the increase in DMI because of the rumen fill; therefore, the density of NE in dairy rations has been elevated as milk production increased in the last 30 years. For instance, the dietary NE density of dairy cattle rations has increased from 1.23 in 1980 to more than 1.6 Mcal/kg in 2006 (Eastridge, 2006). Thus, it can be inferred that some of the improved efficiency due to increased milk production is withdrawn by increasing the dietary energy concentration in terms of expenses. Furthermore, as Vandehaar (1998) concluded the linear relationship between milk production and efficiency may change in the future. Therefore, these concerns drive researchers to define net energy efficiency using concepts such as RFI, which is independent of production and maintenance in dairy cattle.

2.2.2.2. Body Weight

Body weight influences the energy efficiency through its relationship with milk production and digestive capacity. Heritability of body weight (**BW**) has been estimated to be within the range of 0.26 to 0.88 (Veerkamp, 1998), and it is genetically correlated with milk production. A wide range of genetic correlation between BW and milk production from -0.42 (Vallimont et al., 2010) to 0.45 (Veerkamp, 1998) was reported in the literature. The inconsistent results could be due to the different mean of BW and milk production among the populations under estimation. It could also suggest that there is an optimum point for the relationship between BW, milk production, and consequently energy efficiency. In order to illustrate the optimum relationship, Vandehaar (1998) modelled the relationship between body size, milk production, and energy efficiency. He considered two possible relationships in which the digestive capacity was a function of BW (Figure 2.3). In the first scenario, he assumed that the digestive capacity was not a function of BW; indeed, the animal has constant digestive capacity irrelative to its BW. Therefore, increased BW enhances the maintenance requirements and, consequently, decreases energy efficiency. In the second scenario, the digestive capacity was assumed to be a function of BW. Then by increasing BW, digestive capacity would increase and a large cow would be more efficient. However, the larger cow should produce relatively more milk. For example, consider two cows with BW of 625 and 825 kg; the second cow should produce 60 kg/day more milk to become more efficient than the first. Finally, Vandehaar (1998) concluded that the relationship between body size and efficiency depends on the relation between digestive capacities with body size (Vandehaar, 1998), and there is an optimum point of relationship between BW and energy efficiency.

2.2.2.3. Body Tissue Changes

From an evolutionary point of view, mammals use their stored energy reserves to produce milk and support their young ones when their requirements exceed the consumed DMI. As the calf grows older, it gradually relies less on the mothers' milk. Then, the mother has an opportunity to regain energy resources for the next lactation (Bewley et al., 2008). Similarly, in dairy industry, the animals have a mechanism to use their body reserves to support milk production in early lactation and regain the body reserves in late lactation (Coffey et al., 2001; Bewley et al., 2008). Indeed, in early lactation when energy intake is less than that used for milk, maintenance, and activity, the cows are in a negative energy balance (**NEB**). Then, they sacrifice their body resources in this period to meet their requirements. Changes in energy resources practically are measured by changes in BW and body condition score (**BCS**). BCS is a management technique used to appraise the body fat reserves in cattle (Coffey et al., 2001), and it is measured on either a 5 or a 9 point scale. The ability to manage the body reserves varies among the animals, and they have different patterns of BW and BCS changes during and across lactations (Bewley et al., 2008). Depending on the stages of lactation, the range of heritability estimation for BW changes and BCS changes were reported from 0.10 to 0.60 (Veerkamp, 1998; Vallimont et al., 2010; Bewley et al., 2008).

Body tissue changes increase gross energy efficiency by supporting milk production through tissue mobilization. The negative and positive correlations have been reported between milk yield and the BW changes (-0.41 to 0.45) (Veerkamp, 1998) depending on stage of lactation. However, it is demonstrated that one unit of BCS (5 point scale) is equivalent to ~400 Mcal of ME, and its conversion ratio to milk is estimated at 0.82. Therefore, losing one unit of BCS supports around 2000 kg of increased milk production over 305 days, and it is expected to increase GEE from 25 to 26.5% in a cow with a production of 8000 kg milk (Vandehaar, 1998). The lost energy reserves are replaced by cows in their late lactation period. Although the body reserves replenishments' conversion ratio is less (0.7) than that estimated for that which was lost (0.82) (Moe, 1981), loss of BCS still increases the efficiency (Vandehaar, 1998).

Although energy efficiency increases by lose of BCS, some researchers pointed out the side effects of losing energy reserves on other traits such as reproduction (Vandehaar, 1998; Bewley et al., 2008). They reported that excessive BCS losses at calving predispose the animal to metabolic disorders (Spain, 1996; Bewley et al., 2008). Finally, researchers proposed that there is a curvilinear relationship between BCS at calving and milk production; furthermore, the maximum milk production is associated with 3.25 to 3.5 BCS at calving (Roche et al., 2007; Bewley et al., 2008). In fact, during the early lactation period, controlled losses of the body condition score from 0.5 to 1.0 unit (5 unit scale) are associated with an optimal milk production, health, and reproductive performance.

2.2.2.4. Age at First Calving

Age at first calving (**AFC**) represents the length of the period between an animal's birth and first calving. It is a period when an animal impose housing, feeding and veterinary care (yardage expenses) chargers for the farmer, which represents 15 to 20% of animal expenditures toward the cost of milk production (Mayer et al., 2004). Life time efficiency (LTE) is mainly affected by AFC (section 2.2.1 of chapter 2) and can be increased by lowering AFC (Mayer et al., 2004, Vandehaar and St-Pierre, 2006). The aim of the breeding programs is reducing the AFC without compromising the animal's weight at calving. This goal could be achieved by combining increased average daily gain and decreased age at breeding (Mayer et al., 2004). If reduced AFC is not accompanied by the optimum breeding weight, it would have a negative effect on subsequent milk production (Vandehaar and St-Pierre, 2006). For example, the results show that milk yield would be reduced about 70 kg for every 10 kg body weight below the optimum weight (Vandehaar and St-Pierre, 2006). The optimum AFC and weight right after calving for Holstein cows are 22 to 24 months and 570 kg. Indeed, the economic benefit of a decreased AFC is not well understood, and there is a need for further investigation.

2.2.2.5. Environmental Factors

Temperature, humidity and photoperiod are the major environmental factors that affect animal performance and efficiency. The thermoneutral zone is a range in which animals do not spend energy to maintain their normal body temperature. The upper critical range for dairy cattle is 25 to 26 ^{0}C, and the lower critical range depends on the animal’s DMI and the production levels. For example, an animal at the maintenance intake level has the lower critical points of 2 ^{0}C. While as she produces milk her lower critical point decreases; if she produces 10 or 20 kg of milk, her intake level increases and consequently her lower critical points goes down to -4 and -10 ^{0}C, respectively. Therefore, dairy cows in cold stress relatively do not need to change their energy requirements due to the higher amount of heat increment production. It is concluded that, mild cold stress does not affect energy efficiency significantly in high producing dairy cattle; while, mild to severe heat stress increases the maintenance requirements from 0.7 to 2.4 %, respectively, and decreases DMI and feed efficiency (NRC, 2001).

Photoperiod which is another environmental factor affects lactation, growth, reproduction, and immune function. Most of the research studies have been conducted to study the effects of short or long day photoperiod concepts on animals’ reproduction and production performance. Their results demonstrated that the physiological basis of attainment of puberty is controlled by photoperiod rather than ambient temperature. Long photoperiod causes early puberty that is associated with rapid growth in calves and greater mammary parenchyma (Collier et al., 2006), which results in lower AFC and more milk production, and consequently improves energy efficiency.

In addition, other temporary environmental factors such as milking frequencies can also affect milk production and energy efficiency. For example, Wall and McFadden (2007) concluded that milking 2 times more frequently than usual (4 vs. 2 times/day) for a 3-week interval during early lactation significantly increases milk production and energy efficiency

2.2.3. Indirect Effects of Selection for Energy Efficiency on Some Other Traits

To maximize the genetic selection gain, the genetic base of energy efficiency and its association with other traits should be determined. Although reports on the association between energy efficiency and other traits such as reproduction are scarce in dairy cattle, it has been documented in different species. It has been shown that energy efficiency has moderate heritability in different species. For instance, a range of 0.12 to 0.36 for the heritability estimations of GEE, FCR and RFI have been reported in dairy cattle (Van Arendonk et al., 1991; Parke et al., 1999; Vallimont et al., 2011). The weighted mean of 28 and 9 estimates of heritabilities for FCR and GEE were reported as 0.32 ± 0.02 and 0.37 ± 0.05, respectively in beef cattle (Koots et al., 1994). In addition, the weighted mean of 35 estimates of heritabilities for RFI across 7 species was reported 0.25 ± 0.02 (Pitchford, 2004). However, due to a lack of reports in dairy cattle, association between the efficiency with reproduction, activity, organs, body composition, metabolites, and health were reviewed across species in this section (Table 2.1). The association among production and conformation traits in dairy cattle and possibility of shortening test period in the literature were also reviewed.

3.2.3.1. ***Reproduction***

Very few studies investigated the association between feed efficiency and reproductive performance in dairy cattle (Berry and Crowley, 2013). However, it has been shown that the genetic trend of average daughter fertility in Canadian Holsteins cows had a 2% reduction per year over 14 years, from 101.9 in 1995 to 99.9 in 2009 (Van Doormaal, 2010); while, the milk production and energy efficiency substantially increased during those years. Although the association between energy efficiency and reproductive performance has not been well-documented in dairy cattle, there are some reports to support that the animals' reproductive performance is mostly affected by their energy balance status at their early lactation. For instance, it has been shown that the time of first estrus is closely related to negative energy balance during the first 2 - 3 weeks after calving (Coffey et al., 2006) and "cows appear to resume their reproductive activity only after the nadir point of the negative energy balance has passed" (Veerkamp, 1998). Overall, any gain in feed efficiency could be diminished due to the reduced fertility in dairy cows. Therefore, association between feed efficiency and reproductive performance merits future investigation (Berry and Crowley, 2013).

Some researchers studied the indirect effects of selection for energy efficiency on reproduction traits in beef cattle. For example, Shaffer et al. (2010) allocated the beef heifers into three groups based on their feed efficiency performance (low, medium and high RFI) and studied the indirect effects of selection for efficiency on reproduction performance. They reported a negative relationship between RFI and age at puberty. The efficient animals reached their puberty later than inefficient animals, but it did not affect their pregnancy or conception rates. This research team also quantified this negative relationship and reported that each unit increase in RFI corresponds to a decrease of 7.5 days in age at puberty (Shaffer et al., 2010). In another study, the effect of RFI on bull's reproductive performance and fertility has been also studied (Wang et al., 2012). A total of 20 high RFI (inefficient) and 22 low RFI (efficient) beef bulls in a multi-sire breeding system in pasture were considered in the study, and the association between RFI with semen quality traits (density, progressive motility, and morphology) and some other reproductive traits were examined. They concluded that there was no evidence that selection for RFI has a negative effect on reproductive performance and fertility of bulls bred in multi-sire groups in pasture (Wang et al., 2012).

The effects of selection for energy efficiency on reproductive performance have been studied over generations in other species due to their shorter generation intervals. For example, Nielsen et al. (1997) divergently selected mice for energy efficiency based on their heat loss over 15 generations. They categorized the mice into control, high, and low efficient groups. Then, indirect effects of selection for energy efficiency on reproduction performance (litter size, ovulation rate, number of foetuses at 7 days of gestation, and ovulation success) of mice were measured. The results showed that the high efficient line (low heat loss) had 20% smaller litter size at the first parity in the 15^{th} generation and 23% lower ovulation rate in the second parity at the 12^{th} generation compared to the inefficient group. However, the high efficient line on average had a higher ovulation success rate (86%) than the low efficient line (84%), but the differences were not significant (Nielsen et al., 1997). A report on the reproductive performance of pigs demonstrated that efficient animals also had a lower litter size compared to the control group (Estany et al., 2002). However, Morisson et al., (1997) divergently selected hens for RFI over 18 generations and studied the effects of selection for energy efficiency on reproduction and sperm characteristics. Contrary to the mice and pigs reports, the efficient hen line had a better hatchability performance (Morrisson et al., 1997), which is also supported by other researchers who selected hens for low RFI without reducing the egg production (Bordas et al., 1992). They found that a high efficient line of hens had only 6% unfertilised eggs compared with 30% in a low efficient line, and early mortality rate in the efficient line was half of than in the inefficient line. Overall, it could be inferred that in some species litter size is sacrificed to maintain energy and take better care of the remaining fetus.

3.2.3.2. Feeding Behavior and Activity

It has been shown that the animals in different energy efficiency groups have various feeding behaviours; therefore, these traits are most likely affected by selection for energy efficiency. Connor et al., (2013) have recently reported that meal size and feeding rates are significantly different among the efficient groups in dairy cattle. However, the group effect on pedometer reading, meal duration, and time spent feeding per day were not significant (Connor et al., 2013). In feedlot steers, Durunna et al., (2011) conducted a three-year study on 402 and 419 animals in the grower and finisher diets, respectively. They measured feed intake, feeding duration, head-down time, and bunk visits using the Growsafe system. Their results showed that the efficient steers (Low RFI) exhibited less feeding duration, head down time, and bunk visits among which the less feeding duration of efficient animals was supported by other researchers in finishing heifers (Kelly et al., 2010), beef cattle (Nkrumah et al., 2006), and boars (Von Felde et al., 1996). Contrary to the Durunna et al. (2011) report, a higher feeding frequency was reported by Nkrumah et al. (2006) in efficient beef cattle.

The effect of selection for RFI on activity has been investigated in mice (Hastings et al., 1997; Rauw et al., 2000), hens (Luiting and Urff, 1991), and pigs (Von Felde et al., 1996). Hastings et al. (1997) found that high efficient (low RFI) mice are 67% less active than the low efficient ones. Furthermore, Rauw et al. (2000) reported that high efficient (low RFI) mice run slower in the two types of runaway tests than the control group. Overall, Herd and Arthur (2009) concluded that the positive and high genetic correlation of RFI with feeding time and eating sessions per day indicates that feeding behaviour and RFI are controlled by some common genes. Thus, the feeding behaviour and activity traits could be potential indicator traits of energy efficiency, and their associations are worth examining.

3.2.3.3. Organs and Body Composition

There is a lack of report, based on our knowledge, on the association between energy efficiency and organs weight in dairy cattle. However, controversial results have been reported on these associations in different species. Overall, in a literature review by Pitchford. (2004), it is concluded that selection for energy efficiency may results in lower proportions of liver and visceral tissues (Pitchford, 2004). In female mice, the results are contradicted with the conclusion made by Pitchford, (2004), and it was reported that the efficient mice (low RFI) have larger livers, caeca, intestines, and stomachs but smaller hearts (Hughes and Pitchford, 2004). In divergently selected cattle for RFI, it has been reported that the weight of gastrointestinal organs and internal organs are not significantly different between efficient and inefficient groups (Richardson et al., 2001).

It is documented that body composition accounts for 5% of RFI variation among the animals. Richardson et al. (2001) have divergently selected steers for RFI, and they showed that animals with low RFI have more whole-body chemical protein and less whole-body chemical fat (Richardson at al., 2001). Basarab et al. (2003) also found that high efficient steers had more empty body water, but less empty body fat than those in low efficient steers. They also reported that the divergently selected steers have almost the same amount of empty body protein (Basarab et al., 2003). In another study, Shaffer et al. (2010) grouped the beef heifers of British breeds into the low, medium, and high RFI groups, and they found that efficient heifers (low RFI) have less lean meat area (cm^2) per 100 kg of BW than inefficient (high RFI) heifers. Finally, Herd and Arthur (2009) concluded that the amount and direction of association between body composition and variation in energy efficiency in cattle depends on age and the stage of maturity. Moreover, Richardson et al. (2001) concluded that variation in ME intake and energy efficiency is due to metabolic processes rather than changes in body composition.

3.2.3.4. Metabolites and Health

Some metabolites such as IGFT-I and blood concentration of urea are the indicators of the animals' production and health. Many researchers examined the associations between these metabolites and energy efficiency either to use them as an indicator of energy efficiency or to determine the indirect effects of selection for energy efficiency on animals' health status. For example, high concentrations of total plasma protein, blood concentrations of urea, and aspartate amino transfer were reported in high RFI cattle (inefficient) compared with low RFI cattle (efficient). These metabolites are indices of the protein turnover, and it was reported that the inefficient cows have higher protein turnover rates compared with the low efficient cows (Herd and Arthur, 2009). In a research focused on the effect of selection for energy efficiency on animals' heath reported that high RFI steers have higher levels of Cortisol, and red and white blood cells. It was concluded that these animals (inefficient) may be more susceptible to stress (Richardson et al., 2004). In another report, a positive correlation between IGF-I, which is a growth metabolite, and RFI was reported in beef cattle (Moore et al., 2005). However, separation of RFI into post weaning and feedlot periods determined that there is a positive correlation of IGF-I with RFI during the post weaning time while this correlation is negative during the feedlot period (Herd and Arthur, 2009). Finally, it was documented that in divergently selected Angus steers for RFI, metabolism including turn over and stress accounts for 37% of the variation in RFI (Herd and Arthur, 2009), and Kelly et al. (2010) concluded that some plasma analytes such as B-hydroxybutyrate may be potential indicators of net energy efficiency in beef cattle.

A few studies focused on the association between energy efficiency and health traits in dairy cattle. If the animals are not healthy enough, all improved energy efficiency and production gains would be ruined. Rauw et al. (1998) reviewed undesirable effects of selection for high efficiency in farm animals and concluded that the selection has a negative correlation with the health traits. In another research, Wassmuth et al. (2000) investigated the relationship between efficiency and diseases in dairy cattle. They used feed intake data of 7752 young dairy bulls (2203 Danish Red, 4527 Danish Friesian and 1022 Danish Jersey), and combined the feed intake data with recorded incidence of mastitis, retained placenta, metritis, sole of ulcer, and ketosis data of 473,613 dairy cows in their early lactation. Then, they defined efficiency as "the feed energy intake per kilogram live weight gain" in bulls. Overall it has been reported that, energy efficiency was positively (unfavourably) correlated with incidence of diseases. Finally, an urgent research on association between energy efficiency and health related traits has recently been recommended (Berry and Crowley, 2013).

3.2.3.5. Conformation Traits

Conformation traits are scored from one biological extreme to another using a linear scale of 1 to 9 points in dairy cattle. Each animal is assessed for twenty-four traits usually in the first lactation, and combinations of these traits are used to derive five major traits (CDN, 2000). In Canada, these traits are routinely collected by breed associations, and this information is provided to Canadian Dairy Network (CDN) for genetic evaluation (CDN, 2000). One of the main goals of the linear classification program is to identify and emphasize traits associated with longevity (Short and Lawlor, 1992). Consequently, strong genetic and phenotypic correlations among longevity traits (length of productive life) and some of the conformation traits such as the mammary system (Morek-Kopec and Zarnecki 2012) and loin strength (Dadpasand et al., 2008) have been reported. However, other studies determined correlations among these traits with many other traits including body weight, production, and feed intake to use the conformation traits as indictor for other traits. High and significant ($P < 0.01$) genetic correlations were reported between body weight and stature (0.51 to

0.82), chest width (0.75 to 0.86), body depth (0.59 to 0.81), and rump width (0.56 to 0.74) (Verkamp and Brotherstone 1997; Banos and Coffey, 2012). Therefore, equations with R-squares greater than 0.75 were developed to predict the animals' live weights from their routinely recorded conformation traits (Coffey et al., 2003; Banos and Coffey, 2012). Moreover, dry-matter intake had the moderate genetic correlation with chest width (0.25 to 0.28) and body depth (0.20 to 0.34) (Veerkamp and Brotherstone 1997). It was also suggested that the traits that were highly correlated with body weigh could be used as indicators to predict animals' feed requirements for maintenance (Veerkamp et al., 2013). Therefore, some of the conformation traits are related to body weight and production could be potential indicator traits of energy efficiency, and their associations are worth examining.

2.2.4. Reducing the RFI Test Periods

Feed efficiency traits including RFI may be defined throughout an animal's entire lifetime or at a particular stage of life, but difficulty and costs of feed intake measurements are still the main obstacles to feed efficiency research in dairy cattle. Reducing test period without compromising data accuracy and reliability would greatly help the industry to decrease test duration and, consequently, test costs (Wang et al., 2006). However, an accurate estimation of feed efficiency requires the minimum period of feed intake and production traits measurements (Berry and Crowley 2013). There are some reports that examined the possibility of reducing RFI test period in dairy cattle (Lopez-Villalobos et al., 2008; Prendiville et al., 2009; Connor et al., 2012). They conclude that RFI estimation after 100 DIM may provide a reliable estimate of animal feed efficiency over the whole lactation period (Connor et al., 2012). The available reports (Lopez-Villalobos et al., 2008; Prendiville et al., 2009) had very limited numbers of actual feed intake measurements (maximum of five observations over lactation) and none of the reports have investigated the genetic correlation among RFIs and its component traits. Therefore, further investigation is required into the possibility of reducing the RFI test duration by examining genetic correlations among different periods for RFI and its component traits.

2.3. THE RANDOM REGRESSION TECHNIQUE AND ITS APPLICATION IN ANIMAL SCIENCE

The traits that are measured sequentially over time are called repeated measurements, which researchers are particularly interested in studying the changes of these traits over time (Van der Werf, 2001). These traits are traditionally analyzed by repeatability and multivariate models. The traditional models are not capable of considering the continuous nature of these traits and studying the traits over the trajectory. However, the random regression model (RRM) is a useful technique to analyze repeated measurement traits and to define their correlation structure over time. RRM constructs a (co)variance structure which relies on the time difference between measurements, and this (co)variance structure could be defined based on different regression models such as Legendre polynomial. In this part, the source of variations of repeated measurement traits, traditionally used models to analyze these traits, and RRM have been reviewed to provide a general idea about the statistical part of the thesis.

2.3.1. Feature of Repeated Measurements

Repeated measurement traits (Van der Werf, 2001) or longitudinal traits (Schaeffer, 2002) are measured serially on each experimental unit. The common example of these traits is an animal’s body weight at different months of age. The assumptions of homogeneity of error variance and their independency are not applicable to the repeated measurement analysis (Wang and Goonewardene, 2004). Therefore, these traits should be analyzed under a specific form of (co)variance pattern (Van der Werf, 2001; Wang and Goonewardene, 2004). Moreover, it is recommended that precise inferences from this kind of data are considerably dependent upon the modelling of their (co)variance structure (Van der Werf, 2001).

To better understand and also manipulate the changes of longitudinal traits along a trajectory of time, some researchers are interested to model their profiles over time (Van der Werf, 2001). Typical examples of trait changes along the trajectory are the body weight and the milk production curves.

2.3.2. Source of Variations of Repeated Measurements

General formula for variation of observations within an experimental unit has been suggested by Diggle et al. (1994) as: $Var(\varepsilon) = \nu^2 J + \sigma^2 H + \tau^2 I$. Where ν^2, σ^2, and τ^2 are the variance components of an experimental unit, serial correlation, and measurement error, respectively; In the animal breeding concept, an experimental unit variance (ν^2) could be considered as an animal effect or more specifically, as an additive genetic effect of the animal (Van der Werf, 2001); J is a matrix with all elements equal to one, which it means that the animal additive genetic effect is the same on a trait along the trajectory. Serial correlation (σ^2) is associated with the record time of the trait, and H is a specified matrix by a correlation function; indeed, measurements in different days of the records are not independent, and the correlation between two records taken closely in time is stronger than two records that are far away in time (Wang and Goonewardene, 2004). This correlation structure is specified by a correlation function in the H matrix. Finally, I is an identity matrix, referring to the measurement error (τ^2), which is an independent random error term for each observation (Van der Werf, 2001).

2.3.3. Repeatability and Multivariate Model

Traditionally, repeatability and multivariate models have been used to analyze the repeated measurements. The main difference between repeatability and multivariate models is how to construct the (co)variance structure. The repeatability model considers the same additive genetic effect for different records. It is mostly applied to analyse the lactation records in dairy cattle and considers the unity of correlation between records across the lactations. As the correlation between different times can be varied, use of ‘repeatability model’ relies highly on the validity of the unity assumption.

In a multivariate model, each record at different ages is considered a trait; for instance, the growth changes over time have been defined as birth weight and weaning weight (Van der Werf, 2001; Morde, 2005; Speidel et al., 2010). This model demonstrates that the traits are correlated, and the correlation quantities are different between them. Hence, different co(variance) structures, such as autoregressive structure (**AR (1)**), ante-dependence structure (**ANTE**), and unstructured (**UN**) covariance have been proposed for multivariate analysis. Discussion on the details of these co(variance) structures is beyond the scope of this review. However, UN covariance can cover unequal variance over time and also unequal covariance for any pairs of observations, and the other co(variance) structures are the simplified forms of the UN covariance structure.

Animal’s age can be defined in months, days, hours, and even seconds. Therefore, the trait of interest can take a value for each defined time and have a continuous form (Schaeffer, 2002). The repeatability and multivariate models are not suitable for analysing the longitudinal traits due to two main reasons: first of all, these models recognize the longitudinal traits in discontinued form (i.e. year or month) in spite of their continuous nature. Second, these models need more information in the same time period, which is more tedious (Van der Werf, 2001). Therefore, a continuous and flexible correlation structure which relies on the time difference between measurements should be considered to analyse the longitudinal traits. Random regression model accounts for the continuous nature of the traits and is a flexible model in which regression coefficients are different among the animals (Van der Werf, 2001).

2.3.4. Random Regression Model

In a random regression model, the mean of population and each source of variation (animal effect, time effect, and measurement error) could be modelled under different covariance functions (Schaeffer, 2004). The covariance function (**CF**) relies on the time difference and allows the covariance structure to change over time. Also, the variance and covariance of any point in the trajectory can be predicted by CF (Van der Werf, 2001). The covariance structure of the source of variation can be either very complex but typically more simple than the phenotypic trajectory of the mean (Schaeffer, 2004). The basic structure of RRM is the same in most applications, and a simplified RRM for a single trait can be written as (Schaeffer, 2002; 2004):

$Y_{ijknt} = F_i + g(t)_i + r(a,x,m_1)_k + r(pe,x,m_2)_k + e_{ijknt}$, Where Y_{ijknt} is the n^{th} observation on the k^{th} animal at time t; this observation belongs to the i^{th} fixed factor and j^{th} group; F_i is the fixed effects which are independent of time (e.g. herd effects); $g(t)_i$ is a function(s) which accounts for the phenotypic trajectory of the average observations across all animals. This function(s) can be either linear or non-linear, and sometimes is referred to as fixed regression coefficients

(Mrode, 2005); $r(a, x, m_1)_k = \sum_{l=0}^{m_1} a_{kl} x_{ijk:l}$ represents the random regression function in which a is an additive genetic effect of k^{th} animal; x is the vector of time covariates, and m_1 is the order of regression function. Thus, $x_{ijk:l}$ and a_{kl} are the covariables that are related to time t, and the animal additive genetic regression coefficients to be estimated, respectively. $r(pe, x, m_2)_k = \sum_{l=0}^{m_2} pe_{kl} x_{ijk:l}$ is a similar random regression function for the permanent environment (**PE**) effects of k^{th} animal. $e_{ijkn:t}$ is a random residual effect with mean zero and variance ($I\sigma_e^2$). Daily record or the function of t may have different error variance structure $var(e) = dig\{\sigma_{et}^2\}$ (Jamrozik et al., 2008) which introduced earlier in multivariate model section (Section, 2.3.3 in chapter 2) or may be defined by regression function (Schaeffer, 2004). Application of RRM for test day records, growth traits, survival analysis, fertility, and genotype by environment interaction has been well discussed by Schaeffer (2004).

2.3.5. Legendre Polynomial Regression

Several regression functions such as polynomials are used to model each source of the variation for each animal around the average curve (Coffey et al., 2001). Legendre polynomial (LP) is parametric regression model and commonly used (Schaeffer, 2004) compared to non-parametric regression functions such as cubic splines (CS), sinusoidal (SF), and Bessel functions (BF) (Banos et al., 2005). LP has been mostly used by researchers in animal science without any assumptions about the shape of the curve (Mrode, 2005); whereas, applications of other models are in their nascent stages. A polynomial function is a mathematical expression constructed from one or more variables and constants. The operations of addition, subtraction, multiplication, and constant positive whole number exponents have been used for construction; order of polynomial is the largest value of exponent. LP is a version of polynomials that have properties such as good convergence, orthogonal polynomials, and easy to manipulate (Coffey et al., 2004); in addition orthogonal polynomials can provide less correlation between coefficients than ordinary polynomial (Coffey et al, 2004). Numerical examples of CF definition with Legendre polynomial are provided by several researchers (Kirkpatrick et al., 1994; Van der Werf, 2001; Schaeffer, 2002). Although researchers usually decide the order of fit for a trait under LP modelling, the suitable order of fit can be obtained by some statistical criteria such as goodness of fit test, Bayesian information criterion (BIC), log likelihood ratio test (LRT), and mean square of error (Tedeschi, 2006). Although LP is mostly used with RRM as a basic function and makes it possible to model a variety of curves, some undesirable properties related to its capabilities are reported. The main problem of modelling RRM with LP is that genetic variances are much higher at the beginning and end point of the trajectory than the middle point (Schaeffer and Jamrozik, 2008). This can be due to the fact that genetic variances are calculated based on estimated covariance matrices (Schaeffer and Jamrozik, 2008) and may be due to more emphasis on observations at extremes by polynomial models (Meyer, 2005b). Other problems of LP are poor modelling capabilities at the extremes of trajectory (Misztal, 2006) and difficulties in fitting the data in the period with a few observations (Misztal et al., 2000; Nobre et al., 2003; Meyer 2005a; Coffey et al., 2001). Moreover, convergence in higher order may be problematic with large data sets (Robbins et al., 2005).

2.3.6. Literary Evidences of RRM in Animal Science

Application of RRM in animal breeding has been comprehensively reviewed by Schaeffer (2004). Some of the traits analysed using RRM techniques (Table 2.2) include body condition score and feed intake in dairy cattle (Coffey et al., 2002; Banos et al., 2005), weight and back fat thickness in swine and beef cattle (Schaeffer, 2004), conformation traits in dairy cattle (Karacören et al., 2006), milk yield in buffalo (Sesanal et al., 2007), egg production in layer hens (Wolc and Szwaczkowski, 2009), somatic cell and milk yield relationship in Canadian Holstein (Jamrozik et al., 2010), and growth curve in sheep (Sarmento et al., 2011). Most of these projects were conducted to find a suitable order of fit or regression approach, the results of which are summarized in Table 2.2.

2.4. CONCLUDING REMARKS

It could be concluded that there is an optimum point for each of the factors (DMI, milk production, body weight, AFC and environment factors) that influence energy efficiency. Hence, increasing output traits does not necessarily increase net energy efficiency. Therefore, other measures of energy efficiency which are independent from maintenance and production requirements such as RFI should be considered to improve the energy efficiency in dairy cattle. Genetic improvement on energy efficiency can be achieved through selection for RFI in dairy industry, since the heritability estimations for RFI are moderate for most of the species. However, further research is required to accurately define RFI in dairy cattle and to determine the indirect effects of selection for energy efficiency, which may exert on other related traits. It has been also shown that conformation traits could be used as indicator traits for production traits such as BW. Therefore further studies need to investigate the possibility of applying these traits as indicator traits for RFI. Finally, reducing feed efficiency test period in a way that estimated efficiency measure from shorten test be representative of whole location life is of interest.

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Table 2.1. Summary of indirect response of selection for energy efficiency on related traits in different specie

Species	Reproduction	Activities	Organs	Chemical composition	Metabolites	Health
Dairy	Decrease daughter fertility	Data not available.	Data not available.	Data not available.	Data not available.	Increases the incidence of metabolic diseases (Wassmuth et al., 2000)
Beef	Decreases age at puberty, does not affect pregnancy rate (Shaffer et al., 2010). Did not affect bull performance (Wang et al., 2012).	Less feeding duration and less head-down time, (Durunna et al., 2011; Nkrumah et al., 2006; Kelly et al., 2010).	Did not affect tissues of gastro intestinal organs and internal organs (Richardson et al., 2001).	Less body fat (Richardson et al., 2001) more empty body water (Basarb et al., 2003).	Low plasma protein, blood concentration of urea and aspartate amino transfer (Herd and Arthur, 2009) high insulin, glucose and NEFA (Kelly et al., 2010).	Data not available.
Pig	Decreased litter size (Estany et al., 2002)	Less feeding time, less visits per day, less total time in feeder (Von Felde et al., 1996)				
Mice	Decreased litter size, ovulation rate (Nielsen et al., 1997)	Less activities (Hastings et al., 1997; Rau et al., 2000)	Larger livers, caeca, stomachs but smaller hearts (Hughes and Pitchford, 2004)	Fatter (Hughes and Pitchford, 2004)		Data not available.
Chicken	Increased fertility, hatchability, decreased mortality (Morrisson et al., 1997). No losses in egg production (Bordas et al.,1992)	Less activities (Luiting and Urff., 1991)		Controversial results, increase or decrease fat traits (Liting and Urff, 1991)		

Table 2.2 Summary of the studies which applied random regression technique

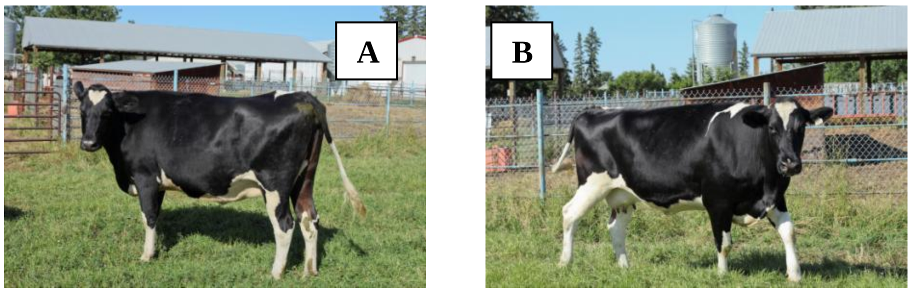
Research team	Trait	Species	Regression function	Order tested	Applied statistical criteria	Conclusion
Coffey et al., 2001	Energy balance	Dairy cattle	LP	1 to 10	AIC ,BIC, LRT, MSE	LP with minimum order of 5
			BS	1 to 10		
			CS	5 to 30 knot		
Liu et al., 2006	Milk yield	Dairy cattle	LP	3 to 8	AIC ,BIC, LRT, MSE	Fifth order for additive effects
Sesana et al., 2007	Milk yield	Dairy buffalo	LP		AIC, BIC	Third order
Wolc and Szwaczkowski, 2009	egg production	Layer hens	LP	1 to 8	AIC	Third order
Sarmento et al., 2011	growth curve	Sheep	LP	2 to 8	RMS, R-square	Third order

LP: Legendre polynomial; CS: Cubic spline; BF: Bessel function;

AIC: Akaike information criteria; BIC: Bayesian information criteria;

LRT: log likelihood ratio; RMS: Residual mean square

Figure 2.1. Schematic concept of residual feed intake (RFI). Two animals which have the same BW and same level of production, are expected to consume the same amount of feed but in reality cow A consumes more than expected while cow B consumes less, so cow B is more efficient than A.



BW = 550 kg, same level of production
Expected feed intake = 19.0 kg/day
Actual feed intake= 20.0 kg/day
RFI= 20 - 19= +1.0 kg/d
Inefficient cow

BW = 550 kg, same level of production
Expected feed intake = 19.0 kg/day
Actual feed intake= 18.0 kg/day
RFI= 18 – 19 = - 1.0 kg/d
Efficient cow

Figure 2.2. Energy transformation processes from gross energy (GE) to net energy (NE). The portion of lost energy in different steps is dependent on DMI level.

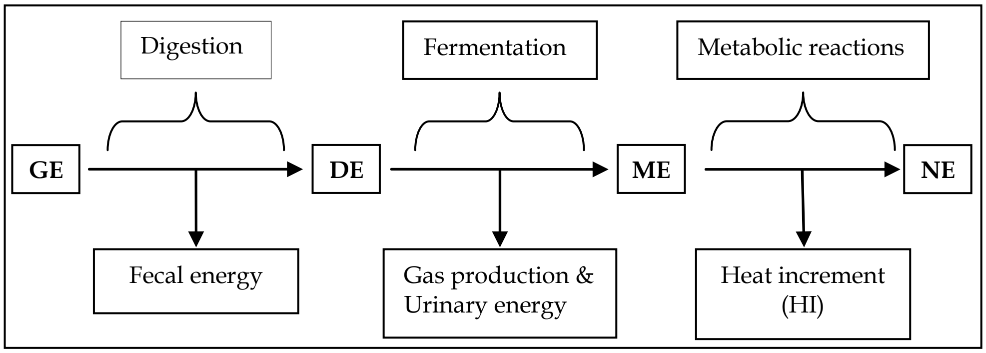
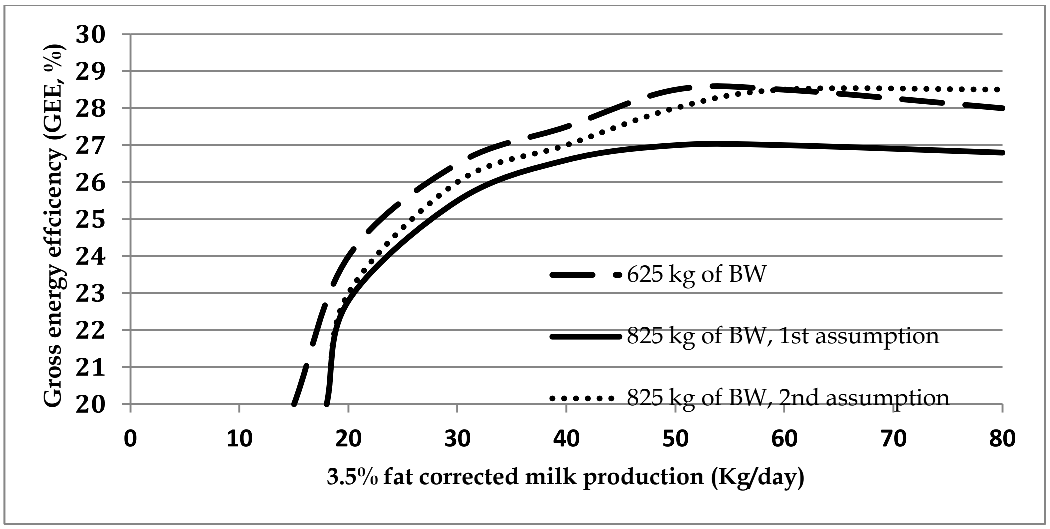


Figure 2.3. Relationship between body weight and gross energy efficiency under two assumptions. The two possible relationships between digestive capacity and BW were discussed. In the first one, digestive capacity was not a function of BW (compare dashed and solid curves) while in the second one the digestive capacity was a function of BW (compare dashed and dot-dashed curves). Adapted from Vandehaar, 1998).



CHAPTER 3. PREDICTION OF RESIDUAL FEED INTAKE FOR FIRST LACTATION DAIRY COWS USING ORTHOGONAL POLYNOMIAL RANDOM REGRESSION[2]

3.1. INTRODUCTION

Feed cost is the single largest expense of dairy production (Vallimont et al., 2011) and has increased substantially over the last few years (Garcia, 2009). Although it is a crucial factor in the profitability of the dairy industry, little attention has been paid to improving feed efficiency through direct selection (Linn, 2006; Zamani et al., 2008). This is mainly due to the difficulties and costs associated with individual feed intake measurements (Kelly et al., 2010). In addition, feed conversion ratio (**FCR**) and gross energy efficiency (**GEE**), which are the most common measures of feed utilization efficiency, have two main problems. FCR is the ratio of input (e.g. feed) to output (e.g. weight gain or milk production) (Crews, 2005). In the dairy industry, GEE is defined as the energy in milk divided by the total energy intake (Veerkamp and Emmans, 1995). Firstly, the energy intake by different animals has different partial efficiencies for maintenance, lactation, and body tissue gain or loss, but FCR and GEE do not distinguish between them (Veerkamp and Emmans, 1995). Secondly, these measures are well known to be phenotypically and genetically correlated with measures of growth, production, and mature size (Crews, 2005). Thus, selection for improvement of FCR and GEE would result in increased growth rate, mature

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size, and consequently increase maintenance requirements (Crews, 2005) in an unbalanced breeding goal. To overcome the aforementioned problems of efficiency measures, an alternative measure of energy efficiency, RFI, has been described. RFI is the difference between an animal's actual energy intake (AEI) and its expected energy intake (**EEI**) based on animal's maintenance requirements and production level and is phenotypically independent of production traits (Koch et al., 1963); an alternative definition of RFI is feed intake adjusted for body size and production level (milk, protein and fat yield and changes in body fat composition). The efficient animals, which have low RFI values, consume less feed without compromising the production level.

Meat producing animals use energy mainly for maintenance and daily weight gain during the growth period. The relationship between energy intake and production is linear in the testing period of meat producing animals (Archer et al., 1999; Basarab et al., 2003; Crowley et al., 2011). As a result, the evaluation methods of individual RFI for meat producing animals during their growth period, has been well studied in beef cattle, swine, and poultry using linear regression models (Archer et al., 1999; Crews, 2005). Unlike the meat producing animals, dairy cows have multi-functional energy requirements for maintenance, growth, pregnancy, and lactation; furthermore, it is established that energy intake and energy expenditures have non-linear profiles during the lactation period in dairy cattle while their individual profiles are different among animals (Coffey et al., 2001; Bewley et al., 2008). Several studies have been conducted to predict RFI in early or whole of the first lactation in dairy cows in the literature, but they used a linear regression model (Van Arendonk et al., 1991; Svendsen et al., 1993; Zamani et al., 2008), utilized limited records of individual AEI (Van Arendonk et al., 1991; Coleman et al., 2010), or used a standard table of estimated requirement values such as NRC (Svendsen et al., 1993; Zamani et al., 2008). The RFI obtained from these studies may not be very accurate, and worthy of further investigation (Zamani et al., 2008). In addition, based on our awareness, no previous research has used the daily actual measured feed intake data, and they collected feed intake data either weekly or monthly in their studies; therefore, their feed intake data collection methods might be insensitive to capture the differences among animals (Vallimont et al., 2011). Moreover, most of the previous studies have not considered the nonlinear profiles of the component (MBW, EBW, and MPER) traits during the lactation period. The objective of this research was to develop a modeling equation to predict RFI in the first lactation dairy cow while accounting for its multifunctional energy requirements and considering the non-linear lactation profiles of the component traits using an orthogonal polynomial random regression technique.

3.2. MATERIAL AND METHODS

3.2.1. Data Acquisition

Daily individual feed intake, monthly body weight, milk production and milk composition of 281 first lactation (1 - 305 DIM) dairy cows from June 2007 to October 2012, were used in the analysis. These animals were housed in a tie-stall system at the Dairy Research and Technology Center (**DRTC**) of the University of Alberta, Edmonton, Alberta, Canada. The animals received one of the three (high, mid, or low energy dense ration) total mixed rations (**TMR**) according to their milk production level. Individual offered feed weight in the morning and refusal feed weight left in the next morning were recorded daily. Offered feed was adjusted weekly in order to keep the individual refusal feed around 10% of the total feed offered. Feed compositions including moisture (%), crude protein (%), and neutral detergent fibre (%) were determined when the TMR ingredients changed, while dietary dry matter (%) was measured monthly. Average dry matter (%) of high, mid and low energy dense TMR over a 5 year study were 52.12, 51.02 and 48.87 respectively, and their net energy density (Mcal/kg dry matter) were 1.85, 1.72, and 1.65, respectively. The individual milk yield and composition data were retrieved from the official Dairy Herd Improvement (**DHI**) Program, which records milk yield and composition once in every 25 to 36 days after calving, but no earlier than 5 DIM. Therefore, milk yield and composition data was available from 5 to 305 DIM. In addition, repeated measurements of individual body weight (**BW**) and body condition scores (**BCS**) of these heifers were measured at their calving and subsequently on their DHI milk sampling days during their lactation. BCS was assessed on a 1 to 5 scale with 0.25 intervals (Edmonson et al., 1989; NRC, 2001) by the same technician over the study period. All procedures of the study were reviewed and approved by the University of Alberta Animal Care & Use Committee.

3.2.2. Data Editing and Traits Derivations

Twenty cows were dropped from the analysis as they had less than four repeated milk yield and composition records, and 25 animals disqualified from the dataset as they had lower than 265 AEI observations over 301-DIM. Two cows also were excluded from the data due to late age at first calving (972 and 1175 days). In addition, 12, 48 and 487 records were removed from the body weight, milk yield, and feed intake data, respectively, because they did not fall within three standard deviations from the population mean on the test day. The remaining 1837, 1766, and 67561 repeated records of body weight, milk yield, and feed intake data, respectively, from 234 cows were used in the analysis.

The daily AEI, MBW, MPER, and EBW for each animal, were derived from the recorded raw data using the following equations:

1) Individual daily actual energy intake (AEI): $AEI(Mcal/day) = DMI \times ED,$

   where DMI (kg/day) is an individual daily dry matter intake and ED (Mcal/kg) is the net energy density of the diet.

   DMI was calculated as: *DMI = ((Offered feed (kg) – Refused (kg)) × DM %*, where DM is the dietary dry matter.

2) Metabolic boy weight (MBW) was defined as (NRC, 2001):

   $MBW\ (kg) = BW^{0.75}(kg),$

where BW is body weight (kg) of the animal. The analysis of BW records between 5 to 305 DIM were not adjusted for fetus growth weight because the energy requirements of fetus growth is negligible in this period of pregnancy (NRC, 2001).

3) MPER was considered as the energy contained in the milk produced, and it is equivalent to sum of the heat of combustion of milk fat, protein and lactose. Heat combustion of milk fat, protein and lactose are reported 9.29, 5.71, and 3.95 Mcal/kg, respectively. Milk lactose content is less variable and is essentially a constant of 4.85 percent of milk (NRC, 2001). Since the DHI program does not record lactose, the MPER was calculated based on fat and protein content (NRC, 2001) and constant value of lactose (4.85% × 3.95) as:

$$MPER\ (Mcal/day) = [(0.0929 \times Fat\%) + (0.0547\ \times Crude\ Protein\ \%) + 0.192] \times Milk\ Yeild\ .$$

4) Changes in BW of dairy cows could be confounded with many factors including water and gastrointestinal content (Bewley et al., 2008), so it may not reflect true changes of tissue energy due to gut fill (NRC, 2001). Therefore, EBW was an adjusted BW for gut fill that could be representative of true changes in body tissue weight (NRC, 2001). EBW on average was considered to be 85% of live BW in dairy (NRC, 2001); however, in this study EBW was calculated using the equations provided by Coffey et al. (2001) to account for individual gut fill at the test day, which was a function

of DMI and the energy content of the diet that each animal consumed at the test day as: $EBW\ (kg) = BW - GF$,

$GF\ (kg) = DMI\ \times (11 - 7(\times MED/15))$,

where MED was the metabolizable energy density (Mcal/kg) of the diet and GF (kg) was gut fill. Descriptive statistics of both measured and derived traits were given in Table 3.1.

3.2.3. Statistical Modeling

The prediction equation of individual lactation RFI was developed in two steps: Firstly, we modeled the daily non-linear profiles of MBW, MPER, and EBW from their respective monthly measurements using the Orthogonal Polynomial Random Regression Model (**RRM**). Secondly, we modeled the lactation multifunctional energy requirements of dairy cows using a multiple linear regression.

3.2.3.1. RRM Development for Individual MBW, MPER, and EBW

RRM is a useful technique to model the longitudinal data for each animal, and each animal could have a predicted daily value for the trait under modeling (Coffey et al., 2001). RRM can be modeled with different regression approaches, and the Legendre polynomial random regression model was used in this study as: $y_{it} = F_{it} + \sum_{m=0}^{k1} \beta_m\, P_m(t) + \sum_{m=0}^{k2} \lambda_{im}\, P_m(t) + \varepsilon_{it}$, where y_{it} was a derived trait (MBW, EBW, and MPER) for animal i on day t, F_{it} represents fixed effects of the population which are independent of time and are used to define contemporary groups. The fixed effects were combined month and year of measurement with ration type (MYR) of 238 levels, which the animal received between two consecutive records; the temperature and humidity index (**THI**) at each test month with a total of 65 levels; and the covariate of animal's age at first calving deviation from the population mean (linear and quadratic). $\beta_m$was the fixed regression coefficients for a particular contemporary group, λ_{im} represented random regression coefficients associated with the animal's additive genetic effects plus its permanent environmental effects, $P_m(t)$ is the m^{th} Legendre polynomial evaluated at a time *(t)*, the parameters *K1* and *K2* were the order of fitted fixed (1-5) and random (1-5) polynomials regression respectively, and $\varepsilon_{it}$was the residual error associated with time *t*. In this study, 25 models originated from the combinations of different five possible orders (1-5) of fixed (**F**) and random (**R**) Legendre polynomial regression were fitted to model the non-linear lactation profiles MBW, EBW, and MPER. These models were denoted as $F_{k1}R_{k2,}$ where k1 and k2 were the order of the fitted fixed and random regression variables, respectively. For example, F_5R_5 was a model with both fixed and random variables with order of five. A prediction equation out of the 25 fitted models was selected as the best prediction equation for each trait based on log likelihood ratio test (**LRT**) and Bayesian information criterion (**BIC**) (Tedeschi, 2006). LRT is a statistical test used to compare the fit of two models, one of which (reduced model) is a special case of the other (full model).

BIC is a criterion for model selection among a finite set of models; it is based on likelihood function and considers a penalty term for the number of parameters in the model by which a model with smaller value is better. In this study, model with both fifth fixed and random order, F_5R_5, was considered as a full model, and then the LRT value was calculated between pairs of the full model and each of the other 24 reduced models as:

$$LRT = 2\,\text{Log Likelihood of full model} - 2\,\text{Log Likelihood of reduced model}$$

The calculated LRT value between the full model and each of the reduced models was compared to a critical value to decide whether to reject the reduced model in favor of the full model. The critical values were determined based on degree of freedom (**D.F**) of change, and significance level ($P < 0.05$) from Chi square distribution. Twenty-four LRT values were calculated and compared to their corresponding critical values for each trait to find the simplified models that did not significantly differ from the F_5R_5 model. If there were more than one models not significantly different from the full model, then the best model was determined based on the BIC criterion among them and used to predict daily profiles for each animal from 5 to 305 DIM. The daily values were only predicted from 5 to 305 DIM for each trait (MBW, EBW, and MPER) because the first 4 days milk (colostrum) production records at each lactation are not included in the DHI recording program. In order to consider the body reserve changes, the differences of predicted EBW between two consecutive days were considered to be the empty body weight change (**EBWC**) between these days. The predicted daily values for each trait of each animal *i* were summed over

301-day to obtain the animal's expected first lactation value for that trait. Smoothing the daily actual feed intake data using predicted values from the developed prediction models is a way to reduce the error noise and capture the real pattern in the data. In smoothing process, daily noise presumably due to error noise is reduced, and the points that are lower or higher than the adjacent points will be increased or decreased which leads to a smooth signal. In order to smooth daily AEI data, RRM with fifth order of fixed and random effects was used to predict individual daily AEI. Then, predicted AEI from 5 to 305 DIM for each animal i were also summed to obtain the individual's 301-day AEI ($\sum_{i=5}^{305} AEI_i$) and called smoothed total AEI. All of the statistical procedures were performed using the MIXED procedure of SAS (SAS Institute, Inc. 2003).

3.2.3.2. Total Lactation EEI and RFI Prediction

A multiple linear and quadratic regression model was used to predict the total lactation individual EEI value. The smoothed total 301-day AEI was linearly regressed on total 301-day predicted traits of MBW, MPER, and EBWC to obtain the individual's 301-day lactation EEI and RFI as:

$$\sum_{i=5}^{305} AEI_i = \beta_0 + \beta_1 \sum_{i=5}^{305} MBW_i + \beta_2 \sum_{i=5}^{305} MPER_i + \beta_3 \sum_{i=5}^{305} EBWC_i + \sum_{i=5}^{305} RFI_i \,.$$

Where, β_0, β_1, β_2, and β_3 were intercept, and regression coefficient of MBW, EBWC, and MPER, respectively. The 301-day first lactation RFI for individual animal i can be obtained by subtracting the total 301-day expected energy expenditures from the smoothed total 301-day actual energy intake of the i^{th} individual as:

$$\sum_{i=5}^{305} RFI_i = \sum_{i=5}^{305} AEI_i - \sum_{i=5}^{305} EEI_i = \sum_{i=5}^{305} AEI_i - (\beta_0 + \beta_1 \sum_{i=5}^{305} MBW_i + \beta_2 \sum_{i=5}^{305} MPER_i + \beta_3 \sum_{i=5}^{305} EBWC_i).$$

The daily average lactation RFI for each individual over 301-day can be obtained by dividing the total lactation RFI by animal's days in record. The quadratic regression model had the same independent variables as described in the linear regression; just their quadratic relationship with total AEI was also examined.

3.3. RESULTS

Descriptive statistics of measured and derived traits were given in Table 3.1. Number of observations per cow for measured (BW, BCS, milk yield and compositions) and derived (MBW, EBW and MPER) traits over 301-day ranged from 4 to 11 (Table 3.1). However, the number of observations per cow for AEI was 289 on average and ranged from 265 to 301 (Table 3.1). The average of recorded daily AEI against DIM was shown in Figure 3.1; the average daily derived and predicted MPER, EBW, and MBW were shown in Figures 3.2, 3.3, and 3.4, respectively. The peak of AEI occurred around 100 DIM (Figure 3.1); while, the peak of MPER occurred around 60 DIM (Figure 3.2). Animals began to lose their body reserves to support their milk production before the peak of AEI, and the nadir point of EBW was around 60 DIM (Figure 3.3).

The LRT and BIC statistics for all models that were not significantly different from the full model by LRT test were presented in Table 3.2 for the three (MBW, EBW, and MPER) traits. The models of F_5R_3, F_5R_3, and F_5R_2 were selected to predict the individual's daily values for MBW, EBW, and MPER, respectively. Scatter plots for the average daily predicted vs. the average daily derived values of MPER, EBW, and MBW against DIM were shown in Figures 3.2, 3.3, and 3.4, respectively. It can be seen that the predicted values were matched well with its derived values for all of the three traits in their respective graphs.

The developed EEI prediction equation is given below with an R-Square of 0.68.

$$\sum_{\mathrm{i}=5}^{305} \mathrm{EEI_i} = -2518.61 + 0.22 \times \sum_{\mathrm{i}=5}^{305} \mathrm{MBW_i} + 0.84 \times \sum_{\mathrm{i}=5}^{305} \mathrm{MPER_i} - 1.51 \times \sum_{\mathrm{i}=5}^{305} \mathrm{EBWC_i}$$

and the 301-day individual lactation RFI can be predicted as:

$$\sum_{i=5}^{305} RFI_i = \sum_{i=5}^{305} AEI_i - [-2518.61 + (0.22 \times \sum_{i=5}^{305} MBW_i) + (0.84 \times \sum_{i=5}^{305} MPER_i) - (1.51 \times \sum_{i=5}^{305} EBWC_i)].$$

The mean of predicted daily average lactation RFI was 0.0 and ranged from -6.58 to 8.64 Mcal NEL/day (Figure 5). Fifty-one percent of the animals had a RFI value below the mean (efficient) and 49% of them had a RFI value above the mean (inefficient).

3.4. DISCUSSION

3.4.1. Advantages of the Developed Model

The objective of this study was to develop a prediction equation to calculate lactation RFI for dairy cows during their whole first lactation period and to account for the animals' multifunctional energy requirements. The developed prediction model also considered the non-linear lactation profiles of RFI component traits and used smoothed daily actual feed intake data during the whole lactation period. In this research, measured AEI data was smoothed to remove the error noise in RFI prediction equation. However, applying measured AEI data in RFI prediction equation provided very close results compared to the smoothed AEI data. The correlation between predicted RFI from measured AEI and smoothed AEI was 0.96. Therefore, 289 repeated measurements of AEI over 301 days may be good enough to capture the real pattern of feed intake in dairy cattle, and smoothed data may be more useful to remove error noise when less repeated data points over lactation are recorded. Several previous RFI prediction studies (Van Arendonk et al., 1991; Svendsen et al., 1993; Zamani et al., 2008;

Coleman et al., 2010; Vallimont et al., 2011) for dairy cattle in the literature were summarized in Table 3.3. Van Arendonk et al. (1991) predicted RFI in early lactation (105-DIM) using linear regression of average daily energy intake on average daily MBW, average daily fat and protein corrected milk, and average daily weight gain. In this study, we used the actual daily feed intake records from the entire lactation to develop a RFI prediction equation for the first lactation dairy cow (301-DIM) rather than early lactation (15 to 105-DIM). Furthermore, Van Arendonk et al. (1991) used the average of body weight gain over 77-day in the prediction model. Applying an average of body weight in early lactation could give a biased result, since measuring BW around the nadir point is important to ensure accurate appraisal of BW gain or loss. It is also well established that dairy animals lose their energy reserves (BW and BCS) to support milk production in early lactation and start to regain their reserves after energy intake peak occurs (Coffey et al., 2001; Bewley et al., 2008), which is also supported by the results found in the current study (Figure 3.3). For example, consider a cow that had 0.15 kg weight loss in the first 50 days in test and 0.27 kg weight gain for the rest of 27 days in test (from 50 to 77 days in test) in the study by Van Arendonk et al. (1991). The cow might have zero average body weight gain during 77-days if her nadir point occurred at the 50th day. In order to accurately consider the body reserve changes, RFI may be predicted in a shorter time such as weekly; then total lactation RFI could be calculated to be sum of weekly predicted RFI over lactation. In this research, RFI component traits including EBWC were summed over the lactation period to calculate total lactation RFI ($RFI_{Lactation}$). Moreover, we calculated individual weekly RFI, and then the total individual lactation RFI was calculated by summing up the weekly RFI (RFI_{Weekly}) over lactation. The two methods have yielded very close results: Mean (standard deviation) of $RFI_{Lactation}$ and RFI_{Weekly} were 0.0 (2.42) and 0.0 (2.46), respectively, and RFIs obtained from these two methods had a correlation of 0.97. Summing up the RFI component traits' method is much easier computationally and more applicable compared to weekly approach.

Coleman et al. (2010) developed a RFI prediction equation for first lactation cows from 16 to 288 DIM in a pasture-based system (Table 3.3). They predicted RFI by regression of estimated daily DMI on predicted daily energy expenditures (fat yield, protein yield, lactose yield, MBW, body weight change and BCS) over 272-days. On one hand, Coleman et al. (2010) estimated individual DMI by n-alkane technique on 6 occasions from 16 to 288 DIM. The estimated observations were then used to develop a prediction equation based on a Cubic Spline regression method, to obtain an estimated daily DMI for each animal over 272-days. On the other hand, they predicted DMI based on animals' energy expenditures (fat yield, protein yield, lactose yield, MBW, body weight change and BCS). Then, they considered individual RFI as the difference between daily estimated DMI from the Cubic Spline regression data with predicted DMI based on animal's energy expenditures. However, RFI prediction is the difference between daily actual dry matter or energy intake with predicted dry matter or energy intake based on animals' energy expenditures. Therefore, the main difference of our study with Coleman et al. (2010) was that they used estimated daily DMI in their study while we used the actual daily DMI measurements in the RFI prediction to subtract predicted DMI based on animals' energy expenditures. Wang et al. (2006) reported that an accurate RFI test results required at least 63 day of observations on actual daily DMI in a period of 90-days feed lot trial of RFI prediction for beef cattle. Although their results may not directly applicable to the dairy industry, at least their results indicate that an adequate number of DMI data measurements are required to have an accurate RFI prediction even with linear prediction in beef. Coleman et al. (2010) had a limited number of daily actual dry matter intake data than our study (6 vs. 289), so they might suffer from loss of prediction accuracy.

Two other studies, Svendsen et al. (1993) and Zamani et al. (2008) predicted RFI for the first two trimesters and the entire first lactation period (Table 3.3), respectively. Both of these research teams used the table values of the standard NRC nutrients requirement to estimate energy expenditures instead of using actual individual feed intake measurements. Moreover, the standard requirements tables such as NRC were prepared based on population average and were not applicable to identify an efficient individual. In this study, both group means efficiency (the fixed effects) and the individual deviation of efficiency (the random effects) from the group mean were modeled and the latter allowed us to identify efficient animals within the group.

3.4.2. Model Development and Selection

Twenty-five Legendre Polynomial RRM models were fitted for each of the energy expenditures components (MBW, EBW, and MPER), and then LRT along with the BIC were used to select the best prediction equation for the energy expenditures. RRM is a useful technique for analyzing longitudinal traits such as feed intake, milk production and BCS (Schaeffer, 2004). It is a flexible model that allows regression coefficients to be different among animals, giving each animal a specific model (Schaeffer and Dekkers, 1994). In RRM, an average curve of a trait for all animals in a particular group is fitted as a fixed regression, and deviation of each animal from this average curve is modeled using random Legendre Polynomial (Coffey et al., 2001; Schaeffer, 2004). Legendre Polynomial has advantages of having good convergence and lower correlation between coefficients as the coefficients are orthogonal compared to an ordinary polynomial (Coffey et al., 2001; Schaeffer, 2004). The common statistical criteria such as mean square of error, or R-Square were not useful for our model selection because the numbers of parameters to be estimated were different for all possible combinations of the RRM models. Therefore, we first used LRT to test proficiency of reduced models in comparison to the full model, and then BIC was used to select the best model among the models that were as efficient as full model.

The preliminary results of the tested fixed and random regression orders of 1 to 10 for the traits showed that most of the orders greater than 5 had a convergence problem. Therefore, five possible orders (1-5) of fixed (F) and random (R) Legendre-polynomial regression models were tested to model the daily non-linear lactation profiles of MBW, EBW, and MPER with time. For the 3 derived traits fixed regression of order 5 (F_5) was selected, whereas random regression of order 3 (R_3), 3 (R_3), and 2 (R_2) were selected for MBW, EBW and, MPER and were used to predict their respective daily values for each animal. There are several reports that used Legendre-polynomial RRM technique to model BW, energy balance, and milk yield within the first lactation period (Coffey et al., 2001; Banos et al., 2005; Liu et al., 2006). They considered a fixed regression order of five to model average records across all animals for the tested traits. Random effects order of 5 and more were suggested to be used for modeling of energy balance, which was a derived trait from BW, and BCS (Banos et al., 2005). It is noted that the random regression model consists of fixed and random parts. The random part of the model could be partitioned in different parts including animal additive and permanent environmental effects (Coffey et al., 2001). If the random part did not partition, it will be a combined effect of animal additive and permanent environmental effects. Currently, random effects order of 5 is being used for both additive and permanent effects in the Canadian Holstein Dairy Cattle for modeling of milk yield within the first lactation (Liu et al., 2006). However, Liu et al. (2006) tested Legendre-polynomial random effects order of 3 to 8 to select the best order of fit for milk yield using some statistical criteria including LRT, and BIC. They also compared the selected model with the currently used model (order of 5 for both additive and permanent random effects) by the Canadian Holstein Dairy Cattle and found that the random orders of 5 and 7 were the best orders for additive and permanent random effects, respectively. Therefore, they concluded that the current model used in the Canadian Holstein dairy evaluation was not the best, based on a single criterion, but was optimal when considering all criteria including LRT, and BIC. However, in the current research, pedigree information was not included in the analysis, as we were interested to predict phenotypic RFI. Therefore, the animal's random effect was a combination of animal additive and permanent effects. Overall, the selected models in the current study were the best models that fitted the traits (Figures 3.2, 3.3, and 3.4), and they were in line with comparable results in the literature.

3.4.3. Expected Energy Intake Equation and RFI Calculation

The linear and quadratic relationships between smoothed total AEI and total MBW, EBWC, and MPER were examined. The linear RFI prediction equation had R-Square of 0.68. The quadratic multiple regression adds just 2% in R-Square to the linear model, and none of the quadratic terms in the non-linear prediction equation were statistically significant ($P > 0.34$). R-Square determines the percentage of the variation of the dependent variable (AEI) that is explained by independent variables (MBW, EBWC, and MPER). It is a good indicator to compare the different RFI prediction modeling approaches. Ideally, we should compare the R-Square of our prediction equation with other available RFI predictions in the previous literature. However, based on our awareness of published results, just Connor et al. (2013) reported R-Square of 0.72 for their RFI prediction equation in early location stage of dairy cattle. The reported higher R-square value by Connor et al.(2013) compare to the current study could be due the fact that they predicted RFI in early lactation (first 110 DIM) and had less sparse method of BW data collection method (every two weeks). .

Individual actual energy intake and expected energy intake, which is predicted based on animal's maintenance and production requirements, are necessary to calculate individual RFI. RFI calculation method has been well established in beef cattle during growth period. Generally, daily DMI and biweekly body weight are recorded over 90-days in beef during their growth period. Then linear regression of measured weight over time is used to model the growth curve for each animal, and predict its MBW and average daily gain (**ADG**) (Basarab et al., 2003; Wang et al., 2006; Kelly et al., 2010). Basarab et al. (2003) used linear regression to model the growth curve of beef steers to predict the mid test body weight and ADG of animals during the feedlot test period and reported that all animals had a growth curve with an R-Square of more than 95%, indicating that the growth during this phase was linear and the selection of a linear regression model was an appropriate approach. Consequently, expected dry matter intake was calculated from linear regression of actual daily DMI on estimated MBW and ADG. As a result, R-Square of RFI prediction equation ranged from 0.72 to 0.82 in beef (Basarab et al., 2003; Basarab et al., 2007). However, energy requirements of dairy cows are complicated and they need energy to produce milk, grow, conceive, and bring their calves to term, while maintaining themselves as biological entities, staying healthy, and keeping up with general activities (Banos et al., 2005). In dairy cattle, the amount of energy intake and that dispensed by an animal determines its body energy state. Almost all lactating animals tend to lose their body reserves to support lactogenesis, especially in high milk producing cows (Coffey et al., 2001). Therefore, accounting for non-linear lactation profiles for multifunctional energy requirements of expected individual energy intake over DIM is the key success to obtaining an accurate RFI prediction for dairy cows. In this study, the non-linear lactation profiles of energy expenditures were accounted for by using RRM and a summation of individual daily values over the trajectory. For multiple requirements, the authors initially considered smoothed AEI as functions of total MBW, MPER, and BW over 301-day and accounted for 56 % of variation in AEI. Including BCS in the initial model produced an equation with an R-Square of about 0.58. However, after adjusting BW for gut fill, EBW, then calculating the EBWC and replacing with BW and BCS provided a model that accounted for 68% of variation in AEI. Among published results just Connor et al. (2013) reported R-Square for RFI calculation which was almost as same as our R-Square; however, the achieved R-Square value for RFI prediction equation was close to the lower range of beef studies (Basarab et al., 2003; Basarab et al., 2007). In this study, the mean of average daily lactation RFI was 0.0 (SD = 2.42 Mcal NEL/day; 1.33 kg DM/day) and ranged from -6.58 to 8.64 Mcal NEL/day (-3.59 to 4.77 kg DM/day). Other researchers in dairy also reported an average of zero for RFI in dairy (Van Arendonk et al., 1991; Coleman et al., 2010), and Conner et al. (2013) reported standard deviation of 4.64 Mcal ME/d in the first 105 DIM. The standard deviation of RFI estimation in growing beef was reported almost 0.56 kg DM/day and the range of RFI values has been reported from -2.5 to +2.2 kg DM/day (Basarab et al., 2003; Wang et al., 2006; Kelly et al., 2010) with average of zero.

3.5. CONCLUSIONS

The F_5R_3, F_5R_3, and F_5R_2 RRM models were selected as the best models to model the daily non-linear profiles and to predict individual daily values of MBW, EBW, and MPER, respectively. The results indicated that the first lactation RFI is predictable and could be used in the dairy industry to increase profitability by selecting animals that are genetically superior in energy efficiency based on the RFI without compromising the production level, through indicator traits such as conformation traits, marker assisted selection and other genomic approaches. However, further investigations are required to develop a prediction equation to calculate RFI across the lactations. In addition, there is a need to investigate the phenotypic and genetic correlations between RFI and conformation traits, fertility and lifetime profitability, and to investigate indicator trait(s) in an effort to ensure that the measurement of feed intake and consequently RFI calculation is more cost effective.

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Table 3.1. Descriptive statistics for daily value of measured and derived traits (N = 234)

Trait	Number of records	Mean	SE	Min	Max
Measured traits					
Body weight (kg)	1,837	566.83	53.93	427.00	754.00
Body condition score	1,837	3.00	0.25	2.00	3.75
Milk (kg)	1,766	30.91	6.16	12.00	54.00
Fat %	1,766	3.58	0.79	1.24	7.59
Protein %	1,766	3.08	0.26	2.34	4.50
Dry matter intake (Kg/day)	67,561	19.47	4.06	1.66	38.52
Age at first calving (Days)	234	699.56	35.5	621.00	855.00
Temperature and humidity index	65	43.04	15.47	13.42	66.78
Derived traits					
Actual energy intake (Mcal NE_L/day)	67,561	35.06	7.35	3.02	69.32
Metabolic body weight ($kg^{0.75}$)	1,837	116.35	7.99	94.26	143.88
Milk production energy requirements (MJ)	1,766	21.58	4.39	7.35	40.93
Empty body weight (Kg)	1,837	381.58	54.11	193.45	559.68

Table 3.2. Maximum log likelihood, LRT, and BIC values of different models, which were not significantly different from the full model (F_5R_5) for MBW, MPER, and EBW

		Trait[1]								
		MBW			MPER			EBW		
Model[2]	D.F[3] Change	Max. Log likelihood	LRT[4]	BIC[5]	Max. Log likelihood	LRT	BIC	Max. Log likelihood	LRT	BIC
F_4R_2	12	---	---	---	-4,901.5	23.6	9,870.0	---	---	---
F_4R_3	7	---	---	---	-4,899.0	18.5	9,842.8	---	---	---
F_5R_2[6]	15	---	---	**---**	**-4,897.3**	**15.0**	**9,834.2**	---	**---**	**---**
F_5R_3	11	**-5,418.6**	**17.8**	**1,0912.5**	-4,894.8	10.1	9,846.3	**-9,298.4**	**17.1**	**7,128.6**
F_5R_4	6	-5,414.6	9.9	1,0924.4	-4,892.9	6.0	9,871.0	-9,293.7	3.5	7,148.8
F_5R_5		-5,409.6		1,0944.0	-4,889.7		9,904.3	-9,289.8		7,180.3

[1]Traits: MBW = Metabolic body weight; MPER = Milk production energy requirements; EBW = Empty body weight.

[2] The models were designated by $F_{k1}R_{k2}$, where k1 and k2 are the order of fixed and random regression, respectively.

[3]D.F = Degree of freedom; [4]LRT = Likelihood ratio test; [5] BIC = Bayesian information criteria; [6] The selected model based on Maximum log likelihood, LRT, and BIC values are bolded.

Table 3.3. Summary of available RFI prediction reports in the literature

		Current study	Vallimont et al., 2011	Coleman et al., 2010	Zamani et al., 2008	Svendsen et al., 1993	Van Arendonk et al., 1991
Breed		Holstein	Holstein	Holstein	Holstein	Dual	Holstein
Raised system		Tie-stall	Tie-stall	Pasture	Tie-stall	Tie-stall	Tie-stall
N		281	970	265	906	353	360
Test duration		300	305	267	365	168	105
Regression approach to model energy sink profiles		NL[7]	NL	NL	NP[8]	NP	L[9]
Regression approach to model relationship between energy intake and sinks		L NL	L	L	L	L	L
Recorded actual feed intake/cow		289	6	6	52	NP	44
R^2 of RFI prediction equation		0.68	NP	NP	NP	NP	NP
Components included in expected energy intake equation	MBW[1]	*	--	*	*	*	*
	MYC[2]	*	*	*	*	*	*
	EBWC[3]	*	--	--	--	--	--
	BW[4]	--	*	--	--	--	--
	BCS[5]	--	*	*	*	--	--
	ADG[6]	--	--	*	*	*	*
RFI	Mean	0.00 Mcal NEL/d	NP	0.03 DM/d	4.64 Mcal/d	NP	64.2 MJ ME/kg
	Min	-5.71	NP	-0.38	-9.43	NP	42.1
	Max	7.96	NP	0.44	18.6	NP	86.4

[1]MBW = Metabolic body weight; [2] MYC = Milk yield and components; [3] EBWC = Empty body weight changes; [4]BW = body weight; [5]BCS = Body condition score; [6] ADG = Average daily gain; [7]NL = Non linear; [8]NP = Not provided; [9]L = Linear

Figure 3.1. Average actual energy intake (NE_L Mcal/day) against DIM

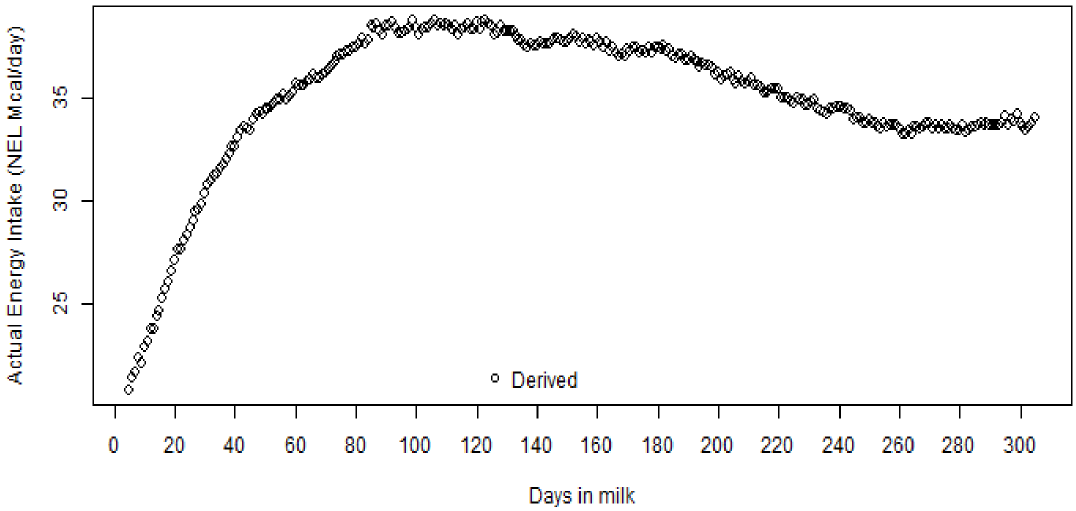


Figure 3.2. Average daily derived (White Diamond) and predicted (Black circle) milk production energy requirement (Mcal NE_L) against DIM

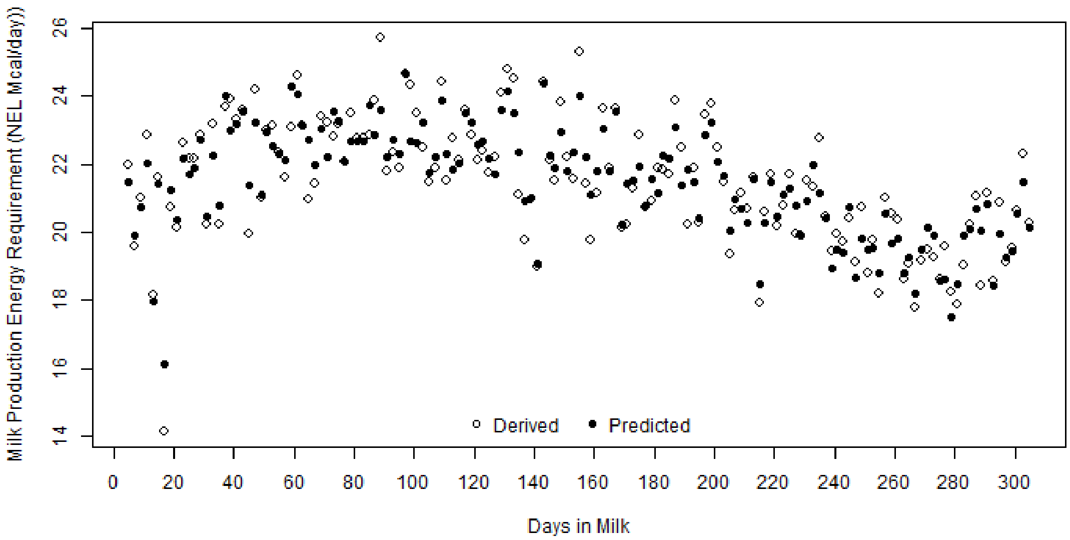


Figure 3.3. Average daily derived (White diamond) and predicted (Black circle) empty body weight (kg) against DIM

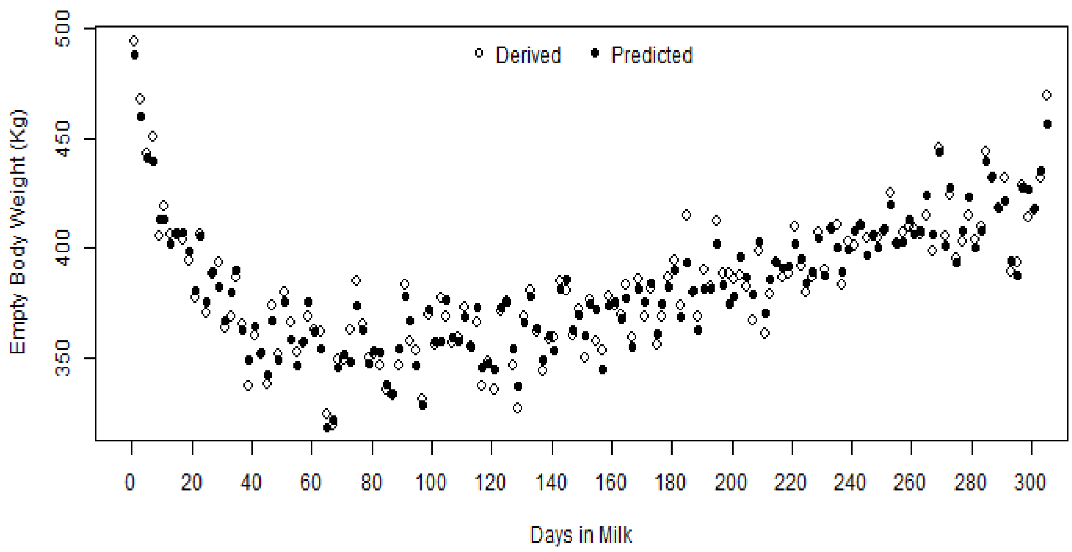


Figure 3. 4. Average daily derived (White Diamond) and predicted (Black circle) metabolic body weight (kg$^{0.75}$) against DIM

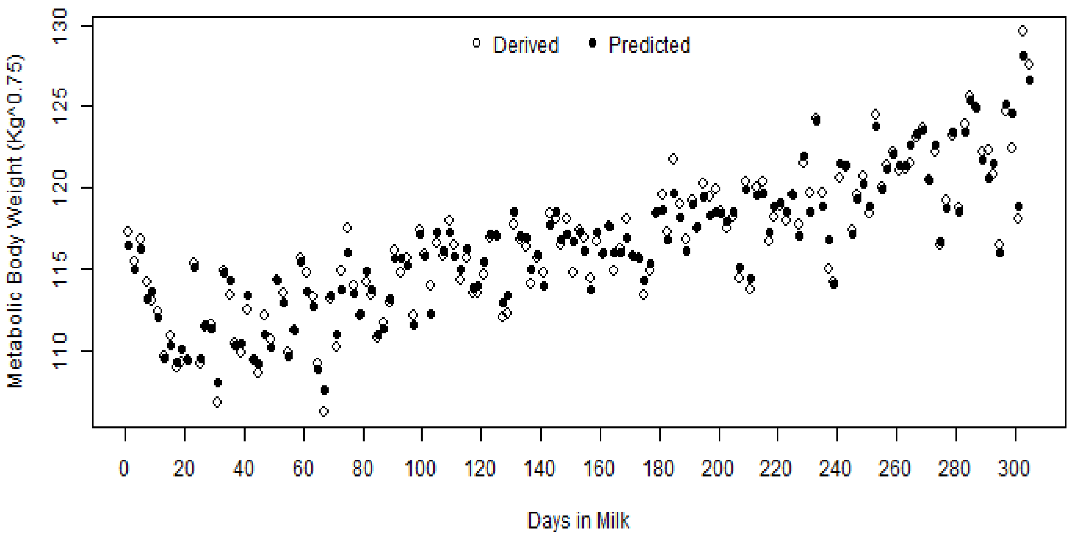
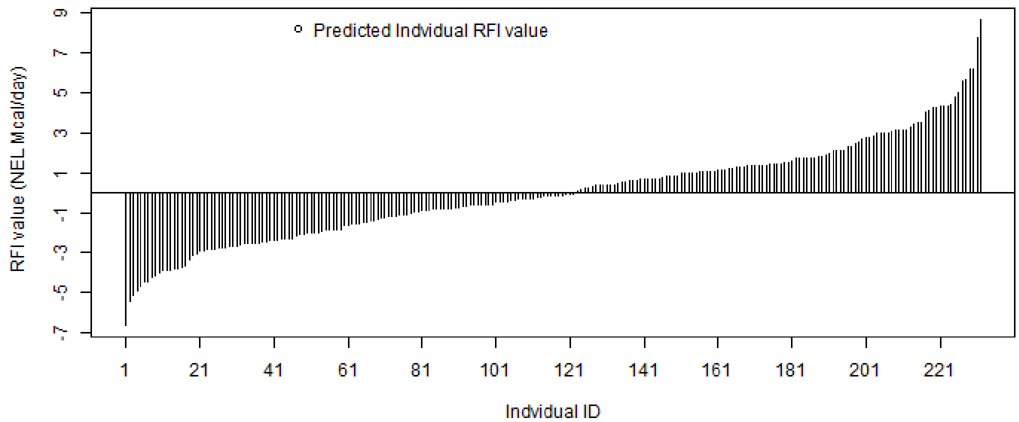


Figure 3. 5. Average daily RFI; each bar indicates daily RFI (NE_L Mcal /day) for each dairy cow



CHAPTER 4. OPTIMUM TEST STAGE OF LACTATION FOR RESIDUAL FEED INTAKE PREDICTION IN FIRST LACTATION DAIRY COWS

4.1. INTRODUCTION

Residual feed intake (**RFI**) is an alternative measure of feed efficiency. The results over a decade of research in beef cattle on RFI have shown that the genetic selection of efficient animals for lower RFI is a viable option to improve feed efficiency, to reduce environmental pollution, and to decrease maintenance and production energy requirements without compromising production (Connor et al., 2012). Research suggested that selection for RFI in beef cattle could reduce feed intake by 10 to 12%, green house gas emission by 25 to 30%, and nutrient losses in manure by 15 to 17% (Alberta Agriculture, Food and Rural Development, 2006). Consequently, RFI research in dairy cattle is gaining popularity in studying similar opportunities of feed efficiency improvement as those available in beef cattle (Van Arendonk et al., 1991; Lopez-Villalobos et al., 2008; Prendiville et al., 2009; Coleman et al., 2010; Vallimont et al., 2011; Connor et al., 2012). However, the measurement of individual feed intake is the necessary requirement for feed efficiency study. Difficulty and costs associated with this measurement have often prohibited this type of research and its applications in dairy breeding since special equipment, labor, and time have to be invested. Therefore, shortening the RFI test period is of interest to reduce the costs and time of the test. To examine the possibility of reducing the RFI test period in dairy cows, three research studies (Lopez-Villalobos et al., 2008; Prendiville et al., 2009; Connor et al., 2012) have been conducted to compare RFIs predicted from data in different stages of the lactation periods with RFI predicted from the whole lactation. Their results indicated that the RFI measurements after 100 DIM may provide a closer estimate of feed efficiency for the whole lactation. However, two of the available research projects (Lopez-Villalobos et al., 2008; Prendiville et al., 2009) studied RFI using grazing dairy cows with a limited number of individual actual feed intake measurements (maximum of 5 times during 300 days in milk). The other research team (Connor et al., 2012), conducted a study in indoor-stall with a limited number of animals (n=32) without reporting feed intake measurement frequencies. To the best of the authors' knowledge none of the available reports on RFI prediction have used individual daily actual feed intake measurements throughout the whole lactation period. Therefore, the aforementioned studies may not be sensitive enough to capture the differences among the animals (Vallimont et al., 2011) during lactation. Additionally, none of the published reports have examined genetic correlations among RFIs between different stages of the lactation, which are necessary for genetic evaluation in improving RFI in breeding programs using the shortened RFI test. Therefore, the objectives were to study the possibility of shortening the RFI test period and to determine genetic correlations between the shortened RFI test periods and the whole lactation for RFIs and its component traits.

4.2. MATERIALS AND METHODS

4.2.1. Data Acquisition and Edition

The data acquisition process was described in detail in section 3.2.1. of chapter 3. In this study, the acquired data throughout the whole lactation (5 to 305 DIM) were subdivided into three stages of the lactation from 5 to 105, 106 to 205, and 206 to 305 DIM as early, mid and late lactation test periods, respectively. The four test periods in this study consisted of three shortened test periods along with the whole lactation period (from 5 to 305 DIM; Whole).

In the data edition process, 59 animals were dropped from the analysis since they were lower than 260 days in record throughout the whole lactation for feed intake measurements. Twenty-two animals were also excluded from the analysis as their number of feed intake observations were lower than 70 within each stage of the lactation periods. In addition, any observations that failed to fall within the three standard deviations from the population mean on the test days were excluded from the analysis. The remaining 1,570, 1,509, and 57,745 repeated records, respectively for body weight, milk yield, and feed intake data from 200 cows were used in the analysis. All cows were cared for in accordance with the guideline of the Canadian Council on Animal Care (McWilliam et al., 1993).

4.2.2. Traits Derivation and RFI Model Development

The traits derivations process within each shortened test period was the same as the procedure used for the whole lactation period, which was described in detail in section 3.2.2 of chapter 3. In summary, four derived traits from the acquired data were calculated: daily individual actual energy intake (**AEI**), monthly milk production energy requirement (**MPER**), monthly metabolic body weight (**MBW**), and monthly empty body weight (**EBW**). The model development process using the RRM technique within each shortened test period was also the same as that applied for whole lactation to predict daily individual values for MPER, MBW, and EBW, which was described in section 3.2.3.1 in Chapter 3. In short, one model out of each of the 25 tested models was selected for each trait and was used to estimate daily individual values over each test period for that trait. The daily predicted MBW, EBWC, and MPER for each animal *i* within each test period was summed up to obtain the total MBW $\left(\sum_{d1}^{d2} MBW_i\right)$, EBWC($\sum_{d1}^{d2} EBW_i$) , and MPER($\sum_{d1}^{d2} MPER_i$), respectively. AEI over each test period for each animal was also summed up to obtain the individual's total AEI ($\sum_{d1}^{d2} AEI_i$) within each test period; where, d1 and d2 were the start and the end days of each test period.

The applied statistical model to predicted expected energy intake and individual total RFI was described in detail in section 3.2.3.2 of Chapter 3. Briefly, a multiple linear regression of total AEI on total MBW, EBWC, and MPER was used to predict total expected energy intake in each test period. The individual total RFI over each test period was obtained from the difference between total actual energy intake and total expected energy intake (**EEI**) within each test period.

4.2.3. Animal Grouping

To study the consistency of RFI prediction equation, three efficiency groups were defined within each test period: Low/Efficient (RFI < 0.5 SD), Medium (0.5 SD < RFI < 0.5 SD), and High/Inefficient (RFI > 0.5 SD from mean). Animals were assigned to one of the three efficiency groups based on their RFI values. Compared with the whole lactation, a numbers of the animals remained in the same RFI classes, changed their classes between 0.5 to 1.0 SD from either low to medium or medium to high and vice versa, and changed their classes greater than 1 SD from low to high or vice versa were determined for each of the shortened period. To determine the extent to which ranks changed within each test period compared with the whole lactation period, the Spearman's rank correlation statistics between each reduced test period with whole lactation period was calculated. In addition, concordance correlation coefficient was calculated between each of the reduced test period and whole lactation period. The concordance correlation coefficients measures the agreement between two variable and evaluate reproducibility or for inter-rater reliability (Lawrence, 2000).

4.2.4. Parameter Estimates

A bivariate animal mixed model was used to estimate heritabilities, phenotypic, and genetic correlations for each pair of traits. The mean of the traits and the number of observations within each of the test periods were considered as fixed effects for the parameter estimations. In addition, the animal additive genetic effect was added to the model as a random effect. An additive genetic relationship matrix is constructed based on the pedigree file containing 18091 animals, in which their ancestry was traced back to as many as 45 generations. A non-zero error correlation was considered between two traits, since the same animals were used in all of the test periods. The applied model was $\begin{bmatrix} y_1 \\ y_2 \end{bmatrix} = \begin{bmatrix} X_1 & 0 \\ 0 & X_2 \end{bmatrix} \begin{bmatrix} b_1 \\ b_2 \end{bmatrix} + \begin{bmatrix} Z_1 & 0 \\ 0 & Z_2 \end{bmatrix} \begin{bmatrix} a_1 \\ a_2 \end{bmatrix} + \begin{bmatrix} e_1 \\ e_2 \end{bmatrix}$. Where y_1 and y_2 were the vectors of phenotypic measurements for any two traits (for example, early RFI as trait 1 and total RFI as trait 2); X_1 and X_2 were incidence matrices relating the fixed effects to the vectors of phenotypic measurements of trait 1 and 2; b_1 and b_2 were the vectors of fixed effects for traits 1 and 2; Z_1 and Z_2 were incidence matrices assigning the phenotypic observations to the vectors of additive genetic effects for trait 1 and 2, and e_1 and e_2 were the vectors of random residual for trait 1 and 2, respectively. The expectations and variances of the model were:

$$E\begin{bmatrix} y_1 \\ y_2 \end{bmatrix} = \begin{bmatrix} X_1 & 0 \\ 0 & X_2 \end{bmatrix} \begin{bmatrix} b_1 \\ b_2 \end{bmatrix}$$, and

$$V\begin{bmatrix} a_1 \\ a_2 \\ e_1 \\ e_2 \end{bmatrix} = \begin{bmatrix} A\delta_{a\,1}^2 & A\delta_{a\,12} & 0 & 0 \\ A\delta_{a\,21} & A\delta_{a\,1}^2 & 0 & 0 \\ 0 & 0 & I\delta_{e\,1}^2 & I\delta_{e\,12} \\ 0 & 0 & I\delta_{e\,21} & I\delta_{e\,2}^2 \end{bmatrix}$$

ASREML-W software (Gilmour et al., 2010) was used to perform the parameters estimation. Heritability estimates originated from bivariate analysis were averaged to obtain the final heritability estimate for each trait.

4.3. RESULTS AND DISCUSSION

4.3.1. Means and Heritability Estimations

4.3.1.1. RFI Predictions

Means and heritability estimates of RFI in the four study periods are presented in Table 4.1. As expected and based on its definition, the mean of RFI estimates were zero for all of the test periods, and it was consistent with other research finding (Van Arendonk et al., 1991; Coleman et al., 2010; Connor et al., 2013). The heritability estimate of RFI was low (0.11) in early lactation (5 to 105 DIM) and relatively similar in the other periods (0.23 for mid lactation and 0.21 for late and whole lactation periods). The heritability estimate of RFI in the early period (0.11) was similar to that reported (0.11) by Connor et al. (2013) in the first 90 DIM. Moreover, the trend of the heritability estimation results was consistent with Lopez-Villalobos et al. (2008) who predicted RFI in grazing Holstein cows every 30-day from 8 to 296 days in milk; they also reported a low (0.06) heritability estimate of RFI for early lactation (90-DIM) and relatively stable heritability estimate after 90-DIM. Nevertheless, RFI was moderately repeatable (0.51 ± 0.04, respectively) across the stages of lactation, and almost the same magnitude of repeatability (0.47) was reported by Connor et al. (2013). In contrast, the heritability estimate of RFI across the stages of lactation in our study (0.21 ± 0.09) was higher than that reported by Vallimont et al. (2011) at 0.07 for 305-DIM, and it was lower than that of Lopez-Villalobos et al. (2008) at 0.38 for 296-DIM. The higher estimates in our study compared to the value reported by Vallimont et al. (2011) could be due to the use of daily actual feed intake data versus the monthly records used in their study. Therefore, they may have used less accurate method of feed intake data collection to capture the genetic differences of RFI among animals (Vallimont et al., 2011). Moreover, Lopez-Villalobos et al. (2008) pointed out that their heritability estimate over 296-DIM should be looked at with caution, since a few records of dry matter intake were available in their study.

4.3.1.2. RFI Component Traits

Means and heritability estimates of RFI component traits in the four periods are also presented in Table 4.1. The RFI component traits were actual energy intake, metabolic body weight, empty body weight change, and milk production energy requirements.

The animals lost on average 0.54 kg/day of their empty body weight in the early lactation period, while they compensated their loss in the mid and late lactation periods (Table 4.1). It is also shown by others (NRC, 2001; Lopez-Villalobos et al., 2008) that dairy cows could lose as much as 0.70 kg/day of their body weight in the early lactation period. The means of milk production energy requirements were higher in the early and late lactation periods than in the mid lactation period. Since the milk production energy requirement trait was defined as a function of milk yield and its components, the trend was expected since the peak of milk production and fat% occurring in the early and late lactation period, respectively.

The heritability estimates were 0.28, 0.32, 0.31, and 0.38 for actual energy intake, metabolic body weight, empty body weight change, and milk production energy requirements, respectively, across the stages of lactation. The heritability estimates for each trait varied in different test periods, but the differences were not statistically significant ($P > 0.05$). The estimates were within the ranges reported in the literature (Van Arendonk et al., 1991; Koenen and Veerkamp, 1998). Finally, the results of RFI component traits were supported by the findings of other researchers (Hooven et al., 1972; NRC, 2001; Prendiville et al., 2009; Connor et al., 2013) who concluded that dairy animals undergo a cycle through lactation. In this cycle, they lose their body reserves after calving to support higher amounts of milk production in early lactation. Then, animals replenish their reserves in the mid and late lactation to support the next parity lactogenesis.

4.3.2. Consistency of RFI Prediction Equation

R-square estimates of the RFI prediction models were 0.47, 0.49, 0.79, and 0.68 for early, mid, late, and whole lactation period, respectively. Connor et al.

(2013) reported a R-square of 0.72 for the RFI prediction model in the first 90 DIM in which they considered metabolic body weight, average daily gain/loss, and energy corrected milk in their RFI prediction model. The higher R-square of their prediction equation in the early lactation period compared to this study (0.72 vs. 0.47) could be due to the fact that they had a less sparse method of data collection on body weight (twice in a week) in comparison to this study (almost once in a month) to capture body reserve partial regression effect for RFI prediction. To our knowledge, there are no published results reporting R-square of RFI prediction equation in different periods, so we compared the results of this section with crossbreed steers in different test period. Although the results reported in crossbred steers may not be directly applicable to dairy, at least our achieved R-square estimates of the RFI prediction equations were within the range of values (0.50 to 0.79) reported for crossbred steers at different ages (Basarab et al., 2003; Durunna et al., 2012; Durunna et al., 2013).

The results of RFI classification showed that 56.5, 65.5, and 49.5% of the animals remained in the same RFI classes (no-change) in early, mid, and late lactation periods, respectively, compared with the whole lactation period (Table.4.2). A closer look at RFI value changes revealed that 41.5, 32.5, and 43.0% of the animals changed their RFI class between 0.5 to 1.0 SD for early, mid, and late lactation periods compared with the whole lactation, respectively, while 2.0, 2.0, and 7.5% changed their RFI values greater than 1.0 SD (Table 4.2). Since larger numbers of the animals remained in their respective group in this study compared with the whole lactation, it could be suggested that RFI prediction in mid lactation stage may be a more reliable indicator of the whole lactation RFI prediction. The authors are unaware of other studies in dairy that examined animals' RFI group changes to compare our results with. However, in crossbred replacement heifers, Durunna et al. (2011) reported that approximately 49% of the heifers maintained their RFI group from the first feeding period to the second (Durunna et al., 2011).

The results of Spearman correlation showed early, mid, and late lactation period, respectively, had 0.63, 0.76, and 0.54 correlations with whole lactation period. Greater rank correlation between mid and whole lactations periods, compared to two other reduced test periods, shows RFI ranks for animals were more similar. The Concordance correlation coefficient between early, mid, and late lactation period with whole lactation period were 0.61, 0.77, and 0.56, respectively. The higher concordance correlation between mid test period with whole lactation period suggests that reproducibility or inter-rater reliability between these two period is higher compared to the other reduced test period.

4.3.3. Correlations among RFIs in Different Test Periods as well as Its Component Traits

Although whole lactation RFI had high and significant ($P < 0.01$) phenotypic correlations with RFI prediction in each of the three test periods, it only had a significant ($P < 0.01$) genetic correlation with mid RFI (Table 4.3). Moreover, mid test period RFI not only had a significant ($P < 0.01$) genetic correlation with whole lactation RFI, but it also had moderate phenotypic and high genetic correlations (*$P < 0.01$*) with both the early and late RFIs. Mid lactation period was adjacent to the early and late periods, and a moderate correlation among the traits in the adjacent periods was expected (Hooven et al., 1972; Koenen and Veerkamp, 1998). However, late and early lactation RFI had near zero phenotypic correlations and these weak correlations could be due to the fact that the animal factors such as production priority (e.g. milk or body gain) and age, as well as the management techniques, such as feeding diet were reasonably different in these two periods during which feed efficiency differs throughout the lactation (Kirkland and Gordon, 2001). The main priority of dairy cows is to produce milk even by losing their body reserves in early lactation, whereas the priority modifies in the late stage of lactation to regain body reserves and to be prepared for the next parity.

Actual energy intake within whole lactation was highly correlated with the other test periods (Table 4.3). The magnitudes of these correlations were significantly different from zero ($P < 0.01$), except the genetic correlation between AEI within whole with the early lactation period. Pendiville et al. (2009) also reported a higher phenotypic correlation (greater than 0.76) between dry matter intake at each stage of lactation with the whole production cycle. In the current study, the actual energy intake in the early and mid periods had the lowest phenotypic correlation (0.31), which was in agreement with Koenen and Veerkamp (1998). In addition, metabolic body weight among the four test periods were significantly correlated (Table 4.3). However, empty body weight change correlations among the four different test periods were not significantly different (*P > 0.05*) from zero, neither genetically nor phenotypically, except for the phenotypic correlation between early and total lactation period.

4.3.4. Correlations among RFI and Its Component Traits within Each Test Periods

Genetic (r_g) and phenotypic (r_p) correlations between RFI with its component traits within each of the four study periods are presented in Table 4.4. RFI prediction had high and significant (*P < 0.01*) phenotypic and genetic correlations with actual energy intake in all of the test periods. The strong phenotypic and genetic correlations between RFI and intake traits were also supported by other researchers (Van Arendonk et al., 1991; Vallimont et al., 2011). RFI prediction in all of the four test periods had close to zero phenotypic correlations with energy expenditure traits (metabolic body weight, empty body weight change and milk production energy requirement), which were expected from the RFI calculation. Van Arendonk et al. (1991) also reported similar phenotypic correlations among RFI and energy expenditure traits. However, RFI prediction was genetically correlated with metabolic body weight and energy requirements for milk production in all of the test periods. Among all the published research on RFI prediction in dairy cattle, just Van Arendonk et al. (1991) examined the genetic correlations among RFI and its component traits in the first 105 DIM and reported zero correlation among them, which was different from the current study. The estimated genetic correlations between RFI and its energy expenditure traits in this study were low and not significant ($P > 0.05$) due to a large standard error; however, these results need to be further validated.

4.4. CONCLUSION

RFI had moderate heritability and repeatability across the stages of lactation, which implies there is an opportunity to improve animal feed efficiency through selection for RFI. Mid RFI were strongly correlated with the whole, early, and late lactation RFI genetically and phenotypically. Moreover, the predicted mid RFI may be more reliable for use to predict the animal's lactation energy efficiency since compared with the whole lactation most of the animals (65.5%) remained in the same RFI classes. Hence, mid stage lactation could be considered as the best test period of RFI prediction among the shortened periods. However, mid RFI had positive significant genetic and phenotypic correlations with actual energy intake and low but not significant negative genetic correlation with metabolic body weight and energy requirement for milk production. It means that selection for mid RFI will decrease the amount of energy intake without phenotypically compromising other production traits; however, further research is suggested to validate the results and overcome the long term concerns of genetic correlation between mid RFI and metabolic body weight and energy requirement for milk production.

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Table 4.1. Mean and heritability estimates of residual feed intake and its component traits at different test periods

		Test period			
Trait		Early	Mid	Late	Total
Residual feed intake (Mcal NE_L/d)	Mean ± SD	-0.09 ± 3.37	0.09 ± 3.72	0.04 ± 3.19	0.03 ± 2.43
	h^2 ± SE	0.11 ± 0.12	0.23 ± 0.16	0.21 ± 0.14	0.21 ± 0.15
Actual energy intake (Mcal NE_L/d)	Mean ± SD	33.08 ± 4.48	34.65 ± 5.09	37.62 ± 4.82	35.16 ± 3.83
	h^2 ± SE	0.25 ± 0.19	0.28 ± 0.15	0.23 ± 0.18	0.28 ± 0.16
Metabolic body weight ($Kg^{0.75}$)	Mean ± SD	112.37 ± 6.72	118.64 ± 6.91	120.73 ± 6.69	116.56 ± 6.29
	h^2 ± SE	0.39 ± 0.16	0.32 ± 0.16	0.29 ± 0.16	0.32 ± 0.17
Empty body weight change (Kg/d)	Mean	-0.54 ± 0.35	0.46 ±0.26	0.12 ±0.24	-0.09 ± 0.09
	h^2 ± SE	0.13 ± 0.12	0.24 ± 0.12	0.21 ± 0.14	0.31 ± 0.15
Milk production energy requirements (Mcal NE_L/d)	Mean ± SD	22.15 ± 2.96	20.63 ±3.22	22.12 ± 2.52	21.78 ± 2.53
	h^2 ± SE	0.22 ± 0.16	0.36 ± 0.17	0.31 ± 0.15	0.38 ± 0.17

Early = From 5 to 105 DIM; Mid = From 105 to 206 DIM; Late= From 206 to 305 DIM; Total = From 5 to 305 DIM

Table 4.2. Number of animals based on their group changes and direction from any shortened to the total lactation period

Group changes and direction	Early to total lactation	Mid to total lactation	Late to total lactation
Changed from high to low by 1 SD (%)	1.00	1.00	4.00
Changed from high to low by 0.5 SD (%)	21.5	19.50	21.5
Maintained the same group (no change) (%)	56.5	65.50	49.5
Changed from low to high by 0.5 SD (%)	20.00	13.00	21.5
Changed from low to high by 1 SD (%)	1.00	1.00	3.5

Table 4.3. Genetic (below diagonal) and phonotypic (upper diagonal) correlations of RFIs and component traits between different test periods

		Early	Mid	Late	Total
		Residual feed intake (Mcal NE_L/d)			
Residual feed intake (Mcal NE_L/d)	**Early**		$0.23 \pm 0.06^{**}$	0.05 ± 0.07	$0.62 \pm 0.04^{**}$
	Mid	$0.85 \pm 0.49^{*}$		$0.45 \pm 0.06^{**}$	$0.76 \pm 0.02^{**}$
	Late	0.94 ± 0.89	$0.98 \pm 0.32^{**}$		$0.57 \pm 0.05^{**}$
	Total	0.78 ± 0.49	$0.99 \pm 0.12^{**}$	0.75 ± 0.23	
		Actual energy intake (Mcal NE_L/d)			
Actual energy intake (Mcal NE_L/d)	**Early**		$0.31 \pm 0.07^{**}$	$0.61 \pm 0.04^{**}$	$0.74 \pm 0.03^{**}$
	Mid	0.48 ± 0.33		$0.67 \pm 0.04^{**}$	$0.79 \pm 0.02^{**}$
	Late	$0.72 \pm 0.25^{**}$	$0.98 \pm 0.18^{**}$		$0.89 \pm 0.04^{**}$
	Total	0.46 ± 0.51	$0.95 \pm 0.12^{**}$	$0.97 \pm 0.06^{**}$	
		Metabolic body weight ($Kg^{0.75}$)			
Metabolic body weight ($Kg^{0.75}$)	**Early**		$0.72 \pm 0.03^{**}$	$0.82 \pm 0.02^{**}$	$0.89 \pm 0.02^{**}$
	Mid	$0.99 \pm 0.07^{**}$		$0.81 \pm 0.02^{**}$	$0.91 \pm 0.01^{**}$
	Late	$0.98 \pm 0.04^{**}$	$0.82 \pm 0.21^{**}$		$0.94 \pm 0.00^{**}$
	Total	$0.99 \pm 0.03^{**}$	$0.95 \pm 0.07^{**}$	$0.96 \pm 0.04^{**}$	
		Milk production energy requirements (Mcal NE_L/d)			
Milk production energy requirements (Mcal NE_L/d)	**Early**		$0.45 \pm 0.05^{**}$	$0.49 \pm 0.05^{**}$	$0.82 \pm 0.02^{**}$
	Mid	$0.99 \pm 0.32^{**}$		$0.57 \pm 0.05^{**}$	$0.74 \pm 0.03^{**}$
	Late	$0.99 \pm 0.27^{**}$	$0.91 \pm 0.21^{**}$		$0.82 \pm 0.02^{**}$
	Total	$0.99 \pm 0.12^{**}$	$0.97 \pm 0.07^{**}$	$0.93 \pm 0.08^{**}$	
		Empty body weight change (Kg/d)			
Empty body weight change (Kg/d)	**Early**		0.11 ± 0.07	-0.09 ± 0.06	$0.42 \pm 0.06^{**}$
	Mid	0.56 ± 0.67		-0.09 ± 0.07	0.02 ± 0.07
	Late	-0.61 ± 0.56	-0.72 ± 0.76		0.02 ± 0.07
	Total	0.69 ± 0.56	-0.42 ± 0.57	-0.44 ± 0.55	

** = Significant at level *P < 0.01;* * = Significant at level *P < 0.05*; Early = From 5 to 105 DIM; Mid = From 105 to 206 DIM; Late = From 206 to 305 DIM; Total = From 5 to 305 DIM

Table 4.4. Genetic and phenotypic correlations between residual feed intake with its component traits within each test period

	Actual energy intake (Mcal NE_L/d)		Metabolic body weight ($Kg^{0.75}$)		Empty body weight change (Kg/d)		Milk production energy requirements (Mcal NE_L/d)	
	r_p	r_g	r_p	r_g	r_p	r_g	r_p	r_g
				Early (From 5 to 105 DIM)				
RFI	0.73 ± 0.03**	0.66 ± 0.25**	0.07±0.07	-0.17 ± 0.98	-0.09 ± 0.07	-0.06 ± 0.72	0.03 ± 0.06	0.14 ± 0.46
				Mid (From 105 to 206 DIM)				
RFI	0.77 ± 0.02**	0.69 ± 0.23**	0.04 ± 0.08	-0.22 ± 0.54	-0.06 ± 0.07	-0.06 ± 0.90	0.03 ± 0.07	-0.06 ± 0.42
				Late (From 206 to 305 DIM)				
RFI	0.53 ± 0.06**	0.78 ± 0.21**	-0.02 ± 0.07	-0.11 ± 0.52	-0.03 ± 0.07	0.09 ± 0.63	-0.06 ± 0.07	-0.18 ± 0.49
				Total (From 5 to 305 DIM)				
RFI	0.69 ± 0.04**	0.65 ± 0.19**	0.02 ± 0.08	-0.11 ± 0.32	0.03 ± 0.07	0.02 ± 0.38	0.00 ± 0.07	-0.05 ± 0.38

** = Significant at level $P < 0.01$; r_p = Phenotypic correlation; r_g = Genetic correlation; RFI = Residual feed intake (Mcal NE_L/d)

CHAPTER 5. GENETIC AND PHENOTYPIC CORRELATIONS AMONG FEED EFFICIENCY, PRODUCTION AND SELECTED CONFORMATION TRAITS IN DAIRY CATTLE

5.1. INTRODUCTION

The relatively high cost of measuring individual feed intake is a primary limiting factor for researching feed efficiency (Kelly et al., 2010) and implementing effective genetic improvement programs for dairy feed utilization. Indirect selection contributed to overall genetic trend via the use of indicator trait(s), and can be used to increase accuracy of genetic evaluation when data density of primary breeding objectives is limited. Individual feed intake measurements are rarer than indicators because the indicators can be easily and routinely measured. Ideally, indicator trait(s) should be moderately to highly heritable, moderately to highly correlated with the breeding objective, relatively inexpensive and easy to record, and measurable in early life, specifically before selection decisions are made (Kelly et al., 2010). Conformation traits (first classification linear type traits) are those that are moderately heritable (Schaeffer, 1983), routinely recorded in a dairy recording program mostly during the animal's first lactation period (Canadian Dairy Network, 2006), and are easily measurable at a low cost (Kelly et al., 2010). Researchers are interested in using these traits as indicators, especially if they are correlated to feed intake and can therefore be used to improve feed efficiency. Some research teams estimated genetic and phenotypic parameters among a few conformation traits with production and common measures of feed efficiency, including the feed conversion ratio (**FCR**) and gross energy efficiency (**GEE**), in dairy cattle (Van Arendonk et al., 1991; Parke et al., 1999; Vallimont et al., 2010). This research has showed that combinations of some conformation traits, such as chest width and pin width, may be useful indicators of feed efficiency and production traits. The challenges that ratio traits such as FCR and GEE pose in genetic improvement programs have been reviewed by some researchers (Gunsett, 1984; Kennedy et al., 1993; Van der Werf et al., 2004) and are discussed in details in section 3.1 of Chapter 3. Besides, Vallimont et al. (2011) recently concluded that estimated genetic parameters for FCR and GEE may be inflated during the lactation period, since the contribution of energy from body tissue changes is not taken into consideration. To address these problems, alternative efficiency measures have been extensively proposed (Crews, 2005), effectively distinguishing upon their contribution to increasing data and accuracy of evaluating feed intake, and the need for estimating parameters of feed intake and its potential indicators (Parke et al., 1999; Vallimont et al., 2011).

Residual feed intake (**RFI**) is an alternative measure for characterizing feed efficiency (Koch et al., 1963). In fact, Kennedy et al. (1993) and Van der Werf et al. (2004) both showed that RFI was equivalent to a restricted selection index for decreased feed intake, holding other energy deposition constant. However, RFI prediction still requires individual feed intake records, which limits its application in the industry. RFI's dependence on individual feed intake measurement (especially during early production and growth phases) further underscores how important it is to increase the accuracy of feed intake genetic evaluation. Finding indicator traits such as conformation traits may increase adoption of feed utilization improvement using RFI and similar multiple trait tools for application industry-wide. Recently published reports of parameters of RFI and conformation traits in dairy cattle are generally lacking. Moreover, RFI *per se* is phenotypically independent of production level, but (co)variances involving feed intake are needed to address the potential issues of long term correlated response in other related economically important traits due to selection for RFI. The objective of this study was to estimate genetic and phenotypic parameters among intake, production, and efficiency traits over a 301-d lactation, and selected first lactation type classification traits.

5.2. MATERIALS AND METHODS

5.2.1. Data Acquisition

Feed intake, body weight (**BW**), and body condition score (**BCS**) data acquisition was described in detail in section 3.2.1 of chapter 3. In the current chapter, 239 first lactation dairy cows were considered in the analysis. Each animal's projected milk, fat and protein yield data was retrieved from the official Dairy Herd Improvement (DHI) program. The first lactation type classification (conformation traits) records for these animals were extracted from the Canadian Dairy Network (**CDN**) data base. The type classification was evaluated at a seven-month interval or "round," and in most cases, each animal was classified one time during its first lactation period (Canadian Dairy Network, 2006). Twenty-four descriptive traits were recorded on a linear scale ranging from 1 to 9, and combinations of these traits were used to determine scores for five major classification traits. Five major and 10 descriptive traits out of the 24 were selected to include in this analysis. The five major traits were overall conformation (**OC**), mammary system (**MS**), dairy strength (**DS**), rump (**RU**), and feet and legs (**FL**); and the selected linear classification traits were angularity (**AN**), udder depth (**UD**), udder texture (**UT**), rear attachment height (**RAH**), rear attachment width (**RAW**), stature (**ST**), height at front (**HF**), chest width (**CW**), body depth (**BD**), and pin width (**PW**). All procedures involving animals were reviewed and approved by the University of Alberta Animal Care & Use Committee, and all cows were cared for in accordance with the guideline of the Canadian Council on Animal Care (1993).

5.2.2. Data Preparation

5.2.2.1. Intake Traits

Individual daily dry matter intake (**DMI**) was calculated using recorded daily offered and refused feed information, for each animal. Individual daily actual energy intake (**AEI**) was calculated using DMI and energy density of the diet. The applied equations to calculate DMI and AEI were described in section 3.2.2 of chapter 3. In the current chapter, it was proposed to calculate efficiency traits over the lactation period, with the objective to calculate lactation DMI and AEI over 301-d for each animal. All animals had a minimum of 260 intake observations over 301-d. The missing values of DMI and AEI for each animal with more than 260 and less than 301 observations were estimated using the fifth-order fixed and random effect Legendre polynomial random regression developed in section 3.2.3 of chapter 3. Total DMI and AEI values over 301-d were calculated and described to be lactation dry matter intake (**LDMI**) and actual energy intake (**LAEI**) for each animal, respectively.

5.2.2.2. Production Traits

Milk yield and composition data obtained from the DHI was used to derive 301-d total lactation 3.5% fat corrected milk (**LFCM**) (NRC, 2001) and lactation energy corrected milk (**LECM**) for 3.5% fat and 3.2% protein (Tyrrell, and Reid, 1965) over 301-d as:

$$\text{LFCM (kg)} = [\text{301-d Milk yield (kg)}] \times \left[0.423 + \frac{(16.216 \times \text{Fat (\%)})}{100}\right],$$

$$\text{LECM (kg)} = [\text{301-d Milk yield (kg)}] \times \left[\left(\frac{(12.82 \times \text{Fat (\%)})}{100}\right) + \left(\frac{(7.13 \times \text{Protein (\%)})}{100}\right) + 0.323\right],$$

Furthermore, the means of BW and BCS observations were calculated for each animal and were described as an average of BW (**ABW**), and BCS (**ABCS**) over 301-d.

5.2.2.3. Feed Efficiency Traits

Lactation feed conversion ratio (**LFCR**), gross energy efficiency (**LGEE**), and residual feed intake (RFI) over 301-d were described to be feed efficiency traits. LFCR was calculated as the ratio of LDMI to LFCM (Crews, 2005).LGEE was defined as LECM divided by LAEI (Veerkamp and Emmans, 1995). Based on the LFCR and LGEE definitions, efficient animals had lower LFCR values but higher LGEE values. Individual lactation RFI values over 301-d obtained from the first study are reported in section 3.3 of Chapter 3, along with detail of the RFI calculation method. In summary, to obtain the individual RFI over 301-d, a total of 301-d actual energy intake values was linearly regressed on total of 301-d estimated traits of metabolic body weight, milk production energy requirement, and empty body weight change. In a population, the mean RFI for all individuals is always zero, and half of all animals have RFI values below and the other half above the mean. Animals with RFI less than zero are generally considered more efficient (Basarab et al., 2007; Crews, 2005).

5.2.3. Parameter Estimation

SAS PROC GLM (SAS 9.3) was used to determine which fixed effects were significant ($P < 0.10$) for each of the derived intake, production, efficiency and selected conformation traits. The significant terms were: mean for all traits; total days in milk, Year×Season, and calving age for LFCM, LECM, LFCR, and LGEE; number of observations for ABW and ABCS; round, and stage of lactation for the type traits. A bivariate animal mixed model was used to estimate heritabilities and phenotypic and genetic correlations for the traits based on the series of pair wise analyses. The fixed effects were specified for each trait, and animal additive genetic effects were added for parameter estimation. The applied bivariate model and its elements were described in detail in section 4.2.4 of Chapter 4. The pedigree file was the same as used .in Chapter 4. Prior estimates of additive and phenotypic variance and covariance were obtained from univariate analyses and then genetic and residual (co)variances and related parameters were estimated using bivariate models as described above using ASREML-W (Gilmour et al., 2010). Estimated (co)variance components were from the bivariate analyses as well as from the relevant genetic and residual parameters and their associated standard errors.

5.3. RESULTS AND DISCUSSION

5.3.1. Descriptive Statistics

Descriptive statistics for intake, production, and efficiency traits are shown in Table 5.1. The average of lactation fat corrected milk, dry matter intake, actual energy intake per day and body weight were 30.9 (kg), 19.5 (kg), 35.1 (Mcal NE_L), and 570.0 (kg), respectively (Table 5.1). The mean of 3.5% fat corrected milk, energy intake, and body weight in this study were higher than those reported by Canadian researchers (Moore et al., 1990; Parke et al., 1999), but slightly lower than the average reported by Vallimont et al. (2010) in the United States. Parke et al. (1999) studied 36,115 first lactation Holstein cows from 4,466 herds and reported an average fat corrected milk, energy intake, and estimated body weight of 20.2 (kg), 27.7 (Mcal NE_L), and 532.8 (kg), respectively in Quebec, Canada. The higher average fat corrected milk in this study compared to other Canadian studies (Moore et al., 1990; Parke et al., 1999) could be attributed to genetic and management improvements in the last 20 years. This is at least partially supported by the 107 kg/cow/d increase in milk production from 1991 - 2011 in Holsteins by DHI (2012). It may also be inferred that Canadian dairy cattle are under intense selection for milk, fat, and protein production (Parke et al., 1999), similar to genetic trends reported in the United States and other countries outside North America.

The association of dry matter and energy intakes with milk production may justify the higher DMI and AEI found in this study similar to finding of other studies (Veerkamp and Brotherstone, 1997; Parke et al., 1999). Applying measured body weight values in the present study led to mean values of BW that differed from values in other studies that used estimated BW values from heart girth (Moore et al., 1990; Vallimont et al., 2010). In addition, the average of lactation gross energy efficiency was higher (0.90 vs. 0.75) than that reported by Parke et al. (1999), which could be attributed to the higher amount of milk yield in this current study and dilution of maintenance requirements and positive auto-correlation between milk production and feed efficiency.

All of the linear conformation traits had a scale of 1 to 9, while each of the major traits had a different range. The overall conformation trait ranged from 640 to 840, and the mammary system trait ranged from 40 to 85; Dairy strength and rump traits ranged from 46 to 90 and from 50 to 88, respectively. All the ranges were similar to previous reports on conformation traits in dairy cows (Canadian Dairy Network, 2006; Miglior et al., 2008).

5.3.2. Heritabilities

Average estimated heritabilities and their associated standard errors generated from bivariate analyses for intake, production, and efficiency traits are reported on the diagonal of Table 5.2. The estimate for lactation actual energy intake (0.27 ± 0.07) was within the range of heritabilities reported in the literature (0.16 to 0.48) (Veerkamp and Emmans, 1995). However, the energy intake heritability estimate (0.27 ± 0.07) was higher than the 0.21 reported by Parke et al. (1999) and the 0.18 reported by Vallimont et al. (2010). Higher heritability estimations for intake traits in the current study may reflect the accuracy of individual feed intake measurements, or it may be due to the sampling variance attributable to the present population size and numbers of records.

Estimated heritability for lactation fat corrected milk was slightly larger (0.37 ± 0.05) but similar to what was reported in previous studies (0.33) by Lee et al. (1992), Parke et al. (1999), and VanRaden et al. (2009). Estimated heritability of average body weight was higher than that of reported by Moore et al. (1990) at 0.23 but lower than Vallimont et al. (2010) at 0.60, whose study estimated the BW from heart girth measurements. In the literature, a wide range of heritability estimates has been reported for BCS (0.08 to 0.60), where previous studies' results varied with respect to stage of lactation (Bewley et al., 2008). The difference between our results and those available in the literature may be due to the average of BW and BCS over the 301-d lactation period in our study, rather than within specific subsets of time within a lactation period.

The estimated heritability for LFCR (0.25 ± 0.02) in this study, was similar to that reported by Parke et al. (1999) who also considered FCR as a ratio of FCM and the total energy intake over 305-d. However, the estimate of LGEE was lower than (0.29 vs. 0.38) that reported by Van Arendonk et al. (1991), whose study was restricted to the first 15 weeks of lactation rather than over 301-d. The difference could be due to the length of the study period, since a range of 0.12 to 0.63 was reported in the literature for feed efficiency traits (FCR and GEE) depending on the stage of lactation (Parke et al., 1999). Estimated heritability for RFI over 301-d, (0.20 ± 0.03) was similar to that reported by Van Arendonk et al. (1991) for the first 105-d of lactation, but it was different from the results of Vallimont et al. (2011) at 0.07 over 305-d. Vallimont et al. (2011) measured feed intake six times over 305-d during lactation and concluded that their method of feed intake measurement was not sensitive enough to capture the difference among the animals.

Estimates of heritability for conformation traits are presented in Table 5.4 and ranged from 0.07 for udder texture to 0.47 for stature. Schaeffer (1983) estimated the heritabilities of 28 conformation traits and reported a range from

0.07 for udder texture to 0.42 for stature. In addition, the Canadian Dairy Network (2007) analyzed 29 conformation traits, and reported heritability estimates ranging from 0.13 for foot angle to 0.53 for stature. Overall, most of the heritability estimates for the conformation traits considered in this study were higher than those reported by Schaeffer (1983), but comparatively lower than those reported by the Canadian Dairy Network (2007) although the ranking of the estimates by magnitude were similar.

5.3.3. Phenotypic and Genetic Correlations among Intake, Production, and Efficiency Traits

Phenotypic (upper diagonal) and genetic (below diagonal) correlations, along with their standard errors among intake, production and efficiency traits are shown in Table 5.2. It is noteworthy that in most cases, standard error (**SE**) associated with genetic correlation estimates in this study were comparable in magnitude to the correlation estimates themselves, reflecting relatively small numbers of animals with records. As expected, LDMI with LAEI, and LFCM with LECM had genetic and phenotypic correlations that were greater than 0.90, and LFCR genetically (-0.94) and phenotypically (-0.91) was highly correlated with LGEE. The traits with strong phenotypic and genetic correlations, generally 0.90 or higher, could be considered genetically equivalent, such that the two traits could share nearly equivalent genetic control and/or an extensive part-whole relationship. Hence, amongst the highly correlated traits, LDMI, LFCM, and LFCR were considered genetically similar with regard to their association with production and efficiency traits hereafter.

The lactation dry matter intake and fat corrected milk had highly positive phenotypic (0.54) and genetic (0.69) correlations, which were comparable with literature values reported by Van Arendonk et al. (1991) and Vallimont et al. (2010). Positive correlations were expected, since dairy cows were fed based on their level of milk production. Lactation dry matter intake and average body weight had positive phenotypic (0.51) and genetic (0.46) correlations, and these positive correlations are similar to those previously reported in other studies (Van Arendonk et al., 1991; Veerkamp and Brotherstone, 1997; Vallimont et al., 2010), indicating that animals with larger BW consume more feed. However, the lactation fat corrected milk had a positive phenotypic correlation (0.17), but a negative genetic correlation (-0.37) with average BW in this study. A wide range of genetic (-0.42 to 0.48) correlations between FCM and BW have been reported in the literature (Veerkamp and Emmans, 1995; Parke et al., 1999; Vallimont et al., 2010). These results indicate that large cows may not necessarily produce more milk. This conclusion is supported by Vandehaar (1998), whose results suggest an optimum point of relationship between milk production and BW.

Both LDMI and LFCM had near zero phenotypic and moderately negative genetic correlations with ABCS. These results were not in agreement with Vallimont et al. (2010), who reported positive genetic correlations of 0.37 and 0.38 for BCS with both DMI and FCM, respectively. The inconsistency of our results with those of Vallimont et al. (2010) may be because we used an average BCS over 301-d in this study, rather than analyzing it in different stages of lactation. The moderately negative correlation in this study suggests that on average, losing BCS may be accompanied with an increase in LFCM. This is supported in a review by Bewley et al. (2008) who summarized that losing one unit of BCS increases milk production by around 2000 kg over a 305-d lactation period (Bewley et al., 2008).

Lactation FCR and DMI had low phenotypic and genetic correlations of 0.12 and 0.03, respectively. Lactation FCR had positive phenotypic and genetic correlations of 0.15, and 0.18, respectively, with average BW, but negative correlations of -0.75, and -0.78, respectively with lactation FCM. The direction of the correlations followed the results of Parke et al. (1998). Results also suggested that LFCR was most likely influenced by production (ABW and LFCM) rather than by dry matter intake, indicating that phenotypically and genetically, LFCR would favour the animals with smaller body weight and higher milk production. RFI, however, had strong positive genetic and phenotypic correlations with LDMI, which is supported by reports from other dairy researchers (Van Arendonk et al., 1991; Vallimont et al., 2011), and is similar to results from beef cattle showing highly positive genetic correlations of DMI and measures of body weight and size during performance tests (Archer et al., 1999; Crews, 2005). The phenotypic correlations of RFI with lactation FCM (0.07) and average BW (0.06) were near zero, yet genetic correlations of RFI with lactation FCM (-0.13) and average BW (-0.29) were negative. The phenotypic correlation results were in agreement with the study of Van Arendonk et al. (1991), who also reported almost zero phenotypic correlations between RFI with BW and FCM over 105-d. However, the genetic correlation results were not in agreement with Van Arendonk et al. (1991), who reported near zero genetic correlations of RFI with both BW and FCM over 105-d. The contrast in these results may be due to the duration of the RFI test, the difference in age at measurement, and the method of RFI prediction. The genetic correlations between RFI and production traits were supported by other researchers in beef cattle (Mao et al., 2013), pigs (Hoque and Suzuki, 2011), and with simulated data (Kennedy et al., 1993). Kennedy et al. (1993) showed that RFI is by definition phenotypically independent of its component traits, but can have non-zero genetic correlation with production. Subsequently, Kennedy et al. (1993) proposed an alternative RFI prediction method which utilizes genetic information with the resulting metric termed genetic RFI (**RFIg**). RFIg, *per se*, is genetically independent of the production traits, which has been further discussed by others (e.g., Crews, 2005). Therefore, RFIg may provide breeders with a tool to select efficient animals without compromising the production level (Kennedy et al., 1993). Further investigations are encouraged to calculate RFIg and its correlations with other traits.

5.3.4. Genetic and Phenotypic Correlations of Intake, Production, and Efficiency with Conformation Traits

Phenotypic and genetic correlations between the 15 selected conformation traits and intake, production, and efficiency traits are presented in Tables 5.3 and 5.4, respectively. Phenotypic correlations of LDMI with conformation traits were from near zero with FL (-0.03) to moderately positive with RAW (0.43); most of these moderate correlations differed significantly from zero ($P < 0.01$) (Table 5.3). Lactation dry matter intake had a negligible genetic correlation with UT (0.05), but moderate to high correlations with BD (0.44), AN (0.44), FL (-0.45), ST (0.45), DS (0.50), RAW (0.51), HF (0.57), and CW (0.68). The genetic correlations among lactation dry matter intake with stature and chest width were significant ($P < 0.05$). The previous studies have determined correlations between intake, production, and feed efficiency traits with limited numbers of conformation traits (stature, and rump width), similarly strong phenotypic and genetic correlation values have been previously reported (Parke et al., 1999; Vallimont et al., 2010).

Average BW had moderate to high positive phenotypic and genetic correlations with DS and its component traits (ST, HF, CW, and BD), but weak and negative phenotypic and genetic correlations with MS (0.02, and 0.09, respectively) and its component traits (UD, UT, RAH, and RAW). The moderate to high phenotypic correlations among average BW with DS and its component traits were significant ($P< 0.01$) (Table 5.3), but their genetic correlations were not significant most likely because of high standard error of estimation ($P > 0.05$) (Table 5.4). These results were comparable with those reported for similar traits in other previous studies (Parke et al., 1999; Berry et al., 2004; Vallimont et al., 2010) and, along with the present results, suggest the potential for using DS and its component traits to predict phenotypic and genetic variability of BW in dairy cattle.

Phenotypic correlations of lactation FCM and conformation traits were near zero, but the corresponding genetic correlations ranged from near zero for OC (-0.05) to moderately negative for PW (-0.39). The phenotypic correlations between lactation FCM and most of the selected conformation traits, especially MS and its component traits, were significant ($P < 0.01$). However, lactation FCM had significant ($P < 0.05$) genetic correlation with UD and PW. Short and Lawlor (1992) analyzed correlations between milk yield and some selected conformation traits. They reported parameters for four conformation traits in their study (ST, BD, UD, and OC), and like our study found similar phenotypic and genetic correlations between milk yield and those four conformation traits.

Lactation FCR had low phenotypic correlations with all conformation traits except AN (-0.26). It had moderate to high and positive genetic correlations with body size-related traits (DS, ST, HAF, CW, and BD), but strong negative genetic correlations with milk production related traits (RAH and RAW). These results are in agreement with the results reported by Parke et al. (1999) who also supports our earlier conclusion on lactation FCR relationships with BW and milk production that animals with smaller body weight and more milk production were efficient based on lactation FCR.

Phenotypic correlations of RFI with conformation traits were low, except RAW (0.29). However, among these correlations RFI had significant ($P < 0.05$) phenotypic correlations with DS, RAW, CW, and PW. Further, RFI had moderate to high positive genetic correlations with PW (0.39), RAW (0.41), AN (0.41), OC (0.46), MS (0.56), and moderately negative genetic correlations with RU (-0.45), FL (-0.41), and HF (-0.55). However, none of these correlations were significant ($P < 0.05$), most probably due to the large standard error of estimates. Estimated genetic correlations of RFI with eight conformation traits were moderate to high. The combinations of these traits may be useful correlates of selection for RFI. To the best of our knowledge, this is the first study that has attempted to determine the correlations between RFI and various combinations of conformation traits in dairy cattle. As such, we cannot offer an extensive direct comparison of the results of this study with other work. The non-significance of genetic correlations results in the current research was due to a large standard error of estimations, which was caused by the relatively smaller sample size (n=239) and family size (2.16). A smaller family size means lower genetic connectedness between the animals. However, further investigations are encouraged by sharing the data to create a large sample size and to avoid the large standard error of estimations, which consequently is expected to validate the results.

Herd and Arthur (2009) reported that digestion process accounts for 10 % of RFI variation in beef cattle. It is also reported that dairy cows with negative RFI value had better apparent N digestibility than those with positive RFI value (Rius et al., 2012). In addition, Zhou et al. (2009) studied the association among rumen microbial ecology and feed efficiency in 48 heifers of their 10 months old. They reported that the differences among cattle with different feed efficiency capacities could be due to methanogenic ecology in the rumen. Further investigations are encouraged to study whether any associations among rumen microbial function and efficiency in dairy cows exist, which can be used to find indicator traits for RFI.

5.4. CONCLUSION

Results indicated that RFI was moderately heritable and, as expected, largely reflects the (co)variance structure among component traits using in its computation. Therefore, there is potential to develop selection tools to improve feed utilization in dairy cattle using intake. Eight conformation traits had moderate to high genetic correlations with RFI, and their combination may be used as indicators of RFI to overcome difficulties in measuring and costs associated with individual feed intake. It should be noted that RFI had near zero phenotypic correlations with production traits as expected, while having potentially non-zero genetic correlations with production traits. Therefore, animal selection based on phenotypic RFI may raise concerns in a long term response to direct selection, especially with regard to production traits. Future research should focus on using both directly economic dairy traits and their indicators to develop genetic improvement tools with higher accuracy but lower cost.

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Table 5.1. Descriptive statistics for intake, production, and efficiency traits

	LDMI	LAEI[2]	ABW[3]	ABCS[4]	LFCM[5]	LECM[6]	LFCR[7]	LGEE[8]	RFI[9]
Mean	5804.91	10410.00	570.55	3.00	9435.57	9416.58	0.62	0.90	-0.06
Min	3775.47	6393.37	463.00	2.55	4857.48	4840.29	0.46	0.65	-4.38
Max	7929.86	14115.97	738.44	3.50	13456.67	13214.48	0.85	1.17	5.37
SD[10]	655.08	1246.41	42.67	0.18	1398.49	1326.76	0.08	0.09	1.76

[1]LDMI = Lactation Dry matter intake over 301-d (kg); [2]LAEI = Lactation actual energy intake over 301-d (Mcal NE_L/kg); [3]ABW = Average body weight over 301-d (kg); [4]ABCS = Average body condition score; [5]LFCM = Lactation fat corrected milk over 301-d (kg); [6]LECM = Lactation energy corrected milk over 301-d (kg); [7]LFCR= Lactation feed conversion ratio over 301-d; LDMI/LFCM; [8]LGEE= Lactation gross energy efficiency over 301-d; LECM/LAEI; [9]RFI= Average residual feed intake over 301-d (Mcal NE_L); [10]SD= Standard Deviation

Table 5.2. Heritabilities (diagonal), phenotypic (upper diagonal) and genetic correlations (below diagonal) among intake, production and efficiency traits (± SE)

	LDMI[1]	**LAEI**[2]	**ABW**[3]	**ABCS**[4]	**LFCM**[5]	**LECM**[6]	**LFCR**[7]	**LGEE**[8]	**RFI**[9]
LDMI	**0.28±0.06**[10]	0.91±0.05**	0.51±0.05**	-0.04±0.03	0.54±0.05**	0.57±0.05**	0.11±0.07	-0.17±0.07**	0.49±0.05**
LAEI	0.96±0.03**	**0.27±0.07**	0.50±0.05**	-0.07±0.06	0.56±0.05**	0.59±0.06**	0.01±0.07	-0.16±0.06**	0.61±0.08**
ABW	0.46±0.22*	0.47±0.23*	**0.42±0.05**	0.50±0.06**	0.17±0.07**	0.20±0.07**	0.15±0.09	-0.15±0.08	0.06±0.08
ABCS	-0.57±0.41	-0.67±0.43	0.35±0.22	**0.45±0.08**	-0.12±0.09	-0.10±0.08	0.08±0.07	-0.11±0.08	0.02±0.08
LFCM	0.69±0.16**	0.67±0.15**	-0.31±0.45	-0.07±0.22	**0.37±0.05**	0.97±0.01**	-0.75±0.03**	0.67±0.04**	0.07±0.05
LECM	0.71±0.15**	0.70±0.14**	-0.28±0.44	-0.06±0.23	0.97±0.01**	**0.39±0.05**	-0.73±0.04**	0.66±0.04**	0.08±0.06
LFCR	-0.03±0.32	-0.06±0.47	0.18±0.37	0.34±0.34	-0.78±0.14**	-0.77±0.15**	**0.25±0.03**	-0.94±0.01**	0.18±0.07**
LGEE	0.13±0.43	-0.18±0.44	0.07±0.35	-0.29±0.33	0.61±0.19**	0.59±0.19**	-0.90±0.07**	**0.29±0.02**	-0.35±0.06**
RFI	0.41±0.45	0.64±0.36	-0.29±0.54	-0.05±0.53	-0.13±0.59	-0.08±0.59	0.33±0.53	-0.57±0.42	**0.20±0.03**

**Statistically significant at $P < 0.01$; *Statistically significant at $P < 0.05$; [1]LDMI = Lactation Dry matter intake over 301-d (kg); [2]LAEI = Lactation actual energy intake over 301-d (Mcal NE_L/kg);[3]ABW = Average body weight over 301-d (kg); [4]ABCS = Average body condition score; [5]LFCM = Lactation fat corrected milk over 301-d (kg); [6]LECM = Lactation energy corrected milk over 301-d (kg); [7]LFCR= Lactation feed conversion ratio over 301-d; LDMI/LFCM;

[8]LGEE= Lactation gross energy efficiency over 301-d; LECM/LAEI; [9]RFI= Average residual feed intake over 301-d (Mcal NE_L); [10]Diagonal elements are average of heritability estimations ± Standard error of estimates from bivariate analysis

Table 5.3. Phenotypic correlations among intake, production, efficiency, scored conformation and linear conformation traits

	OC[10]	MS[11]	DS[12]	RU[13]	FL[14]	AN[15]	UD[16]	UT[17]	RAH[18]	RAW[19]	ST[20]	HF[21]	CW[22]	BD[23]	PW[24]
LDMI	0.24**	0.15*	0.39**	0.21**	-0.03	0.23**	-0.13	-0.06	0.07	0.43**	0.32**	0.04	0.35**	0.24**	0.17**
SE	0.06	0.07	0.06	0.07	0.07	0.07	0.07	0.07	0.07	0.05	0.06	0.07	0.06	0.07	0.06
LAEI[2]	0.28**	0.15*	0.41**	0.24**	0.01	0.27**	-0.13	-0.02	-0.07	0.42**	0.29**	0.05	0.33**	0.26**	0.18**
SE	0.06	0.07	0.06	0.06	0.07	0.06	0.07	0.07	0.07	0.06	0.06	0.07	0.06	0.07	0.06
ABW[3]	0.11	0.02	0.37**	-0.07	0.11	-0.03	-0.11	-0.13	-0.13	0.25**	0.45**	0.11	0.45**	0.30**	0.20**
SE	0.07	0.08	0.05	0.08	0.07	0.07	0.07	0.07	0.07	0.07	0.06	0.07	0.05	0.07	0.06
ABCS[4]	0.03	0.07	-0.05	-0.17*	0.04	-0.34**	0.08	-0.26**	-0.05	0.11	-0.03	0.05	0.28**	-0.05	-0.04
SE	0.07	0.07	0.07	0.07	0.07	0.06	0.07	0.06	0.07	0.07	0.07	0.07	0.07	0.07	0.04
LFCM[5]	0.14**	0.18*	0.21**	0.09	0.07	0.25**	-0.24**	-0.02	0.08	0.18**	0.08*	-0.02	0.02	0.10*	0.03
SE M	0.04	0.08	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04
LECM[6]	0.15**	0.21**	0.22**	0.10*	0.05	0.24**	-0.23**	-0.03	0.08	0.20**	0.09*	-0.01	0.04	0.09*	0.06
SE	0.04	0.08	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.09
LFCR[7]	-0.11	-0.12	-0.14*	-0.08	0.10	-0.26**	0.12	-0.10	-0.08	-0.12	-0.02	0.07	0.09	-0.05	0.07
SE	0.07	0.07	0.07	0.07	0.07	0.07	0.08	0.07	0.07	0.07	0.08	0.07	0.07	0.08	0.07
LGEE[8]	0.08	0.08	0.11	0.03	-0.08	0.20	-0.11	0.07	0.08	0.09	0.01	-0.08	-0.07	0.02	-0.09
SE	0.07	0.08	0.06	0.07	0.08	0.07	0.08	0.07	0.07	0.08	0.08	0.08	0.07	0.08	0.07
RFI[9]	0.12	0.11	0.14*	0.10	0.04	0.12	0.04	-0.05	0.01	0.29**	0.12	0.01	0.17*	0.09	0.15*
SE	0.07	0.07	0.07	0.08	0.09	0.08	0.08	0.08	0.07	0.07	0.08	0.08	0.08	0.07	0.07

**Statistically significant at $P < 0.01$; *Statistically significant at $P < 0.05$; [1]LDMI = Lactation Dry matter intake over 301-d (kg); [2]LAEI = Lactation actual energy intake over 301-d (Mcal NE_L/kg); [3]ABW = Average body weight over 301-d (kg); [4]ABCS = Average body condition score; [5]LFCM = Lactation fat corrected milk over 301-d (kg); [6]LECM = Lactation energy corrected milk over 301-d (kg); [7]LFCR= Lactation feed conversion ratio over 301-d; LDMI/LFCM;[8]LGEE= Lactation gross energy efficiency over 301-d; LECM/LAEI; [9]RFI= Average residual feed intake over 301-d (Mcal NE_L); [10]OC = Overall conformation; [11]MS = Mammary system ; [12]DS= Dairy strength ; [13]RU= Rump;[14]FL= Fee and Legs; [15]AN = Angularity; [16]UD = Udder depth ; [17]UT = Udder texture; [18]RAH = Rear attachment height; [19]RAW = Rear attachment width; [20]ST = Stature; [21]HF = Height at front; [22]CW = Chest width ; [23]BD = Body depth; [24]PW = Pin width

Table 5.4. Genetic correlations among intake, production, efficiency, scored conformation and linear conformation traits

	OC[10]	**MS**[11]	**DS**[12]	**RU**[13]	**FL**[14]	**AN**[15]	**UD**[16]	**UT**[17]	**RAH**[18]	**RAW**[19]	**ST**[20]	**HF**[21]	**CW**[22]	**BD**[23]	**PW**[24]
LDMI	0.32	0.11	0.50	-0.12	-0.45	0.44	-0.26	0.05	0.11	0.51	0.45*	0.57	0.68*	0.44	0.22
SE	0.61	0.53	0.27	0.50	0.56	0.43	0.25	0.57	0.46	0.29	0.23	0.49	0.31	0.31	0.29
LAEI[2]	0.30	0.11	0.45	0.09	-0.53	0.47	-0.29	0.10	0.41	0.52	0.47*	0.33	0.68*	0.34	0.33
SE	0.70	0.45	0.27	0.29	0.63	0.43	0.26	0.61	0.49	0.29	0.23	0.50	0.34	0.33	0.32
ABW[3]	0.56	0.09	0.39	-0.44	0.39	-0.34	-0.15	-0.09	-0.05	-0.15	0.31	0.42	0.61	0.22	0.20
SE	0.44	0.34	0.24	0.27	0.43	0.38	0.23	0.45	0.41	0.33	0.18	0.37	0.56	0.23	0.21
ABCS[4]	0.34	0.26	0.16	0.06	-0.03	-0.46	0.05	0.33	0.26	0.02	-0.19	0.53	0.31	0.05	-0.14
SE	0.35	0.27	0.85	0.23	0.34	0.29	0.19	0.39	0.33	0.28	0.19	0.37	0.51	0.23	0.21
LFCM[5]	-0.05	-0.16	-0.05	0.16	-0.08	0.09	-0.36*	-0.11	0.27	0.29	0.01	-0.19	0.03	-0.22	-0.39*
SE M	0.37	0.26	0.23	0.21	0.31	0.27	0.14	0.37	0.24	0.22	0.17	0.26	0.25	0.18	0.15
LECM[6]	-0.05	0.16	-0.04	0.12	0.05	0.11	-0.34*	-0.10	0.23	0.33	0.02	-0.14	0.02	-0.25	-0.36*
SE	0.37	0.25	0.23	0.21	0.31	0.27	0.15	0.38	0.24	0.21	0.17	0.26	0.25	0.18	0.15
LFCR[7]	0.19	0.18	0.37	-0.37	0.37	-0.16	0.32	0.03	-0.49	-0.65	0.43	0.64	0.27	0.37	0.33
SE	0.67	0.51	0.43	0.46	0.63	0.54	0.29	0.71	0.46	0.38	0.33	0.54	0.48	0.40	0.30
LGEE[8]	-0.13	-0.19	-0.19	0.08	-0.27	0.01	-0.32	0.09	0.41	0.61	-0.32	-0.43	-0.18	-0.09	-0.41
SE	0.61	0.46	0.39	0.37	0.58	0.51	0.27	0.62	0.44	0.37	0.30	0.53	0.44	0. 36	0.27
RFI[9]	0.46	0.56	-0.18	-0.45	-0.41	0.41	0.11	0.09	0.16	0.42	0.16	-0.55	-0.05	0.11	0.39
SE	0.39	0.36	0.78	0.52	0.71	0.76	0.44	0.45	0.88	0.61	0.45	0.50	0.50	0.36	0.61
h^2	0.13	0.21	0.19	0.29	0.11	0.14	0.46	0.07	0.14	0.18	0.47	0.14	0.19	0.30	0.41
SE	0.09	0.08	0.08	0.03	0.03	0.02	0.04	0.03	0.03	0.03	0.10	0.04	0.09	0.08	0.07

*Statistically significant at $P < 0.05$; [1]LDMI = Lactation Dry matter intake over 301-d (kg); [2]LAEI = Lactation actual energy intake over 301-d (NE_L Mcal kg); [3]ABW = Average body weight over 301-d (kg); [4]ABCS = Average body condition score; [5]LFCM = Lactation fat corrected milk over 301-d (kg); [6]LECM = Lactation energy corrected milk over 301-d (kg); [7]LFCR= Lactation feed conversion ratio over 301-d; LDMI/LFCM; [8]LGEE= Lactation gross energy efficiency over 301-d; LECM/LAEI; [9]RFI= Average residual feed intake over 301-d (NE_L Mcal); [10]OC = Overall conformation; [11]MS = Mammary system ; [12]DS= Dairy strength ; [13]RU= Rump [14]FL= Foot and Legs; [15]AN = Angularity; [16]UD = Udder depth; [17]UT = Udder texture; [18]RAH = Rear attachment height; [19]RAW = Rear attachment width; [20]ST = Stature; [21]HF = High at front; [22]CW = Chest width ; [23]BD = Body depth; [24]PW = Pin width

CHAPTER 6. GENERAL DISCUSSION AND CONCLUSION

6.1. GENERAL DISCUSSION

Because feed cost is the single largest expense of dairy production (Vallimont et al., 2011), and feed efficiency is the greatest factor contributing to variation in carbon footprint (Thoma et al., 2010), improving feed efficiency in dairy cow could reduce production cost and green house gas emissions. Consequently, feed efficiency improvement may make the dairy production a more competitive and environmentally sustainable industry (Connor et al., 2013). The research for this thesis focused on investigating genetic and phenotypic variations of feed efficiency in dairy cattle, and the possibility of reducing the feed efficiency test period. The associations among feed efficiency, intake, production, and conformation traits were also examined.

The first study (Chapter 3) was aimed at developing an appropriate model to predict residual feed intake (**RFI**) in first lactation dairy cows. The developed model predicts RFI over the whole first lactation period accounting for the non-linear energy requirement profiles of metabolic body weight (**MBW**), empty body weight (**EBW**), and milk production energy requirements (**MPER**). Reported RFI prediction models in the literature were developed either using either data resulting from a short period (Van Arendonk et al., 1991; Connor et al., 2013) or whole lactation period with limited number of actual feed intake measurements (Coleman et al., 2010; Vallimont et al., 2011). Moreover, the random regression technique was used in this study to model the lactation profiles of RFI component traits, whereas most of the previous research groups applied the linear regression approach (Van Arendonk et al., 1991; Svendsen et al., 1993; Zamani et al., 2008). The mean of predicted daily average lactation RFI was zero and ranged from -6.58 to 8.64 Mcal NEL/day. The mean of zero for predicted RFI was also supported by other researchers (Van Arendonk et al., 1991; Coleman et al., 2010; Vallimont et al., 2011; Connor et al., 2013), but they reported a different range for predicted RFI. The different reported range for RFI in the literature may be mainly due to using a different energy intake unit, RFI test period, and farm management. The results of the present study indicate that the first lactation RFI can be predicted with an R-square of 0.68 in dairy cattle, and that a wide phenotypic range of feed efficiency existed among the animals based on RFI. The predicted RFI may be used in dairy breeding programs to increase profitability by selecting animals that are genetically superior in energy efficiency.

Shortening the RFI test period to reduce the test costs and make RFI test more applicable is of interest in dairy feed efficiency research. Therefore, the objective of the second study (Chapter 4) was to determine a reduced test period to be representative of the whole lactation period for RFI measures. Compared with the whole lactation period, large numbers (65.5%) of the animals maintained in the same RFI classes in mid stage of lactation than early and late stage. It could be inferred that the RFI prediction in the mid stage (106 – 205

DIM) is more consistent than the RFI prediction in early (5 – 105 DIM) and late (206 – 305 DIM) lactation. Consistent with our results, Connor et al. (2013), who used 32 high-yielding Holstein cows, concluded that RFI measured after 100 DIM may provide better estimates of efficiency during the full lactation cycle than the early lactation. In addition, the present research revealed that the RFI prediction in whole lactation cycle had a high and significant phenotypic correlation with the RFI predication in each of the three shortened test periods (early, mid and late); however, the whole RFI had only a significant genetic correlation with mid RFI. To the best of the author's knowledge, this is the first study about dairy cattle to estimate the genetic correlation among RFIs in different test periods and to investigate RFI class changes in different stage of lactation. It could be suggested that mid-RFI may be a more reliable predictor of the whole lactation RFI, and that future dairy feed efficiency research may consider testing the first lactation animals for RFI at mid the stage of lactation .

The genetic and phenotypic parameters among RFIs obtained from different stages of lactation and their component traits were also examined in Chapter 4. Results of this study revealed that moderate repeatability (0.51 ± 0.04) was estimated for RFI prediction across the stages of lactation which was in line with Connor et al. (2013) at 0.47 for the first 90 DIM. The results showed that RFI had strong and significant phenotypic and genetic correlations with actual energy intake (**AEI**) within each test period, which was consistent with the findings of other researchers (Van Arendonk et al., 1991; Vallimont et al., 2011). RFI had a close to zero phenotypic correlations with its component traits, but it had low and non-significant genetic correlations with MBW and MPER within each test period. Among all the published reports about dairy cattle, only Van Arendonk et al. (1991) examined the genetic correlations between RFI and its component traits and reported that the correlations were close to zero. The phenotypic and genetic correlations of RFI with AEI, MBW, EBWC, and MPER infer that selecting for RFI in any of the test periods could decrease feed intake without phenotypically compromising the production level. Although RFI had the non-significant genetic correlation with MBW and MPER, selection for RFI could raise a long term concern on responses of MBW and MPER in dairy industry.

Individual feed intake measurement is the industry-wide limiting factor to the feed efficiency selection in dairy breeding program. Indirectly selecting for feed efficiency on correlated traits may be an alternative approach to overcome this limitation. Including conformation traits in the present study provided an opportunity to test them as indicator(s) for feed efficiency, particularly RFI, and production traits. The associations among whole lactation RFI with intake and production traits were examined in Chapter 5. Body weight had strong positive phenotypic and genetic correlations with dairy strength and its composite traits (stature, height at front, chest width, and body depth). It could be suggested that dairy strength and its composite traits could be used to predict phenotypic and genetic variability of body weight in dairy cattle, and this result confirms the earlier achievement by Parke et al. (1999) and Vallimont et al. (2011). RFI prediction had low phenotypic correlations with almost all of the selected conformation traits. It had moderate positive genetic correlations with pin width

(0.39), rear attachment width (0.41), angularity (0.41), overall conformation (0.46), and the mammary system (0.56), and moderate negative genetic correlations with the rump (-0.45), feet and legs (-0.41), and height at front (-0.55). This is the first study that examined the association between RFI with conformation traits. Therefore, future discussion and comparison of these results were limited. Overall, correlations among feed efficiency and production traits determined that the feed conversion ratio (**FCR**) was mostly affected genetically and phenotypically by milk production and body weight rather than energy intake. It is also suggested that selecting for FCR would increase milk production and body weight but have less or even no effect on energy intake, which it is not the goal of feed efficiency improvement. In contrast, selecting for RFI would decrease energy intake without compromising production level, so RFI is the more desirable measure of energy efficiency than FCR for the dairy industry. The combinations of highly correlated conformation traits could be used as indicator traits for RFI selection in dairy breeding programs.

6.2. GENERAL CONCLUSION AND FUTURE RESEARCH DIRECTIONS

The results of the present research showed that RFI was predictable during the whole lactation period and within any stages of lactation. There are phenotypic and genetic variations for RFI among first lactation dairy cows. In addition, RFI had moderate heritability and repeatability across the stages of lactation. In contrast with FCR, RFI had a high correlation with feed intake and was independent of production level. Therefore, RFI could be used as a tool to improve feed efficiency in dairy cattle, to increase profitability of the dairy industry, and reducing green house gas emissions. Since the RFI prediction in the mid lactation period had significant genetic and phenotypic correlations with RFI prediction in the whole lactation period, it could be suggested that RFI prediction in the mid lactation period is a more reliable indicator of whole lactation RFI, compared to early and late lactation RFIs. Moreover, the eight conformation traits including overall conformation had moderate genetic correlations with RFI. Combinations of these routinely measured correlated traits may be used as indicator traits for RFI indirect selection in dairy breeding program to avoid difficulties in measuring and costs associated with individual feed intake.

Implication RFI results in the dairy-industry poses some limitations since research on feed efficiency in dairy cattle has been recently promoted; there are still many issues to be addressed. However, results of decade of research on beef cattle could benefit dairy researchers, as there are concerns common to both types of cattle. For example, the results of a survey of 902 beef cattle producers concluded that the “RFI concept is complex and not readily understood when first encountered, even for trained scientists” (Wulfhorst et al., 2010). Therefore, more socio-economic studies are needed on feed efficiency. In addition, the animals used in this research were all Holstein breed and in their first parity under same management system. To apply the RFI results industry-wide, some proposals are required specifically to standardize the test across herds. A standardized test protocol for evaluating RFI in beef cattle includes age restriction, length of test period, frequency of body weight measurements, and length of acclimation feed intake records. In dairy cattle, additional factors including herd, year, season, parity, breed, and milking frequency may need to be standardized across testing sites. Moreover, some research is required on RFI economic potentials for adopting by industry.

A total of 281 animals with relatively small family size (n = 2.16) were used in this study, which was reflected in the high standard error of estimation for most of the genetic correlation estimations. Further researchers are encouraged to enlarge the sample size by either accumulating more data or sharing data with other institutions to further validate the present results. Thus far, all published results including the recent research, irrespective of the definition of feed efficiency, have focused on a specific period of the animals' production life, such as early or whole lactation period. Further investigations are recommended to study feed efficiency in the animals' entire economic life-time. These studies would be able to address the questions related to any ”compensatory effects” after the test period and any impact of selection for efficiency on other traits such as survival in the long term. Any gain in feed efficiency could be neglected due to reduced reproductive performance and health status in dairy cows; therefore, investigating the association between RFI with reproduction and health traits is also recommended. Using the automated GrowSafe feeding system (GrowSafe Systems Ltd., Airdrie, Alberta, Canada) in beef cattle provides more opportunity to study RFI and its association with behavioral traits (Kelly et al., 2010; Durunna et al., 2013). Therefore, with adapting an automated feed intake measurement system in dairy, it is worth investigating further to test some of the behavioral traits such as feeding duration as indicator traits for RFI. Since difference in apparent N digestibility is reported among high RFI and low RFI groups of dairy cows (Rius et al., 2012), it would worth to study the association among rumen microbial function and RFI. Quantitative genetic analysis of phenotypic records with pedigree information has been yielded substantial gain (Berry and Crowley, 2013). However, this approach has some limitation including limitation on the numbers of phenotype records, antagonist genetic correlations among traits, and interaction environment by genetic for most of the traits. To overcome these limitations a lot is to be gained in the investigation of genomic information. Genomic studies for feed efficiency traits can include genome wide association studies, candidate gene, or candidate regions studies.

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