GENETICS OF FEED INTAKE AND EFFICIENCY IN GRAZING DAIRY COWS

A thesis presented in partial fulfilment of the requirements

for the degree of

Doctor of Philosophy

in

Animal Science

MASSEY
UNIVERSITY
TE KUNENGA KI PŪREHUROA
UNIVERSITY OF NEW ZEALAND

Alan Michael Hurley

2017

Abstract

Hurley (2017). Genetics of Feed Intake and Efficiency in Grazing Dairy Cows. PhD Thesis, Massey University, New Zealand

Feed efficiency in dairy cows is widely acknowledged as a highly desirable characteristic to improve because of its well-documented impact on production costs. Traditional measures of feed efficiency have used ratio traits, specifically energy conversion efficiency, but these have undesirable statistical properties. Alternative measures of feed efficiency are those based on the residuals from regression-type statistical models, the most common of which is residual energy intake (**REI**). Residual energy intake is defined as the difference between actual and predicted intake and is usually derived from least squares regression models. The general objective of this thesis was to quantify phenotypic and genetic (co)variances between the feed intake complex, performance, and fertility traits in lactating Holstein-Friesian dairy cows. A total of 8,199 feed intake records from 2,693 lactations on 1,412 grazing lactating Holstein-Friesian dairy cows from experimental farms were used. Several alternative efficiency definitions were developed, each with their own respective strengths and weaknesses. Exploitable genetic variation was demonstrated to exist for the range of alternative efficiency traits, and the magnitude of this variation was sufficiently large to justify consideration of the feed efficiency complex in future dairy breeding goals. The heritability estimates for the different efficiency traits estimated using repeatability models varied from 0.06 to 0.21. Variance components, however, differed across lactation when estimated using random regression models; for example, the heritability of REI varied from 0.04 (34 DIM) to 0.11 (280 DIM) across lactation. Phenotypic correlations among many traits including REI and energy balance (EB) differed not only by stage of lactation but also by cow parity. Moderate to strong genetic correlations existed between REI and EB across lactation (ranging from 0.45 to 0.90). Albeit associated with large standard errors, estimated genetic correlations between feed efficiency and reproductive performance were either neutral or favourable suggesting greater genetic merit for feed efficiency does not appear to be antagonistically genetically correlated with reproductive performance. Selection index calculations using the current economic weights in the Irish Economic Breeding Index, and genetic (co)variances estimated in this thesis, indicate that the inclusion of REI in the index with an economic weight of €0.078/UFL will generate animals with improved REI.

Declarations

This thesis contains no material that has been accepted for a degree or diploma by the University or any other institution. To the best of my knowledge no material previously published or written by another person has been used, except where due acknowledgement has been made in the text.

This thesis has been written with chapters formatted as papers for publication. Therefore there is some repetition of chapter methods; each chapter contains a full discussion, with the final general discussion chapter providing a succinct discussion of key findings of this thesis. Each chapter has been formatted for the Journal of Dairy Science and each chapter has a complete list of references. The submitted manuscripts include supervisors as co-authors; however, for each chapter I planned the study, undertook the analysis and wrote the manuscripts with directions of those co-authors.

Acknowledgements

This PhD provided me with the opportunity to work with a number of remarkably talented and dedicated professionals and friends, for which I am grateful. I would like to acknowledge the opportunity presented to me by Teagasc and Massey University to carry out this work. Funding from the Irish Department of Agriculture, Food and Marine Research Stimulus Fund project GENCOST is greatly appreciated.

I would like to acknowledge the support, advice, and guidance of my supervisors, Prof Nicolas Lopez-Villalobos, Prof Donagh Berry and Dr Jennifer Burke throughout my PhD. I'm very appreciative of having had the opportunity to work with world leaders in computational genetics and genomics. To Prof Nicolas Lopez-Villalobos thank you for your never-ending support and enthusiasm, for immensely stimulating scientific discussions and for guiding and inspiring me with your teachings throughout this research journey. To Prof Donagh Berry, I extend my sincere gratitude for the support you provided me with over past four years. Your teaching in genetic and mathematical statistics is unmatched and has strongly contributed to my growth as a scientist. Without your help I wouldn't be in this position today. You've never been hesitant in sharing your wisdom, you've shown the world what great supervisors are all about. I acknowledge my other co-supervisor Dr Jennifer Burke who was always willing to attend meetings and offer advice wherever possible. Finally, I would also like to thank my other co-authors Dr Sinead McParland, Dr Eva Lewis, Dr Michael O'Donovan and Dr Emer Kennedy whose valuable comments made this thesis what it is today.

The support of IVABs staff and students in particular Prof Kevin Stafford (thanks for the great conversations over coffee!), Miss Debbie Hill and Dr Penny Back are greatly acknowledged. To my friends Nick, Felipe, Charlotte, and Paolo thanks for making my time in New Zealand as enjoyable and rewarding as it was. Huge thanks to Nick, Giulio, and Tara for their insightful comments and encouragement during my doctoral studies. To my fellow students in Moorepark particularly those I shared offices with cheers for all the good times. A special thanks to Sinead for your support and encouragement. To the Irish crew all the St. Croans lads thanks for all the great times together.

Special thanks to Garth and Renee, you guys were a second family to me in New Zealand. Your warm welcome, staunch support, sagacious advice and guidance are truly appreciated. It was great to have a family to come home to in the evenings, chat together and have the craic. Not forgetting Toko and Bo and my great equine friend Pedro. The gym sessions with Garth will always remain with me (I'll be back to HOOFIT soon!). You folks epitomise New Zealand hospitality and moving onto pastures new has definitely made me realise what a great time we had together.

Finally, I would like to thank my family, Mum, Dad, John and Sinead, for all their love and support, and believing in me throughout this project. I wish to dedicate this thesis to my parents, John and Eithne, for the major contributions and sacrifices they have made throughout my education.

Go raibh maith agaibh as bun mo chroí.

"One day, in retrospect, the years of struggle will strike you as the most beautiful"

Sigmund Freud

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List of Abbreviations

AFC = Age at first calving
BCS = Body condition score
BW = Body-weight
$BW^{0.75}$ = Metabolic body-weight
CFS = Calving to first service interval
CIV = Calving interval
CV = Coefficient of variation
DIM = Days in milk
DMI = Dry matter intake
EB = Energy balance
ECE = Energy conversion efficiency
ECE_{adj} = Energy conversion efficiency adjusted
ECE_{maint} = Energy conversion efficiency taking account of maintenance
ECR = Energy conversion ratio
EBI = Economic breeding index
EBV = Estimated breeding values
FC = Fat concentration
FtW = Feed to body-weight
ICBF = Irish cattle breeding federation
KG = Kilogram
KR = Kleiber ratio
LC = Lactose concentration
MEff = Metabolic efficiency
MS = Milk solids
NEI = Net energy intake
NEL = Net energy for lactation
NEM = Net energy of maintenance
NS = Number of services
PEMEP = Partial efficiency of milk production
$PEMEP_{Nut}$ = Partial efficiency of milk production based on nutritional tables
PC = Protein concentration
PRFS = Pregnancy rate to first service
PR42 = Pregnancy in first 42 days of breeding season
PR84 = Pregnancy in first 84 days of breeding season
REI = Residual energy intake
REI_{maint} = Residual energy intake taking account of maintenance
REP = Residual energy production
REP_{maint} = Residual energy production taking account of maintenance
RIEP = Residual intake and energy production
SE = Standard error
SR21 = Submission rate in the first 21 days of the breeding season
UFL = Unité fourragère du lait

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Appendix one

Chapter 1

General introduction

Over the last century, the productivity of dairy cattle has increased substantially in line with scientific advances in several areas. Primarily, the introduction of quantitative genetics beginning in the 1930s has greatly enhanced the rate of change (Gianola and Rosa, 2015). Furthermore, improvements in animal nutrition enabled animals to reach their genetic potential, while improvements in reproductive technologies (e.g., artificial insemination) allowed producers to accelerate genetic gain by only selecting elite animals to reproduce. Technological developments in milking equipment and computerized record-keeping facilitated accurate identification of animals. Genetic evaluations exploited the resulting data to ensure superior genotypes were selected to suit a particular breeding objective, thereby further enhancing genetic gain.

An objective of modern breeding programmes is to increase farm profitability. Feed efficiency is becoming increasingly important as it greatly impacts farm profitability. Improving feed efficiency contributes to a greater percentage of total dry matter intake (DMI) being used for production (i.e., milk, meat). In dairy cows, feed accounts for approximately 80% of total variable costs (Shalloo et al., 2004). In the United States, it has been shown that over her lifetime, an elite dairy cow can partition three times more feed energy towards milk than towards maintenance (VandeHaar and St-Pierre, 2006). In beef cattle, a 5% improvement in feed efficiency could lead to an economic impact four times greater than a 5% increase in average daily gain (ADG) (Basarab et al., 2002). Moreover, Fox et al. (2001) illustrated that a 10% improvement in ADG improved profitability by 18%; however, a 10% improvement in feed efficiency improved profitability by 43%. Reducing DMI, without any repercussions on the other performance traits, is therefore important to maintain competitiveness while also meeting projected consumer demands for animal based protein and energy.

Feed efficiency has been defined in either growing animals or lactating females, but the literature has primarily focused on growing animals (Berry and Crowley, 2013). Feed efficiency is a complex trait for which no single definition is adequate. Since the 1960s, more than two dozen definitions of feed efficiency exist in the scientific literature (Archer et al., 1999). Many efficiency definitions are expressed on an individual animal basis (i.e., ratio or residual traits), while others express efficiency per unit area or on a particular production system (Berry, 2008). Regardless, efficiency should be considered over the lifetime of the individual animal and include maintenance costs and all products produced (e.g., milk, meat) (VandeHaar et al., 2016), but the practicality of achieving this is difficult.

In pigs and poultry, the contribution of breeding to improvements in feed efficiency are well recognized (Cahaner and Siegel, 1986; Havenstein et al., 1994; Havenstein et al., 2003), with feed efficiency traits incorporated in the selection objectives and selection criteria of both species (Fairfull and Chambers, 1984; De Vries and Kanis, 1992). In poultry, the genetic gain in feed efficiency has been substantial; for example, Zuidhof et al. (2014) demonstrated that the kilograms of feed necessary to yield a kilogram of meat (i.e., feed conversation ratio) was predicted to have reduced by 50% and growth rate increased by over 400%, between the years 1960 and 2005. In broilers, Havenstein et al. (2003) demonstrated that approximately 85% to 90% of the improvements in feed efficiency were due to genetics.

In dairy cattle, breeding objectives traditionally focused on selection for revenue-generating traits such as milk, fat, and protein yield (Miglior et al., 2005) with little cognisance of other traits. In the past two decades, however, functional traits (i.e., fertility, health, disease, and survival), as well as production traits, have been incorporated into breeding objectives; nonetheless, feed efficiency is still precluded from most breeding objectives. Its omission is due to both a lack of available data (i.e., DMI) from which to estimate efficiency, but also the lack of a consensus on the most suitable definition of feed efficiency for dairy cattle.

In many species, improvements in feed efficiency is desired, given current international concerns regarding greenhouse gas (GHG) emissions, nutrient losses, and water quality (Leip et al., 2015). It is well established that methane is a major GHG emitted from ruminants (Beauchemin and McGinn, 2005), and a contributing factor to climate change. Methane from ruminant production systems accounts for approximately 12% to 17% of GHG emissions (Beauchemin et al., 2009). Improving feed efficiency could also lead to a reduction in nutrient excretion; for example, in poultry, De Verdal et al. (2010) showed that poultry selected for decreased feed conversation ratio excreted 67.4% less urine than a random control line over a period of four generations. Improving animal characteristics impacting on the environment has several environmental benefits, but animal performance can also improve if achieved through a balanced breeding goal (Berry, 2013).

In growing dairy and beef cattle, previous analyses have clearly shown the presence of heritable genetic variation in feed intake (Berry and Crowley, 2013), suggesting it is indeed possible to breed for improved efficiency. In dairy cows, however, limited knowledge exists on the genetic correlations between feed intake, and other performance traits such as milk production, body-weight, body condition score and fertility traits. Not quantifying such associations prior to inclusion of the feed intake complex into any breeding objective could be seriously damaging.

The general objective of this thesis was to quantify phenotypic and genetic (co)variances between the feed intake complex, performance, and fertility traits in lactating Holstein-Friesian dairy cows. The outcome will be knowledge of the potential improvements in feed efficiency achievable in a national breeding program. To meet this general objective, five specific objectives were developed in this thesis:

1 To derive alternative definitions of feed efficiency in grazing lactating dairy cows and to quantify the inter-relationships among these alternative definitions.

2 To investigate the intra- and inter -relationships within and among the alternative feed efficiency metrics across different stages of lactation and across different parities.

3 To estimate genetic parameters across lactation for measures of energy balance and a range of alternative feed efficiency variables as well as to quantify the genetic inter-relationships between them.

4 To quantify the genetic inter-relationships between reproductive performance and a range of alternative feed efficiency metrics.

5 To quantify the impact of the Irish national dairy cow breeding objective, the Economic Breeding Index (EBI), on genetic change in residual energy intake (REI). The rate of genetic gain in the existing EBI traits by including REI as a goal trait in the EBI was also investigated.

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Chapter 2

Literature review

Introduction

As Ireland's largest indigenous industry, the agricultural-food industry is recognized as the main economic driver in rural Ireland operating at a growing profit of €2.59 billion per annum (CSO, 2016). In Ireland, dairy cows represent approximately 1.4 million of the 2.5 million cows (CSO, 2016) with grassland providing the main feedstuff. The dairy industry, however, is under constant pressure to further improve production efficiency, and reduce greenhouse gas emissions and nutrient losses (Leip et al., 2015). Enhancing feed efficiency provides a potential alternative to help overcome these challenges.

In dairy cows, feed accounts for approximately 80% of total variable costs (Shalloo et al., 2004). Therefore, it is anticipated that genetic selection to reduce feed intake whilst maintaining or improving production can result in significant gains in profit; however this statement has never been substantiated. Considerable research is on-going in feed efficiency. However, all proposed measures of feed efficiency in lactating dairy cows are fundamentally flawed (Berry and Crowley, 2013). Despite many recommending selecting for feed efficiency there is absolutely no information of the impact of selection for efficiency on other performance traits like fertility. Not quantifying such associations prior to any recommendation can be seriously damaging and therefore such associations must be quantified using a large dataset of deeply phenotyped animals.

The focus of this review was to:

1. To present and discuss the current feed efficiency metrics available in the literature.
2. To present genetic parameters of these feed efficiency metrics.

3. To present phenotypic and genetic correlations between the efficiency metrics and production traits.
4. To discuss the inclusion of feed efficiency in a breeding program.
5. To discuss current gaps in knowledge.

Feed efficiency metrics

Growing animals

Ratio traits. The most commonly used definition of feed efficiency in the scientific literature and industry on growing animals is feed conversion ratio (**FCR**) generally defined as the amount of dry matter consumed to produce 1 kg of body weight gain, or its inverse feed conversion efficiency (**FCE**; Brody, 1945) defined as kilograms of body weight per unit of DMI. Feed conversion ratio and FCE on a daily basis can be calculated as:

$$\mathrm{FCR} = \frac{\mathrm{DMI}}{\mathrm{ADG}} \qquad \mathrm{FCE} = \frac{\mathrm{ADG}}{\mathrm{DMI}}$$

where DMI = daily dry matter intake, and ADG = average daily gain. Feed conversion ratio is useful to determine the effects of diet quality, environment, and management practices on the efficiency of production in growing animals (Carstens and Tedeschi, 2006); Both FCR and FCE do not account for mobilization of body tissue.

Partial efficiency of gain (**PEG**; Kellner, 1909) is the ratio of ADG to DMI used for production after accounting for DMI required for maintenance (Archer et al., 1999) and is defined as:

$$\mathrm{PEG} = \frac{\mathrm{ADG}}{\mathrm{DMI} - \mathrm{DMI}_{\mathrm{maint}}}$$

where ADG = average daily gain, DMI = daily dry matter intake, and $\mathrm{DMI}_{\mathrm{maint}}$ = is the daily DMI required for maintenance. Maintenance requirements can be approximated using feed tables (NRC, 2001), or computed using average body-weight (BW) during the test period (Carstens and Tedeschi, 2006). Approximating maintenance requirements using feed tables suggests no differences exist among animals in the efficiency of feed use for maintenance; however, the literature suggests differences in maintenance energy requirements do exist between breeds (Ferrell and Jenkins, 1984, Taylor et al., 1986).

Relative growth rate (**RGR**; Fitzhugh and St CS, 1971) is not a direct measure of feed efficiency *per se*, but is a measure of efficiency. Relative growth rate is defined as growth relative to instantaneous body size and is defined as the logarithm of body weight at the end of the trial period minus that at the start of the trial period, multiplied by 100, and is represented as:

$$\mathrm{RGR} = \frac{100\ \times [\log_{\mathrm{e}}(\mathrm{end\ BW}) -\ \log_{\mathrm{e}}(\mathrm{start\ BW})]}{\mathrm{days\ on\ test}}$$

Kleiber ratio (**KR**; Kleiber, 1947) by definition is not a direct feed efficiency measure *per se*, but can be used as a measure of feed efficiency if all animals on trial are fed the same restricted diet which is similar to RGR. Kleiber ratio is defined as weight gain per unit metabolic BW ($\mathrm{BW}^{0.75}$); thus, more growth can be achieved without increasing maintenance energy costs and is represented as:

$$\mathrm{KR} = \frac{\mathrm{ADG}}{\mathrm{BW}^{0.75}}$$

where ADG = average daily gain, $BW^{0.75}$ is metabolic BW. Bergh et al. (1992) investigated the use of KR as an indirect measure of efficiency as KR only uses growth components in its estimation. And concluded that KR is a valuable and effective trait where feed intake cannot be estimated.

Residual traits. An increasingly common measurement of feed efficiency in beef animals is residual feed intake (**RFI**), also known as net feed efficiency (Koch et al., 1963). Residual feed intake is defined as the difference between actual and predicted feed intake independent of performance and was first proposed by Byerly (1941) in laying hens, although, Koch et al. (1963) later defined RFI as the residuals from the regression of feed intake on various energy sinks and energy sources. The regression model is represented as:

$$Y = \beta_0 + \beta_1 X_1 + \beta_2 X_2 \ldots \beta_n X_n + \varepsilon.$$

where Y is the dependent variable (i.e., DMI), β_0 is the intercept, β_1 and β_2 are regression coefficients, X_1 and X_2 are independent variables, and ε is the residual (i.e., RFI).

The regression model can be developed using standard feed tables (e.g., NRC, 2001), or alternatively, RFI can be derived using least squares regression. Using a least squares approach, mean RFI will equal zero due to the mathematical properties of least squares regression; this however, might not occur if RFI is derived using standard feed tables. If RFI is generated using standard feed tables, phenotypic correlations between RFI and the energy sinks (e.g., BW and ADG) can also exist (Arthur et al., 2001a, Smith et al., 2010). Regardless of the approach, animals in more negative RFI consume less than expected based on their growth and maintenance requirements and are therefore more efficient (Moore et al., 2009). Figure 2.1 shows a two-dimensional plane illustrating expected feed intake based on a regression model of $BW^{0.75}$ and ADG; the regression model is represented as:

$$\varepsilon = DMI - (\beta_1 BW^{0.75} + \beta_2 ADG).$$

where ε = residual feed intake, β_1 and β_2 are regression coefficients, DMI = dry matter intake, $BW^{0.75}$ = metabolic BW, and ADG = average daily gain.

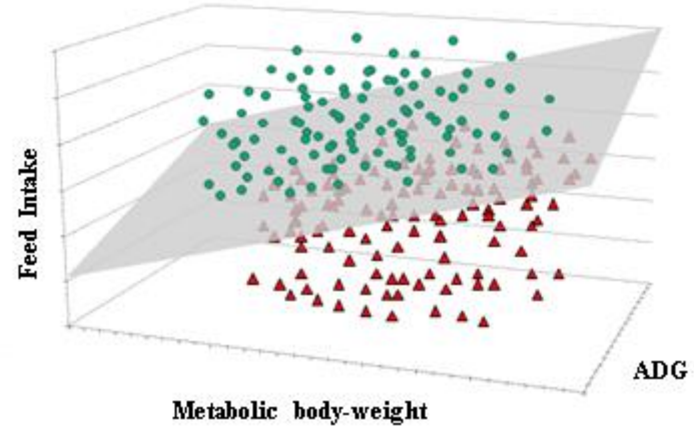

Figure 2.1. Two-dimensional plane illustrating expected feed intake based on a regression model of $BW^{0.75}$ and ADG; circles illustrate positive RFI animals (i.e., less efficient), while triangles illustrate negative RFI animals (i.e., more efficient) (Berry and Pryce, 2014).

In growing cattle, the traditional energy sinks used in the calculation of RFI are ADG and $BW^{0.75}$ which can account for more than 60% of the total phenotypic variation in feed intake (Carstens and Tedeschi, 2006). Metabolic BW is generally defined as BW midway through the test period to the power of 0.75 (Nkrumah et al., 2007, Crowley et al., 2010). Additional energy sinks can be included in the RFI model; for example, the inclusion of activity can be used to reflect feeding frequency (Basarab et al., 2003, Basarab et al., 2011, Durunna et al., 2011, Durunna et al., 2012); 8% to 10% supplementary variation in DMI is accounted for by feeding frequency (Basarab et al., 2011, Durunna et al., 2012).

Koch et al. (1963) proposed another efficiency measure to distinguish variation in feed efficiency among growing animals which they termed residual BW gain (**RG**). Using similar methodology to calculate RFI, Koch et al. (1963) defined RG as the residuals from a regression model of ADG on both feed intake and $BW^{0.75}$; consequently, improved RG is associated with faster growth rates on average. However, dissimilar from RFI, the more efficient animals have positive RG values indicating greater growth rates than anticipated. Residual body-weight gain can be represented as:

$$RG = ADG - (\beta_1 DMI + \beta_2 BW^{0.75})$$

where RG = residual BW gain, β_1 and β_2 are regression coefficients, DMI = dry matter intake, $BW^{0.75}$ = metabolic BW.

Berry and Crowley (2012) proposed an alternative definition of feed efficiency by an amalgamation of both RFI and RG to create residual intake and gain (**RIG**). Residual intake and gain was calculated by standardizing both RFI and RG to have equivalent variances and then summed both standardized traits after inverting the sign of RFI; therefore, a positive RIG value represented more feed efficient animals. Residual intake and gain is represented as:

$$\text{RIG} = [(-1 \times \text{RFI}) + \text{RG}]$$

Residual intake and gain is a linear combination of RFI and RG; therefore, it is expected that RIG offers the benefits of both components of feed efficiency traits. Residual intake and gain is negatively phenotypically correlated with DMI and positively phenotypically correlated with ADG; therefore, the likelihood of a slow growing animal ranking highly on RIG is reduced (Berry and Crowley, 2012). Berry and Crowley (2012) showed that during the finishing period, superior RIG animals consumed less feed and had greater ADG than superior RFI or RG animals. Table 2.1 shows some sample calculations for a selection of feed efficiency metrics on growing animals, and Figure 2.2 illustrates the plotted values for RFI on the sample population of growing cattle.

Table 2.1. Sample calculations for some feed efficiency metrics on growing animals.

Animal	DMI	$BW^{0.75}$	ADG	RFI	RG	RIG
1	12.12	117.21	1.23	0.54	-0.03	1.59
2	13.18	111.43	1.34	1.33	-0.01	3.46
3	11.47	109.62	1.16	0.75	-0.01	1.25
4	12.58	117.38	1.24	0.95	-0.04	2.12
5	10.56	109.16	1.08	-0.33	-0.003	2.48
6	10.49	96.75	1.01	0.26	0.02	2.79
7	13.10	119.95	1.33	0.78	-0.01	1.45
8	13.86	118.32	1.34	0.36	0.01	1.89
9	11.47	113.63	1.16	-0.13	0.04	2.46
10	11.67	111.84	1.17	-0.17	-0.001	1.23

DMI = dry matter intake (kg/d); $BW^{0.75}$ = metabolic BW ($kg^{0.75}$/d); ADG = average daily gain (kg/d); RFI = residual feed intake (kg/d); RG = residual BW gain (kg/d); RIG = residual intake and gain (kg/d).

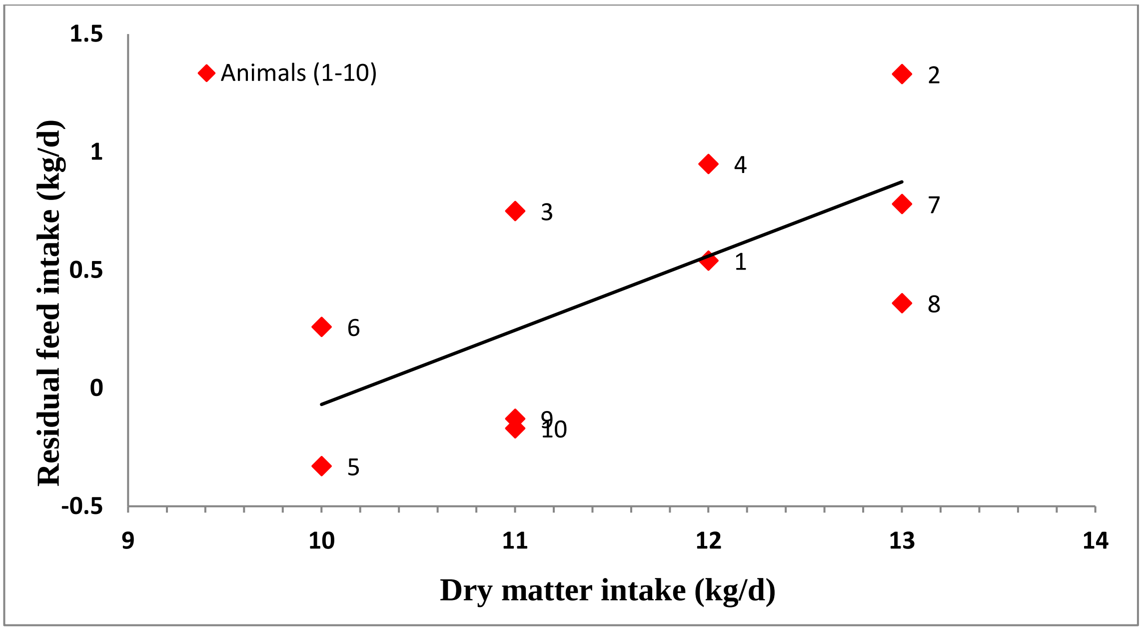

Figure 2.2. Plotted values for residual feed intake on the sample population of growing cattle from Table 2.1.

Dairy cows

Ratio traits. The simplest and most common ratio trait measurement of feed efficiency in lactating dairy cows is feed conversion efficiency (**FCE**), defined as the ratio of milk solids (MS; fat and protein yield) yield to DMI (Connor, 2015) represented as:

$$\mathrm{FCE} = \frac{\mathrm{MS}}{\mathrm{DMI}}$$

where MS = milk solids and DMI = dry matter intake. Usually the numerator includes either energy corrected milk or total MS while the dominator is expressed as either energy intake or DMI. Gross feed efficiency measured on a yearly basis does not account for both anabolism and catabolism of body tissue throughout lactation used for milk production; the energy from feed used to recover body weight is also not accounted for.

Other ratio trait measures of feed efficiency in lactating dairy cows have been proposed. These include milk solids (MS) yield per kilogram body-weight (BW) (Coleman et al., 2010) defined as:

$$\text{Milk solids per kilogram BW} = \text{MS}/\text{BW}$$

or DMI per kilogram BW (Coleman et al., 2010, Prendiville et al., 2011) defined as:

$$\text{Total DMI per kilogram BW} = \text{DMI}/\text{BW}$$

Residual traits. An increasingly common measure of feed efficiency in lactating dairy cows is RFI (Berry and Crowley, 2013, Connor, 2015). In growing dairy heifers, RFI is computed the same as growing beef animals, where the RFI model includes mid-test $BW^{0.75}$ and ADG (Williams et al., 2011, Lin et al., 2013). In lactating dairy cows, however, the definition of REI is more complex and differs among studies (Coleman et al., 2010, McParland et al., 2014); consequently, the applications and benefits of these definitions are different. In lactating dairy cows, RFI is estimated as the difference between actual feed intake (or energy intake) measured during an extended controlled evaluation period (or multiple short periods), minus predicted feed intake (or energy intake) based on the energy necessary for the cow to support body maintenance, production, and pregnancy (during the production cycle). A typical RFI model for lactating dairy cows is:

$$\text{RFI} = \text{DMI} - (\text{MS} + \text{BW}^{0.75} + \text{BCS} + \Delta\text{BW})$$

where RFI = residual feed intake, DMI = dry matter intake, MS = milk solids, $BW^{0.75}$ = metabolic BW, BCS = body condition score, and ΔBW = change in BW.

Coleman et al. (2010), using lactating Holstein-Friesian cows defined RFI by regressing DMI on milk, fat, protein, and lactose yield, as well as $BW^{0.75}$, BCS, and change in BW (ΔBW) throughout lactation; year was also included as a fixed effect to remove temporal effects. If mobilization of body tissue is not properly accounted for in the RFI definition then RFI is mathematically equivalent to energy balance (EB) (Veerkamp, 2002); therefore, it is important to accurately measure BW and BCS regularly to account for mobilization of body tissue.

Using similar methodology to calculate RFI, an alternative approach used to quantify feed efficiency in lactating dairy cows is residual solids production (**RSP**) (Coleman et al., 2010), defined as the residuals from the regression of MS on various energy sinks and energy sources (e.g., DMI, $BW^{0.75}$). Residual solids production can be represented as:

$$RSP = MS - (\beta_1 DMI + \beta_2 BW^{0.75}).$$

where β_1 and β_2 are regression coefficients, MS = milk solids, DMI = dry matter intake, and $BW^{0.75}$ = metabolic BW. Contrasting with RFI, positive RSP values signify more feed efficient cows. Residual solids production might be easier to understand by the end user as increased MS production is straightforward to visualize. Coleman et al. (2010) demonstrated that positive RSP in early lactation was associated with increased pregnancy rate and cow survival. Overall, RSP could be superior to RFI as a selection criterion to improve feed efficiency in lactating dairy cows given results obtained by Coleman et al. (2010), but genetic correlations between RSP and other production traits have yet to be quantified. Genetic selection for RFI and RSP will require accurate estimates of several traits (e.g., feed intake) which could prove problematic as these traits are expensive to measure and not routinely recorded. Table 2.2 shows some sample calculations for some feed efficiency metrics on lactating dairy cows; Figure 2.3

illustrates the plotted values for RFI on the sample population of lactating dairy cows. The advantages and disadvantages of both ratio and residual traits in lactating cows are in Table 2.3.

Table 2.2. Sample calculations for some feed efficiency metrics on lactating dairy cows.

Animal	DMI	$BW^{0.75}$	ΔBW^{+}	ΔBW^{-}	MY	MS	RFI	RSP
1	17.85	109.79	0.37	0.00	19.24	1.51	2.01	0.28
2	19.46	114.63	0.58	0.00	31.34	2.19	-0.39	1.39
3	20.77	121.86	0.51	0.00	34.99	2.83	-1.58	3.25
4	16.92	104.34	0.00	-0.14	34.46	2.67	-2.07	3.00
5	12.77	122.64	0.00	-0.66	31.80	2.21	-4.45	0.45
6	14.88	116.29	0.00	-0.94	36.80	2.32	-3.60	0.80
7	15.42	120.10	0.00	-0.91	34.14	2.28	-2.91	1.02
8	16.08	116.96	0.22	0.00	18.23	1.13	-0.43	-2.77
9	16.64	118.76	0.00	-0.02	22.24	1.57	-0.97	-0.56
10	17.48	119.09	0.22	0.00	22.71	1.87	-1.51	1.96

DMI = dry matter intake (kg/d); $BW^{0.75}$ = metabolic BW ($kg^{0.75}$/d); ΔBW^{+} describes animals gaining BW ($kg^{0.75}$/d); ΔBW^{-} describes animals losing BW ($kg^{0.75}$/d); MY = milk yield (kg/d); MS = milk solids yield (kg/d); RFI = residual feed intake (kg/d); RSP = residual solids production (kg/d).

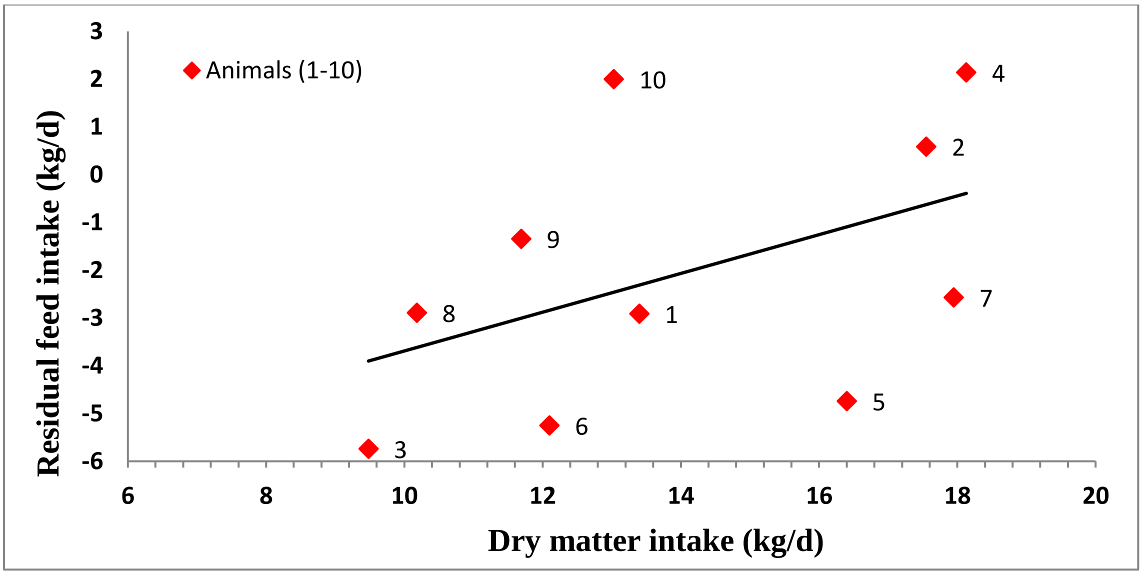

Figure 2.3. Plotted values for residual feed intake on the sample population of lactating dairy cows from Table 2.2.

Table 2.3. Advantages and disadvantages of both ratio and residual traits in lactating cows.

Advantages	Disadvantages
Ratio traits	
Easy to calculate and interpret	Fail to account for the energy used for separate functions (Kolath et al., 2006)
Good predictors available (e.g., mid-infrared spectroscopy)	Increased error variance as a proportion of the total variance (Lison, 1958). Strongly correlated with component traits (Berry, 2008) Difficult to add to selection index especially as other traits are likely to be present in the index
Residual traits	
Can account for anabolism/catabolism of body tissue	Complex calculation and difficult to understand (i.e., negative RFI is more efficient) (Wulfhorst et al., 2010)
A genomic prediction equation can be derived to predict RFI	Phenotype cannot be calculated on an individual as the regression coefficients are dependent on the population used to estimate them
Can slot in to current breeding goals easily	Comparing animals across populations without access to the original data is not possible unless DMI is predicted using regression coefficients from feed tables (Berry and Crowley, 2013) Currently low reliability due to the limited DMI data availability There is true error in RFI as well as variation in efficiency Possible genetic antagonisms with other performance traits (e.g., fertility and health traits)

Factors associated with RFI

Apart from measurement error of its component traits, variation in RFI is attributable to differences in biological processes. In ruminants, the main biological processes that contribute to variation in RFI are thought to be feed intake, digestibility, metabolism, activity, and thermoregulation (Richardson and Herd, 2004). The total partitioning of the variation in feed efficiency explained by the aforementioned biological processes are summarized in Figure 2.4.

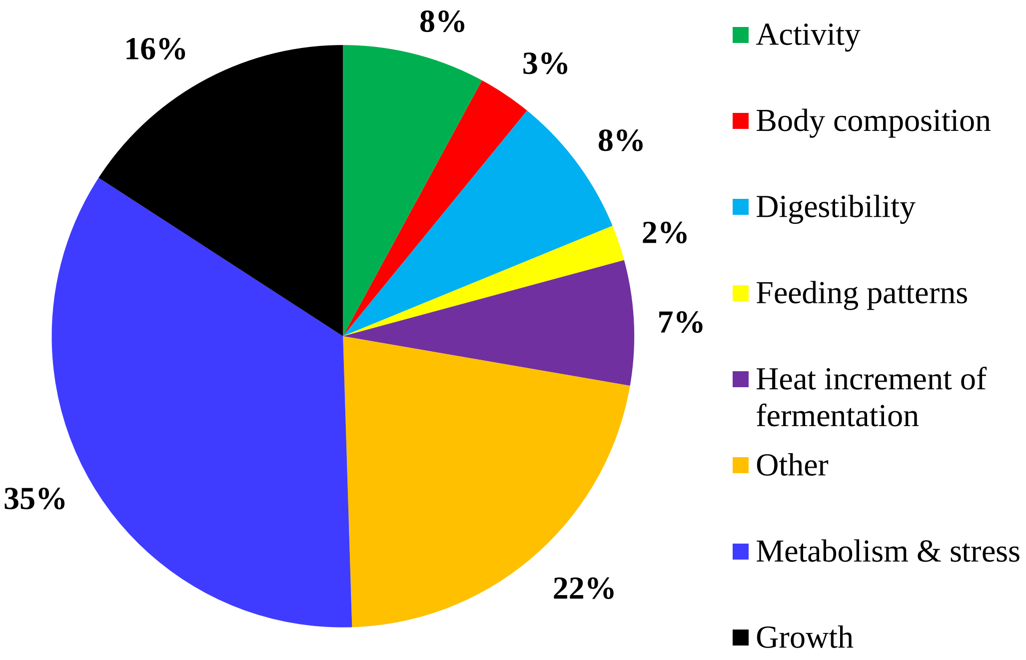

Figure 2.4. Contributors to the variation in RFI determined from divergently selected beef cattle (Richardson and Herd, 2004).

Feed intake. Various studies have illustrated how feed intake is highly associated with maintenance requirements of ruminants (Webster et al., 1975, Herd and Arthur, 2009). Increased feed intake leads to increased visceral organ size and thus greater energy expense, resulting in poorer animal efficiency (Herd and Arthur, 2009). Adam et al. (1984) reported that the rate of ingestion and meal duration are key factors to determine the energy costs of consuming forages.

Digestibility. Digestibility provides an estimate of how successful an animal is at making ingested feed energy available for absorption. In beef cattle, Richardson et al. (1996) reported that significant digestibility differences existed between animals divergent in RFI. Moreover, in beef cattle, Richardson and Herd (2004) concluded that nutrient digestibility accounts for approximately 8-10% of the variation in RFI.

Metabolism. The deposition of the same weight of lean tissue and fat has different energy costs. In beef cattle divergently selected for RFI, Richardson et al. (2001) illustrated that chemical composition was correlated with genetic variation in RFI; as a result, progeny from negative RFI parents (i.e., more efficient) had less whole body fat and more whole body chemical protein than progeny from high RFI parents (i.e., less efficient).

Activity. Activity includes energy expanded through ruminating, consuming forage, and locomotion (Richardson et al., 1999). In beef cattle, differences in activity contribute to 8-10% of the variability in RFI (Herd and Arthur, 2009). In poultry, activity contributes to a considerable proportion of the variation in RFI (Luiting et al., 1991). Luiting et al. (1991) concluded that 80% of genetic differences in RFI between lines of chickens divergent for RFI could be related to differences in activity. In mice, Mousel et al. (2001) illustrated that less efficient mice had higher heat loss than efficient mice as they were twice as active as the more efficient mice.

Thermoregulation. Luiting et al. (1994) reported that hens with negative RFI (i.e., more efficient) had less exposed body area through which they could lose energy. Luiting et al. (1994) concluded that in poultry, this may be a contributing factor to the variation in RFI.

Measuring feed intake

Accurate feed intake measurement is essential to quantify feed efficiency (Ferreira et al., 2004). Several methods of measuring feed intake exist.

Automated feeding systems. Automated feed monitoring systems are the most common way (internationally) of measuring feed intake. The system (e.g., GrowSafe® system) uses radio-frequency identification to record intakes of individual animals but can now also record other phenotypes such as the number of eating bouts per day, time spent at the feeder, and head down. A disadvantage of using automated feed monitoring systems to track DMI on large groups of animals is the limited feeding capacity of the automated feed bunks. When automated feed systems are used to track DMI on lactating dairy cows, a fresh and constant feed supply must be available to prevent a reduction in DMI. As a result, the number of animals that can be assigned per feed bunk is limited; therefore, the cost of measuring DMI is increased. Additionally, these systems only operate effectively indoors or on feed pads.

N-Alkanes. The n-alkane technique was developed in the early 1980s and 1990s as an alternative method to estimate herbage intake (and digestibility) of an individual animal. N-alkanes are long chain (C_{25} to C_{35}) hydrocarbons present in the cuticular wax of plants. The concept of using these hydrocarbons as markers for the estimation of herbage intake was first proposed by Mayes et al. (1984). In grassland species, the odd numbered chain lengths alkanes (C_{29}, C_{31}, and C_{33}) predominate over even numbered chain lengths (Dove and Mayes, 1991). N-alkanes are widespread in plant waxes and relatively easy to analyze (Grace and Body, 1981). The n-alkanes technique is based on the relationship between odd chain alkanes, naturally present in the epicuticular wax of plants (tritriacontane), and synthetic even chained alkanes orally administered in daily doses (dotriacontane); herbage intake can then be estimated by using n-alkanes as faecal markers. Mayes et al. (1986) proposed a double alkane procedure for estimating intake, where animals were dosed with a known quantity of even-chain alkanes and consume herbage which is sampled and contains a certain amount of naturally occurring odd numbered alkane; therefore, herbage intake can be calculated from the intake dose, alkane content of the herbage dose and the ratio of dosed and natural alkane in the faeces as:

$$\text{Intake (kg DM/d)} = \frac{\frac{\text{Fi}}{\text{Fj}} \text{ x Dj}}{\text{Hi} - \left(\frac{\text{Fi}}{\text{Fj}} \text{ x Hj}\right)}$$

where Dj = daily dose of the even-chain alkane (C32), Fi = faecal concentrations of the odd-chain alkane (C33), Hi = herbage concentrations of the odd-chain alkane (C33), Fj = faecal concentrations of the even-chain alkane (C32), Hj = herbage concentrations of the even-chain alkane (C32). The n-alkanes procedure provides a measure of DMI averaged across 6 days of sampling.

Synthetic alkanes can be administered to grazing ruminants in several ways; for example, using intra-ruminal controlled release devices (CRD), (Dove and Mayes, 1991), gelatine capsules (Dove et al., 2000), suspension (Marais et al., 1996), and pellets (Hameleers and Mayes, 1998) which all continually release alkanes in the rumen. The n-alkane method of estimating herbage intake has been found to have an error of less than 5% (Dove and Mayes, 1991).

Mid-infrared spectroscopy. Mid-infrared (**MIR**) spectroscopy is used globally to determine the fat, protein, and lactose concentration in milk (McParland et al., 2012). In dairy cows, McParland et al. (2014) reported that the MIR spectrum of milk samples can predict DMI with an accuracy of 80% and can predict RFI with an accuracy of 60%.

Energy feeding systems

Yan et al. (2003) described and compared different energy systems for dairy cattle. The most common energy systems currently adopted are those in North America [National Research Council (NRC), 2001], France [Van Es, 1978; Institute National De la Recherche Agronomique (INRA), 1989], and the United Kingdom [Agricultural and Food Research Council (AFRC), 1993].

The major goal of developing the NRC (2001) was to ensure energy supply equalled energy output. The NRC (2001) is expressed in Mcal and relies heavily on a computer model to dynamically predict dietary nutrient requirements. The dietary energy requirements take into account feedstuff digestion dynamics as well as the energy requirements for maintenance, growth, lactation, reproductive status and activity of the animal. The NE system recognizes that the energy requirement of ruminant animals is the sum of their energy requirements for maintenance, production (milk, BW gain) and fetal growth, each of these functions use ME into NE with different efficiencies. Total net energy requirements are calculated as:

$$NE_{req} = NE_m + NE_l + NE_g + NE_{preg}$$

where NE_{req} = total NE requirement; NE_m = NE requirement for maintenance; NE_l = NE requirement for lactation; NE_g = NE requirement for BW gain; and NE_{preg} = NE requirement of pregnancy (Dijkstra et al. 2005). The NE_L content of feeds and diets are not considered to be constant. As DM intake increases, NE_L concentrations will decrease and as the proportion of grain in a diet increases, the NE_L concentration of a diet will increase at a decreasing rate.

The French Net Energy System is expressed in unité fourragère du lait (UFL) where one UFL represents the NE requirements for lactation equivalent of 1 kg standard air-dried barley (Jarrige et al., 1986) which is equivalent to 7.11 MJ net energy or 11.85

MJ metabolisable energy or 1.730 Mcal. In common with most other energy systems is the fact that it is based on the metabolizable energy (ME) content of feedstuffs and on the efficiencies of ME utilization for maintenance, lactation and gaining body condition. However, what is different from the other energy systems is it uses a more analytical approach is used to calculate the NE values of feedstuffs and diet. The ME content of feedstuffs is calculated from their chemical composition, energy digestibility and the ME/DE ratio, therefore, gross energy content and energy digestibility of the feedstuffs are better accounted for. This is different from other energy systems where ME content of feedstuffs is calculated either from their digestible organic matter (DOM) content, their contents of digestible components contents, or from their DE content using a constant ratio: ME/DE = 0.81. The relationships used to calculate the NE contents of feedstuffs for milk production are the same as in most of the NE systems. Nonetheless, expressing the NE values of feedstuffs in relation to those of barley, as in the Scandinavian feed unit system has an advantage as the results obtained in feeding trials relative to comparisons of feedstuffs or diets can be easily used in the UFL systems. In the rationing of dairy cows, the UFL system takes into account the effect of feeding on the NE supply of rations, as well as the effects of forage quality (cell-wall lignification) and percentage of concentrates. Finally, data on the energy requirements and recommended allowances of many types of ruminants are available.

The UK ME feeding system was first developed by Blaxter (1962), for use in the UK in 1965 by the Agricultural Research Council (ARC, 1965). The energy unit used in the UK ME feeding system is the Joule, which is equivalent to 4.184 calories. Metabolizable energy is defined as gross energy minus faecal energy, urinary energy and energy in combustible gasses (methane) and represents the maximum amount of energy that is available for an animal for milk production, maintenance, live-weight gain and pregnancy. Metabolizable energy requirements are calculated as:

$$ME_{req} = NE_m/k_m + NE_l/k_l + NE_g/k_g + NE_{preg}/k_p$$

where ME_{req} = total ME requirement; NE_m = NE requirement for maintenance; NE_l = NE requirement for lactation; NE_g = NE requirement for BW gain; and NE_{preg} = NE requirement of pregnancy; k_m = the efficiencies of utilization of ME for maintenance; k_l = the efficiencies of utilization of ME for lactation; k_g = the efficiencies of utilization of ME for BW gain; k_p = the efficiencies of utilization of ME for pregnancy (Dijkstra et al. 2005).

The content of ME in feedstuffs are published in nutritional feed tables. The values have been derived from digestibility and urine output measurements, conducted at maintenance levels of feeding, and adjusted for estimates of methane production. Alternatively, for forages and compound feeds, frequently ME contents are predicted from laboratory assessments (e.g. in vitro digestibility) and previously derived relationships. It is difficult to assess to what extent these procedures bias the estimate of ME content. In general, however, current approaches to determine ME content and hence ME intake are considered satisfactory, but estimates of the efficiency of utilization of ME for maintenance (k_m), BW gain (k_g) and lactation (k_l) are subject to doubt. When accessing six different energy systems including the NRC (2001), UFL, and UK ME systems. De Brabander et al. (1982) showed that there is very little difference between the different energy systems studied.

Feed efficiency and methane emissions

In lactating dairy cows, RFI is strongly genetically correlated with methane emissions (de Haas et al., 2011), suggesting selection for lower RFI (i.e., more efficient) has the potential to reduce methane emissions. However, the analysis by de Haas et al. (2011) only models GHG emissions and is not based on actual data. One subtle point, however, is that methane production expressed per unit of feed is actually higher at lower levels of feed intake (de Haas et al., 2011; Blaxter and Clapperton, 1965; Pickering et al., 2015). Nonetheless, modelling by Pickering et al. (2015) has demonstrated that feed efficiecny still produces a net benefit in reducing GHG emissions. The relationship between feed efficeincy and methane is not straight forward as a pure positive one.

Genetic parameters of feed efficiency

Growing animals. Heritability estimates for different feed efficiency traits in growing animals vary from 0.06 (RFI; Robinson and Oddy, 2004) to 0.62 (FCR; Archer et al., 1997). Minimum heritability estimates for RFI and FCR in growing animals were 0.06 and 0.07, respectively; maximum heritability estimates for RFI and FCR were 0.46 and 0.62, respectively. Heritability estimates for KR varied from 0.21 to 0.52 in growing animals, while heritability estimates for RGR in growing animals varied from 0.14 to 0.33. Heritability estimates for RG in growing cattle ranged from 0.28 and 0.62 (Koch et al., 1963, Crowley et al., 2010).

Dairy cows. Several studies have estimated the heritability of RFI in confinement systems. Heritability estimates among lactating dairy cows range from 0.01 to 0.40 (de Haas et al., 2011, Connor et al., 2013), and from 0.22 to 0.40 in growing dairy heifers (Pryce et al., 2012, Lin et al., 2013). In lactating dairy cows, when feed intake, milk yield, and BW were included as parameters in the RFI model, the heritability for RFI varied from 0.05 to 0.08 (Parke et al., 1999; Søndergaard et al., 2002; Vallimont et al., 2011). From a meta-analysis of the available literature on lactating dairy cows, Berry and Crowley, (2013) reported an average heritability of 0.04 for RFI. Heritability estimates for RFI on lactating dairy cows are generally lower in comparison to growing beef animals (Berry and Crowley, 2013). Nonetheless, results clearly indicate that ample genetic variation exists for RFI in lactating dairy cows (Herring and Bertrand, 2002, Williams et al., 2011, Berry and Crowley, 2013, Vallimont et al., 2013), suggesting it is indeed possible to breed for improved efficiency. Feed conversion efficiency is moderately heritable, depending on the stage of lactation evaluated, with heritability estimates ranging from 0.14 to 0.37 (Van Arendonk et al., 1991; Vallimont et al., 2011; Spurlock et al., 2012).

Heritability estimates of RFI in other livestock. In sheep, heritability estimates for RFI range from 0.11 to 0.30 (Cammack et al., 2005; Francois et al., 2002; and Snowder and Van Vleck., 2003). In pigs, the heritability for RFI was 0.23 (Nguyen et al., 2005); a similar heritability for RFI was estimated on large white pigs in a separate study (0.15; Gilbert et al., 2006) where ADG and BW were used as independent variables in the regression model.

Phenotypic correlations

Growing animals. Residual feed intake is phenotypically independent of ADG and $BW^{0.75}$ (Koch et al., 1963), and RG is phenotypically independent of DMI and $BW^{0.75}$ when both RFI and RG are calculated using least squares regression. In beef cattle, to observe phenotypic differences between animals differing in RFI, test groups are set up based on animals divergent on RFI (Basarab et al., 2003; Richardson and Herd; 2004). Baker et al. (2006) documented no differences in ADG between 3 groups divergently selected on RFI. In beef cattle, moderate to strong phenotypic correlations have been reported between RFI and DMI ranging from 0.60 to 0.72 (Basarab et al., 2003). Similarly, moderate to strong phenotypic correlations exist between RFI and ADG which range from 0.53 to 0.70 (Basarab et al., 2003).

Dairy cows. In dairy cows, RFI is phenotypically independent of milk yield and $BW^{0.75}$ when calculated using least squares regression; similarly, RSP is independent of DMI and $BW^{0.75}$ when calculated using least squares regression. Residual feed intake is generally moderately phenotypically correlated with DMI, for example, Manafiazar et al. (2015) presented a phenotypic correlation of 0.50. Residual feed intake is also strongly phenotypically correlated with EB, suggesting that negative REI (i.e., more efficient) animals are also in more negative EB; however, this is not unexpected given their mathematical similarity (Savietto et al., 2014).

Genetic correlations

Growing animals. Kennedy et al. (1993) and Van der Werf (2004) demonstrated how, even though RFI is phenotypically independent of its predictor traits, it may not be genetically independent, and if it is, it will only be so by chance. Kennedy et al. (1993), however, described a way to make RFI genetically independent of the regressors. Nonetheless, Arthur et al. (2001b) observed that RFI is moderately genetically correlated with DMI (0.69 ± 0.03 and 0.79 ± 0.04) and FCR (0.66 ± 0.05 and 0.85 ± 0.05) in Angus male and female weanlings and young Charolais bulls, respectively. In the same study, the genetic correlation in Charolais bulls estimated between FCR and BW was positive (0.24 ± 0.09) while the genetic correlation between FCR and ADG was negative (-0.46 ± 0.08); this suggests that the more efficient animals, as defined by FCR, grew faster but are not expected to be heavier. Additionally, FCR and DMI were positively correlated (0.64 ± 0.07; Authur et al., 2001). Robinson and Oddy (2004) estimated a negative genetic correlation between FCR and BW (-0.62 ± 0.18) in heifers and steers of mixed breeds. Similarly, Hoque et al. (2006) also reported a negative genetic correlation between FCR and BW (-0.57 ± 0.25) confirming that selection on FCR will result in heavier animals.

Dairy cows. Moderate to strong undesirable genetic correlations exist between FCE and BCS, BW, EB and days open (Van Arendonk et al., 1991; Vallimont et al., 2011 and 2013; Spurlock et al., 2012). Selection for negative EB has undesirable consequences on multiple health and fitness traits, including fertility (De Vries et al., 1999, Collard et al., 2000). Vallimont et al. (2013) showed a positive reliability-adjusted correlation between sire EBV for RFI and predicted transmitting ability for daughter pregnancy rate (r = 0.22; $P < 0.05$), suggesting that selection for negative RFI (i.e., more efficient animals) is associated with reduced predicted transmitting ability for daughter pregnancy rate. Additional research is clearly warranted on a large population of lactating cows and growing heifers managed under similar conditions, while consistent RFI models are necessary to allow for improved comparison between studies.

Genomic selection

Genomic selection is a relatively new procedure to predict individual animal breeding values using whole genome information (Meuwissen et al., 2001). These breeding values can be predicted for any genotyped animal, thus providing an indication of the future performance capabilities of that animal and its offspring. The process behind genomic selection includes generating single nucleotide polymorphisms (SNP) effects for a genotyped reference population with recorded phenotypes for a specific trait or number of traits. In this way, the effects of all loci that contribute to the genetic variation are captured, even if the effects of the individual loci are small and not different from zero. Selection candidates (in subsequent generations) are then genotyped and their genotypes are combined with the estimated SNP effects to estimate a genomic EBV (GEBV) for each animal.

Meuwissen et al. (2001) illustrated, using simulations that the correlation between the true breeding value and the predicted breeding value using SNPs alone could be up to 0.85. The main differences between the traditional method of estimating breeding values (i.e., BLUP) and genomic selection are that pedigree recording is essential to traditional BLUP- EBV but not required for genomic selection and unlike BLUP, elite breeding animals (i.e., the selection candidates or their progeny) do not have to be trait recorded (phenotyped) for genomic selection (Meuwissen et al., 2016). The now widespread use of genomic information in dairy cattle breeding programs has opened up the possibility to select for novel and difficult to measure traits (e.g., feed intake). One of the limitations of any trait reliant on feed intake is the limitation of feed intake data on large numbers of cows, phenotypes derived from feed intake are therefore obvious candidates for genomic selection; the costs associated with genotyping are relatively small compared to the cost of phenotyping for feed intake. However, for genomic selection to work the trait must be heritable; the reliability of genomic predictions must also be acceptable to those using the breeding values. The accuracy of genomic prediction of DMI and RFI has been estimated to be approximately 0.40 in dairy and beef cattle studies (Pryce et al., 2013).

Inclusion of feed efficiency in breeding programs

Economic breeding index. In Ireland, the economic breeding index (**EBI**) is a selection index tool that aims of identify profitable dairy females, which can be selected as parents of future replacements in the herd. The EBI was officially launched in 2001 by the Irish cattle breeding federation (ICBF) (Berry et al., 2007). The EBI succeeded the relative breeding index (**RBI**) which was a relative breeding goal comprising milk, fat yield, protein yield, and percentage protein (Berry et al., 2007). When the EBI was established, it was based on the available data which included milk, fat, and protein yield, along with calving interval, and survival. Over the past decade, developments of the ICBF database has led to greater amounts of performance information collected which allowed for the introduction of new traits. A breakdown of the traits currently included in the EBI (ICBF, 2017) with economic weights, trait emphasis, and overall emphasis are in Table 2.4.

Table 2.4. Breakdown of the traits included in the EBI with economic weights, trait emphesis, and overall emphesis (ICBF, 2017).

Sub-Index	Trait	Economic Weight	Trait Emphesis	Overall Emphesis
Production	Milk yield	-€0.09	10.60%	33%
	Fat yield	€1.04	3.40%	
	Protein yield	€6.64	18.90%	
Fertility	Calving interval	-€12.43	24.00%	35%
	Survival	€12.01	10.90%	
Calving	Direct calving diff.	-€3.52	2.80%	9%
	Maternal calving diff.	-€1.73	1.30%	
	Gestation length	-€7.49	4.10%	
	Calf mortality	-€2.58	1.00%	
Beef	Cull cow weight	€0.15	0.70%	9%
	Carcass weight	€1.38	5.10%	
	Carcass conformation	-€10.32	1.70%	
	Carcass fat	€11.71	1.10%	
Maintenance	Cull cow weight	-€1.65	7.20%	7%
Management	Milking time	-€0.25	2.10%	4%
	Milking temperature	€33.69	1.90%	
Health	Lameness	-€54.26	0.60%	3%
	Somatic cell count	-€43.49	1.80%	
	Mastitis	-€77.10	0.80%	

Feed efficiency in breeding programs. There is considerable evidence to suggest that feed efficiency should be included in a selection index or breeding goal (Van der Werf, 2004). The inclusion of RFI has considerable economic weight (i.e., the economic weight of feed intake). Nonetheless, there is no additional benefit of including RFI (or any other feed efficiency measure) in a breeding goal or selection index that already includes feed intake and the component traits. Moreover, feed intake in a breeding goal may be an easier concept to comprehend as RFI is a difficult concept to understand (Wulfhorst et al., 2010). The advantages and disadvantages of including DMI or RFI in a breeding goal are in Table 2.5.

Regardless of whether RFI or feed intake is directly included in a breeding objective or as a breeding goal trait, the greatest obstacle to assessing feed efficiency is the measurement of individual animal feed intakes. Measuring individual feed intake is expensive; therefore, practical and cost-effective means of evaluating feed efficiency among commercial production herds are required.

Table 2.5. Advantages and disadvantages of including DMI or RFI in a breeding goal (Berry, 2015).

Advantages	Disadvantages
DMI in the breeding goal	
Easy to explain and understand	Cannot easily identify efficient animals
Economic weight is relatively easy to calculate	May be mis-understood (positive EBV may be efficient)
Amenable to customized indexes	Correlated with performance
Economic weights on other components reflect reality in the market place (e.g., F:P price ratio)	Independent culling rates may be harmful to overall gain
Good predictors available (e.g., MIR)	Misinterpreted that negative EBV might imply poorer performing animals
Might be less susceptible to GxE	
RFI in the breeding goal	
Economic weight is relatively easy to calculate	Difficult to explain technically
Can ‘easily’ slot into current breeding goals	Low reliability (currently)
(Theoretically) uncorrelated with performance	Possibly more susceptible to GxE
Relatively simple message (if not caught up in details)	Selection index within a selection index
Could materialize in faster genetic gain for efficiency	RFI in lactating mature animals (as currently defined) is not ideal
	EBVs may change as the RFI model changes
	Possibly correlated with fertility

Gaps in knowledge

Although interest in the genetics of feed efficiency is increasing, there are still considerable gaps in knowledge within the literature that need to be addressed. Genetic parameters are population specific, and therefore need to be estimated within the sample population of which they will be used. No estimates of genetic parameters are currently available for feed efficiency in Irish dairy cows.

In dairy cows, definitions of efficiency must account for different functions involved in energy usage and supply over the entire lactation, such as lipid and protein body mass changes (Berry et al., 2006). Some currently used definitions of feed efficiency in lactating cows (e.g., FCE, FCR) do not fully account for body tissue mobilization patterns to energy contribution. The existence of genetic variation in definitions of feed efficiency, as well as the estimation of precise intra- and inter-trait genetic correlations, needs to be quantified prior to consideration in genetic evaluations and subsequent inclusion in breeding objectives. The possibility of altering the trajectories of the efficiency traits to suit a particular breeding objective is unknown. Furthermore, precise estimates of the genetic correlations between feed efficiency with health and fertility traits (and others) are essentially non-existent.

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Chapter 3

Inter-relationships among alternative definitions of feed efficiency in grazing lactating dairy cows

A.M. Hurley[1, 2], N. López-Villalobos[2], S. McParland[1], E. Kennedy[1], E. Lewis[1],
M. O' Donovan[1], J.L. Burke[2], and D.P. Berry[1]

[1]*Teagasc, Animal & Grassland Research and Innovation Centre, Moorepark, Fermoy, Co. Cork, Ireland*

[2]*Institute of Veterinary, Animal and Biomedical Sciences, Massey University, Private Bag 11-222, Palmerston North, New Zealand*

Journal of Dairy Science (2016) 99:468-479.

doi: https://doi.org/10.3168/jds.2015-9928.

Abstract

International interest in feed efficiency, and in particular energy intake and residual energy intake (REI), is intensifying due to a greater global demand for animal-derived protein and energy sources. Feed efficiency is a trait of economic importance, and yet is overlooked in national dairy cow breeding goals. This is due primarily to a lack of accurate data on commercial animals, but also a lack of clarity on the most appropriate definition of the feed intake and utilization complex. The objective of the present study was to derive alternative definitions of energetic efficiency in grazing lactating dairy cows and to quantify the inter-relationships among these alternative definitions. Net energy intake (NEI) from pasture and concentrate intake was estimated up to eight times per lactation for 2,693 lactations from 1,412 Holstein-Friesian cows. Energy values of feed were based on the French Net Energy system where 1 UFL is the net energy requirements for lactation equivalent of 1 kg air-dry barley. A total of 8,183 individual feed intake measurements were available. Energy balance (EB) was defined as the difference between NEI and energy expenditure. Efficiency traits were either ratio-based or residual-based; the latter were derived from least squares regression models. Residual energy intake (REI) was defined as NEI minus predicted energy to fulfil the requirements for the various energy sinks. The energy sinks (e.g., net energy for lactation (NEL), metabolic BW) and additional contributors to energy kinetics (e.g., body-weight loss) combined, explained 59% of the variation in NEI, implying that REI represented 41% of the variance in total NEI. The most efficient 10% of test-day records, as defined by REI (n = 709), on average were associated with a 7.59 UFL/d less NEI (average NEI of the entire population was 16.23 UFL/d) than the least efficient 10% of test-day records based on REI (n = 709). Additionally, the most efficient 10% of test-day records, as defined by REI, were associated with superior energy conversion efficiency (ECE i.e., NEL divided by NEI) (ECE = 0.55) compared to the least efficient 10% of test-day records (ECE = 0.33). Moreover, REI was positively correlated with energy balance implying that more negative REI animals (i.e., deemed more efficient) are expected to be, on average, in greater negative energy balance. Many of the correlations among the 14 defined efficiency traits differed from unity implying that each trait is measuring a different aspect of efficiency.

Keywords: feed efficiency, dairy, residual energy intake, energy balance, feed conversion.

Introduction

The expanding world human population (FAO, 2009) is contributing to increased global demand for animal-derived energy and protein sources. International interest in sustainable resource use efficiency is therefore intensifying. Although global, national, and even herd resource use efficiency is multi-factorial, impacted by animal characteristics such as reproductive performance, longevity and per lactation energy produced (Berry et al., 2015), individual animal feed intake recording as well as the appropriate definitions of efficiency is also fundamental to achieving the necessary gains in efficiency.

The definition of alternative measures of feed efficiency and their respective utility is the subject of extensive discussion. Since the 1960s, more than two dozen definitions of feed efficiency have been presented in the scientific literature (Archer et al., 1999). Feed conversion ratio (FCR) and feed conversion efficiency (FCE) are the traditional measures of feed efficiency in growing and lactating animals, respectively. Residual feed intake, used predominately in growing animals as a measure of feed efficiency (Berry and Crowley, 2013), is now also being used in lactating dairy cow populations (Coleman et al., 2010; McParland et al., 2014; Pryce et al., 2014). The definition of REI in lactating cows does however differ among studies (Coleman et al., 2010; McParland et al., 2014; Pryce et al., 2014). Consequently, the applications and benefits of these definitions are different. A plethora of other definitions of feed efficiency also exist in both growing and lactating animals, all with their respective advantages and disadvantages (for review see Berry and Crowley, 2013). Irrespective of the definition, estimates of feed efficiency in dairy cows must account for different functions involved in energy usage and supply over the entire lactation, for example lipid and protein body mass changes (Berry et al., 2006). Some currently used definitions of feed efficiency in lactating cows (e.g., FCE) do not fully account for body tissue mobilization patterns. Moreover, the inter-relationships among the alternative definitions of feed efficiency traits have not been fully elucidated.

The objectives of the present study were (1) to derive alternative definitions of energetic efficiency in lactating Holstein-Friesian dairy cows, and (2) to quantify the inter-relationships among these alternative definitions. Results from this study may be useful in determining the most appropriate definition of energy efficiency in lactating dairy cows, although one definition is unlikely to meet the requirements of all potential stakeholders.

Materials and methods

Data

Data were available from the Teagasc, Animal & Grassland Research and Innovation Centre, Moorepark, Fermoy, Co. Cork, Ireland (50°7N; 8°16W) from the years 1988 to 2009, inclusive. All studies were undertaken on two adjacent research farms, namely, Curtin’s Research Farm and Moorepark Research Farm. Cows originated from studies which evaluated alternative grazing strategies, nutritional strategies, or strain of Holstein-Friesian animals; see O'Neill et al. (2013) for a description of the database. Animals were fed a basal diet of grazed grass. Swards consisted primarily of perennial ryegrass (*Lolium perenne*) and were managed under a rotational grazing system similar to that described by Dillon et al. (1995). Some animals were supplemented sporadically with concentrates, varying from 0.89 to 3.9 kg DM per cow daily, offered in equal feeds during each milking. All cows were milked twice daily.

Individual cow milk yield was recorded daily; milk fat and protein concentration was determined from successive morning and evening milk samples once per week using mid-infrared spectroscopy (Fos-let instrument, AS/N Foss Electric, Hillerod, Denmark). Net energy requirement for lactation (NEL) was calculated as Agabriel (2007):

$$\mathrm{NEL} = ((0.054 \times \mathrm{FC}) + (0.031 \times \mathrm{PC}) + (0.028 \times \mathrm{LC}) - 0.015) \times \mathrm{milk\,kg}$$

where FC is fat concentration (%), PC is protein concentration (%), and LC is lactose concentration (%).

Individual animal body-weight (BW) was recorded weekly upon exiting the milking parlour using an electronic scale (Tru-Test Limited, Auckland, New Zealand). Animal body condition score (BCS; scale 1 = emaciated, 5 = obese) was recorded every two to three weeks in increments of 0.25 (Edmonson et al., 1989). Cubic splines with 6 knot points at 20, 70, 120, 170, 220, and 270 days in milk (DIM), with a covariance structure fitted among knot points, were fitted through individual BW and BCS test-day records. Body-weight and BCS at each DIM were interpolated from the fitted splines. Forward differencing was used to estimate daily BW and BCS change for each DIM.

Individual animal grass dry matter intake (DMI) at pasture was estimated using the n-alkane technique (Mayes et al., 1986) as modified by Dillon and Stakelum (1989). During the intake measurement period, cows were dosed twice daily before milking with paper bungs, containing 500 mg of C32-alkane (n-dotriacontane) for 12 d. Fecal samples were collected from each cow twice daily during days 7 to 12. Subsequently, samples were bulked per cow giving one sample per cow per intake measurement period; this sample was sub-sampled for gas chromatography analysis. Selected herbage samples were taken following close observation of cows grazing both after morning and evening milking on day 6 to 11 of the intake measurement period. The ratio of herbage C33-alkane (tritriacontane) to dosed C32-alkane was used to estimate DMI as outlined in detail by Dillon (1993).

Individual cow daily total DMI (i.e., grazed pasture DMI plus concentrate DMI) was available, on average, 4.5 times per lactation. Efficiency traits were calculated only when a DMI record was available. Energy values of the pasture and concentrate were based on the French Net Energy system where 1 unité fourragère du lait (UFL) is the net energy requirements for lactation equivalent of 1 kg standard air-dry barley (Jarrige et al., 1986) equivalent to 7.11 MJ net energy or 11.85 MJ metabolisable energy. The energy values and energy sinks were also based on the French Net Energy system.

The UFL concentration of the offered herbage was calculated using the acid detergent fibre and crude protein concentration which were measured in the laboratory (Jarrige, 1989). Concentrate UFL value was also calculated from the chemical composition of the feed. The net energy content of the concentrate fed was calculated for each day; where UFL content of concentrate was not available (28% of test-day records) the year-month average was assumed. Net energy content of the herbage offered (UFL/kg dry matter) was also available; where an offered herbage UFL value was not available (10.3% of test-day records), the year-month average was assumed. The within-year-month variation in the UFL content of both concentrate and offered herbage was low, with a coefficient of variation of 2% and 7%, respectively. Net energy intake (NEI) was defined as the sum of pasture and concentrate net energy intake. In total 8,183 individual feed intake measurements were available from 2,693 lactations on 1,412 pasture-based Holstein-Friesian dairy cows.

Definitions of energy efficiency

Fourteen alternative definitions of energy efficiency, broadly classified into ratio and residual-based traits, were generated. Energy balance was also defined. Energy balance (EB) was calculated as the difference between NEI and energy expended through lactation and maintenance according to Jarrige (1989) where the energy values of the feed were modified for Irish dairy systems by O'Mara (1996):

$$\mathrm{EB} = \mathrm{NEI} - \Delta\mathrm{NE} - \mathrm{NEL} - \mathrm{NEM} - \mathrm{NEP}$$

where NEI is daily net energy intake, ΔNE is an adjustment of daily net energy intake for the proportion of concentrates in the diet, NEL is daily net energy requirements for lactation, NEM is daily net energy requirements for maintenance calculated as $((1.4 + (0.6 \times (\mathrm{BW}/100))) \times 1.2)$, and NEP is daily net energy requirements for pregnancy where UFL requirement for the 6th, 7th, and 8th month of pregnancy were 0.9, 1.6, and 2.6 UFL/d, respectively (O'Mara, 1996).

Residual traits. Residual energy intake for each day of lactation was defined as the residuals from the regression of NEI on energy sinks and other energy sources as:

$$\mathrm{REI} = \mathrm{NEI} - [\mathrm{NEL} + \mathrm{Parity} + \sum_{i=1}^{2} \mathrm{DIM}^{i} + \mathrm{BW}^{0.75} + \mathrm{BCS} + \mathrm{BW}^{0.75} \times \mathrm{BCS} + \Delta\mathrm{BW}^{+} + \Delta\mathrm{BW}^{-} + \Delta\mathrm{BCS}^{+} + \Delta\mathrm{BCS}^{-} + \Delta\mathrm{BW}^{+} \times \mathrm{BCS} + \Delta\mathrm{BW}^{-} \times \mathrm{BCS}]$$

where REI is daily residual energy intake, NEI is daily net energy intake, NEL is daily net energy requirements for lactation, parity (1, 2, 3+), $\sum_{i=1}^{2} \mathrm{DIM}^{i}$ is days in milk included as a continuous variable with a linear and quadratic effect, $\mathrm{BW}^{0.75}$ is metabolic BW, and BCS is body condition score. The energy generated from a 1 kg loss in BW is less than the energy required for a 1 kg gain in BW (O'Mara, 1996); therefore, piecewise regression was applied to BW and BCS in the REI model where $\Delta\mathrm{BW}^{+}$ describes animals gaining BW, $\Delta\mathrm{BW}^{-}$ describes animals losing BW, while $\Delta\mathrm{BCS}^{+}$ describes animals gaining BCS, and $\Delta\mathrm{BCS}^{-}$ describes animals losing BCS. No multicollinearity existed in the multiple regression model.

An alternative definition for residual energy intake (i.e., $\mathrm{REI}_{\mathrm{maint}}$) was defined as the residuals from the previously described regression plus both the regression coefficient on $\mathrm{BW}^{0.75}$

times the actual $BW^{0.75}$ of the individual, and the regression coefficient on the interaction between $BW^{0.75}$×BCS times the respective phenotypic value.

Analogous to residual gain in growing cattle (Koch et al., 1963), residual energy production (REP) for each day of lactation was defined from the residuals of a least squares regression model regressing net energy for lactation on NEI plus energy sinks and other energy sources, similar to that described by Coleman et al. (2010):

$$\mathrm{REP} = \mathrm{NEL} - [\mathrm{NEI} + \mathrm{Parity} + \textstyle\sum_{i=1}^{2} \mathrm{DIM}^{i} + \mathrm{BW}^{0.75} + \mathrm{BCS} + \mathrm{BW}^{0.75} \times \mathrm{BCS} + \Delta\mathrm{BW}^{+} + \Delta\mathrm{BW}^{-} + \Delta\mathrm{BCS}^{+} + \Delta BCS^{-} + \Delta\mathrm{BW}^{+} \times \mathrm{BCS} + \Delta\mathrm{BW}^{-} \times \mathrm{BCS}]$$

where REP is daily residual energy production, NEL is daily net energy requirements for lactation, NEI is daily net energy intake, parity (1, 2, 3+), $\sum_{i=1}^{2} \mathrm{DIM}^{i}$ is days in milk included as a continuous variable with a linear and quadratic effect, $BW^{0.75}$ is metabolic BW, BCS is body condition score, $\Delta\mathrm{BW}^{+}$ describes animals gaining BW, $\Delta\mathrm{BW}^{-}$ describes animals losing BW, $\Delta\mathrm{BCS}^{+}$ describes animals gaining BCS, and $\Delta\mathrm{BCS}^{-}$ describes animals losing BCS. No multicollinearity existed in the multiple regression model.

An alternative definition for residual energy production (i.e., REP_{maint}) was defined as the residuals from the previously described REI model plus both the regression coefficient on $BW^{0.75}$ times the actual $BW^{0.75}$ of the individual, and the regression coefficient on the interaction between $BW^{0.75}$xBCS times the respective phenotypic value.

Analogous to residual intake and gain as defined by Berry and Crowley (2012), residual intake and energy production (RIEP) was defined using both REI and REP, both standardized to have a variance of one:

$$\mathrm{RIEP} = \widetilde{\mathrm{REP}} - \widetilde{\mathrm{REI}}$$

where $\widetilde{\mathrm{REP}}$ is residual energy production standardized to a variance of one, and $\widetilde{\mathrm{REI}}$ is residual energy intake standardized to a variance of one. Standardising both traits to a common variance (i.e., here one) would result in equal emphasis on both REI and REP; otherwise a greater emphasis would be placed on the trait with the greater variance (Berry and Crowley, 2013).

Ratio traits. Energy conversion efficiency (ECE), and its reciprocal, energy conversion ratio (ECR) for each day of lactation were defined as:

$$\mathrm{ECE} = \frac{\mathrm{NEL}}{\mathrm{NEI}} \qquad \mathrm{ECR} = \frac{\mathrm{NEI}}{\mathrm{NEL}}$$

where NEL is the daily net energy requirements for lactation, and NEI is the daily net energy intake.

Energy conversion efficiency was refined to 1) consider the energy kinetics from BW and BCS change in both the numerator and denominator ($\mathrm{ECE}_{\mathrm{adj}}$), and 2) also consider the energy requirement for maintenance plus the interaction between $\mathrm{BW}^{0.75}$ and BCS in the numerator of $\mathrm{ECE}_{\mathrm{maint}}$:

$$\mathrm{ECE}_{\mathrm{adj}} = \frac{\mathrm{NEL} + \mathrm{b\Delta BW}^{+} + \mathrm{b\Delta BCS}^{+} + \mathrm{b\Delta BW}^{+} \times \mathrm{BCS}}{\mathrm{NEI} - \mathrm{b\Delta BW}^{-} - \mathrm{b\Delta BCS}^{-} - \mathrm{b\Delta BW}^{-} \times \mathrm{BCS}}$$

$$\mathrm{ECE}_{\mathrm{maint}} = \frac{\mathrm{NEL} + \mathrm{bBW}^{0.75} + \mathrm{bBW}^{0.75} \times \mathrm{BCS} + \mathrm{b\Delta BW}^{+} + \mathrm{b\Delta BCS}^{+} + \mathrm{b\Delta BW}^{+} \times \mathrm{BCS}}{\mathrm{NEI} - \mathrm{b\Delta BW}^{-} - \mathrm{b\Delta BCS}^{-} - \mathrm{b\Delta BW}^{-} \times \mathrm{BCS}}$$

where NEL is daily net energy requirements for lactation, NEI is daily net energy intake, $\mathrm{b\Delta BW}^{+}$ describes animals gaining BW and the associated regression coefficient (b) from the REI model, $b\Delta BW^{-}$ describes animals losing BW and the associated regression coefficient (b) from the REI model, $b\Delta BCS^{+}$ describes animals gaining BCS and the associated regression coefficient (b) from the REI model, $b\Delta BCS^{-}$ describes animals losing BCS and the associated regression coefficient (b) from the REI model, BCS is body condition score, and $bBW^{0.75}$ is metabolic BW and the associated regression coefficient (b) from the REI model.

Analogous to partial efficiency of growth (PEG; Kellner, 1909) used in growing cattle, partial efficiency of milk energy production (PEMEP) and partial efficiency of milk energy production based on nutritional tables ($PEMEP_{Nut}$) were defined as:

$$\mathrm{PEMEP} = \frac{\mathrm{NEL}}{\mathrm{NEI} - \mathrm{bBW}^{0.75} + \alpha} \qquad \mathrm{PEMEP}_{\mathrm{Nut}} = \frac{\mathrm{NEL}}{\mathrm{NEI} - \mathrm{NEM} + \alpha}$$

where NEL is daily net energy requirements for lactation, NEI is daily net energy intake, NEM is the net energy requirement for maintenance (Jarrige et al., 1986), α is a shift parameter, and $bBW^{0.75}$ is metabolic BW and its associated regression coefficient (b) from the previously described REI model. A shift parameter of 20 was applied.

Metabolic efficiency (MEff) was defined as:

$$\mathrm{MEff} = \frac{\mathrm{NEI} - \mathrm{NEL}}{\mathrm{BW}^{0.75}}$$

where NEI is daily net energy intake, NEL is net energy requirements for lactation, and $BW^{0.75}$ is metabolic BW.

Feed to body-weight (FtW) was defined as:

$$\mathrm{FtW} = \frac{\mathrm{NEI}}{\mathrm{BW}^{0.75}}$$

where NEI is daily net energy intake, and $BW^{0.75}$ is metabolic BW.

Kleiber ratio (KR) (Kleiber, 1961) in growing animals is defined as average daily gain divided by metabolic BW. An analogous Kleiber ratio trait in dairy cattle was defined as:

$$\mathrm{KR} = \frac{\mathrm{NEL}}{\mathrm{BW}^{0.75}}$$

where NEL is the net energy requirements for lactation and $\mathrm{BW}^{0.75}$ is metabolic BW.

Statistical analysis

Pearson correlations were estimated among the different traits. A t-test was used to determine the significance of the difference between groups of animals.

Results

Descriptive statistics

The mean, standard deviation and the coefficient of variation for the production measures are in Table 3.1. The coefficient of variation was greatest for milk yield (32%) and least for $\mathrm{BW}^{0.75}$ (9%). A moderate coefficient of variation existed for the two component traits of ECE, NEI (20%) and NEL (28%). Descriptive statistics for the alternative efficiency traits are in Table 3.2. The coefficient of variation for the different ratio traits varied from 16% ($\mathrm{ECE}_{\mathrm{maint}}$) to 27% (ECR); the coefficient of variation for energy balance was 76%. The coefficient of variation for REI, REP, or RIEP, when estimated using least squares regression, was undefined since the mean of the residuals is, by definition, zero. Using the mean of NEI and NEL as the denominator in the calculation of the coefficient of variation for REI and REP, respectively, the respective coefficient of variation for REI and REP was 13% and 15%.

Table 3.1. Number of observations (N), mean, standard deviation (SD), and the coefficient of variation (CV) for the production traits.

Trait[1]	N	Mean	SD	CV
Milk yield (kg)	8183	21.73	6.99	32.19
Milk fat yield (kg)	8183	0.86	0.25	29.79
Milk protein yield (kg)	8183	0.75	0.22	29.09
Milk lactose yield (kg)	8183	0.72	0.24	33.33
NEL (UFL/d)	8183	7.04	1.97	27.98
NEI (UFL/d)	8183	16.23	3.24	19.98
BCS (scale 1 to 5)	7086	2.80	0.33	11.82
$BW^{0.75}$ (kg)	7086	111.04	9.96	8.97

[1] NEL = net energy for lactation; NEI = net energy intake; BCS = body condition score (scale 1 = emaciated, 5 = obese); $BW^{0.75}$ = metabolic BW.

Table 3.2. Number of observations (N), mean, standard deviation (SD), and the coefficient of variation (CV) for the different efficiency traits and energy balance.

Trait[1]	N	Mean	SD	CV
EB (UFL/d)[2]	7086	3.24	2.46	75.84
ECR	8183	2.43	0.67	27.48
ECE	8183	0.44	0.11	25.43
ECE_{adj}	7086	0.45	0.10	21.88
ECE_{maint}	7086	0.98	0.16	16.24
PEMEP	7086	0.41	0.11	26.46
$PEMEP_{Nut}$	7086	0.23	0.06	24.16
MEff	7086	0.08	0.02	26.82
FtW	7086	0.15	0.02	16.98
KR	7086	0.06	0.02	26.27
REI (UFL/d)	7086	0.00	2.17	13.37[2]
REI_{maint} (UFL/d)	7086	8.56	2.53	29.56
REP (UFL/d)	7086	0.00	1.06	15.06[2]
REP_{maint} (UFL/d)	7086	8.56	1.68	19.63
RIEP (UFL/d)	7086	0.00	1.75	0.00

[1] EB = energy balance; ECR = energy conversion ratio; ECE = energy conversion efficiency; ECE_{adj} = energy conversion efficiency adjusted; ECE_{maint} = energy conversion efficiency taking account of maintenance; PEMEP = partial efficiency of milk production; $PEMEP_{Nut}$ = partial efficiency of milk production based on nutritional tables; MEff = metabolic efficiency; FtW = feed to body-weight; KR = Kleiber ratio; REI = residual energy intake; REI_{maint} = residual energy intake taking account of maintenance; REP = residual energy production; REP_{maint} = residual energy production taking account of maintenance; RIEP = residual intake and energy production.

[2] Mean of NEI (16.23) and NEL (7.04).

The percentage variance in NEI explained by factors defined in the REI model are in Table 3.3. The partial regression coefficient of NEI on NEL was 1.12 UFL/d per UFL/d of NEL (Table 3.3); additionally, the partial regression coefficient of NEI on $BW^{0.75}$ (i.e., an approximation for animal size) was 0.17 UFL/d per kg $BW^{0.75}$ when all interaction terms were included in the REI model. The partial regression coefficient in the REI model for BW gain was negative (-1.76 UFL/d per $kg^{0.75}$/d), but positive (6.31 UFL/d per $kg^{0.75}$/d) for BW loss; BW loss values were represented as negative values in the data. Only ΔBCS^{+} and ΔBW^{+} in the REI model was not ($P > 0.05$) associated with NEI. The proportion of the variance in NEI explained by just the main effects in the REI model was 0.53; including all interaction terms increased the proportion of the variance explained to 0.59. The partial regression coefficient from the REP model of NEL on NEI was 0.28 UFL/d per UFL/d of NEI. Additionally, the partial regression coefficient of NEL on $BW^{0.75}$ was 0.05 UFL/d per kg $BW^{0.75}$. The proportion of the variance in NEL explained by just the main effects in the REP model was 0.67; including all interaction terms increased the proportion of the variance explained to 0.72.

Table 3.3. Percentage variance in net energy intake (NEI), regression coefficients (standard error in parentheses) and the significance of each variable in the residual energy intake (REI) model.

Variable[1]	% variance	Regression coefficient	P-value
NEL (UFL/d)	28.20%	1.12 (0.02)	0.0001
Parity	21.27%	Parity 1: -0.55 (0.08)	0.0001
		Parity 2: 0.25 (0.07)	0.0002
		Parity 3+: 0.00	0.0001
DIM	0.07%	0.04 (0.002)	0.0001
DIM^2	0.24%	0.00009 (0.00001)	0.0001
$BW^{0.75}$ (kg)	27.80%	0.17 (0.02)	0.0001
BCS (scale 1 to 5)	0.06%	3.28 (0.85)	0.0001
$BW^{0.75} \times BCS$	9.42%	-0.03 (0.01)	0.0002
ΔBW^{+} (kg)	1.74%	-1.76 (1.03)	0.0861
ΔBW^{-} (kg)[2]	2.78%	6.31 (1.55)	0.0001
ΔBCS^{+} (scale 1 to 5)	0.89%	-15.15 (27.95)	0.5878
ΔBCS^{-} (scale 1 to 5)[2]	3.04%	95.40 (19.24)	0.0001
$\Delta BW^{+} \times BCS$	1.91%	0.98 (0.36)	0.0068
$\Delta BW^{-} \times BCS$	2.62%	-1.39 (0.51)	0.0071

[1] NEL = net energy for lactation; parity = 1, 2, 3+; DIM = days in milk fitted as linear effect; DIM^2 = days in milk fitted as quadratic effect; $BW^{0.75}$ = metabolic BW; BCS = body condition score (scale 1 = emaciated, 5 = obese); ΔBW^{+} = animals gaining BW; ΔBW^{-} = animals losing BW; ΔBCS^{+} = animals gaining body condition score; ΔBCS^{-} = animals losing body condition score.

REI = NEI – [NEL + Parity + $\sum_{i=1}^{2} DIM^i$ + $BW^{0.75}$ + BCS + $BW^{0.75} \times BCS$ + ΔBW^{+} + ΔBW^{-} + ΔBCS^{+} + ΔBCS^{-} + $\Delta BW^{+} \times BCS$ + $\Delta BW^{-} \times BCS$].

[2] Phenotypic values included in the analysis for loss are negative.

The most efficient 10% of test-day records, as determined by REI (n=709), on average were associated with an NEI of 7.59 UFL/d less (average NEI of the entire population was 16.23 UFL/d) than the NEI associated with the least efficient 10% of test-day records based on REI ($P < 0.05$). Furthermore, the most efficient 10% of test-day records, based on REI, were associated with superior ($P < 0.05$) ECE (0.55) compared to the least efficient 10% of test-day records (0.33 UFL/d). Moreover, the most efficient 10% of test-day records based on REI were, on average, in negative EB (-0.02 UFL/d) throughout lactation ($P < 0.05$) while the least efficient 10% of test-day records were not (i.e., 7.38 UFL/d). No difference ($P > 0.05$) existed between the most and least efficient REI groups for $BW^{0.75}$, BCS, or NEL.

Mean performance of the top ranked (i.e., 10%) test-day records based on REI (n = 709), REP (n = 709) and RIEP (n = 709) are in Table 3.4. The top 10% of test-day records ranked on

REI were, on average, in negative EB (-0.02 UFL/d) (*P* < 0.05) unlike the mean EB of the bottom 10% of test-day records ranked on both REP (1.51 UFL/d) and RIEP (0.25 UFL/d). Test-day records ranked on REP were associated with the greatest (*P* < 0.05) milk yield (28.03 kg) compared to the top test-day records ranked on REI (21.96 kg) or RIEP (25.56 kg). The top 10% of test-day records ranked on RIEP had the greatest (*P* < 0.05) ECE (0.58, *P* < 0.05) compared with either REI or REP (0.55 UFL/d). No difference (*P* > 0.05) in ΔBW, ΔBCS and $BW^{0.75}$ existed among the top 10% of test-day records ranked on either REI, REP, and RIEP.

Table 3.4. Mean performance of the top 10% (most efficient) of test-day records based on residual energy intake (REI), residual energy production (REP), and residual intake and energy production (RIEP).

	ECE	EB (UFL/d)	NEI (UFL/d)	NEL (UFL/d)	MY (kg)	ΔBW (kg)	ΔBW <60d (kg)	ΔBW >200d(kg)	ΔBCS	BW^1 (kg)	REI (UFL/d)	REP (UFL/d)	RIEP (UFL/d)
REI	0.55^a	-0.02^a	12.94^a	7.04^a	21.96^a	0.21	-0.17	0.38^a	-0.001^a	549.71	-3.82^a	1.01^a	2.71^a
REI$_2$	0.56^a	-0.02^a	13.21^b	7.30^b	23.06^b	0.21	-0.12	0.47^b	-0.001^b	551.41	-2.98^b	0.49^b	1.84^b
REP	0.55^a	1.51^b	16.65^c	9.01^c	28.03^c	0.21	-0.12	0.37^a	-0.001^b	546.17	-2.08^c	1.93^c	2.78^{ac}
RIEP	0.58^b	0.25^c	14.49^d	8.24^d	25.56^d	0.20	-0.14	0.38^a	-0.001^b	546.54	-3.38^d	1.69^d	3.16^d

REI = residual energy intake; REP = residual energy production; RIEP = residual intake and energy production; REI$_2$ = Coleman et al., 2010 RFI definition, ECE = energy conversion efficiency; EB = energy balance; NEI = net energy intake; NEL = net energy for lactation; MY = milk yield; ΔBW = animals gaining and losing BW; ΔBCS = animals gaining and losing body condition score.

[1] Metabolic body-weight (BW$^{0.75}$) converted to actual BW.

^{abc}within a column means with different superscripts are significantly different from each other.

Correlations among the efficiency traits

Correlations between the different efficiency traits and EB are in Table 3.5. Absolute correlations between the residual efficiency traits with EB were strong and varied from 0.70 (RIEP) to 0.81 (REI). The absolute correlations between the ratio traits and EB were strong, varying from 0.82 (ECE_{maint}) to 0.99 (MEff). The correlation between both REI and REI_{maint} with EB was 0.81 and 0.80, respectively. Both REI and REP were identically correlated (|0.88|) with RIEP. Kleiber ratio (KR) was uncorrelated with both REI and REI_{maint}.

Correlations between ECE with both ECE_{adj} and ECE_{maint} were 0.96 and 0.65, even though the difference between ECE_{adj} and ECE_{maint} was just the inclusion of maintenance ($BW^{0.75}$) plus the interaction between $BW^{0.75}$ and BCS in the numerator of ECE_{maint}; the correlation between ECE_{adj} and ECE_{maint} was 0.66. The correlation between PEMEP with both ECE_{adj} and ECE_{maint} was 0.87 and 0.50, respectively. A strong correlation existed between ECE_{adj} and KR (0.73) while the correlation between ECE_{maint} and KR (0.15) was much weaker. The correlation between ECE_{adj} and FtW (-0.19) was weak while the correlation between ECE_{maint} and FtW was moderate (-0.64). Both PEMEP and $PEMEP_{Nut}$ were strongly correlated (0.92). Correlations between ECE with both PEMEP and $PEMEP_{Nut}$ were 0.89 and 0.88, respectively.

Table 3.5. Pearson correlations among the different efficiency traits and energy balance (EB).

Trait[1]	1	2	3	4	5	6	7	8	9	10	11	12	13	14
1. EB														
2. ECR	0.70													
3. ECE	-0.80	-0.87												
4. ECE_{adj}	-0.76	-0.89	0.96											
5. ECE_{maint}	-0.82	-0.57	0.65	0.66										
6. PEMEP	-0.64	-0.80	0.89	0.87	0.50									
7. $PEMEP_{Nut}$	-0.49	-0.84	0.88	0.87	0.36	0.92								
8. MEff	0.99	0.67	-0.77	-0.76	-0.83	-0.65	-0.49							
9. FtW	0.71	0.10	-0.19	-0.19	-0.64	-0.10	0.19	0.75						
10. KR	-0.25	-0.74	0.73	0.73	0.15	0.71	0.92	-0.21	0.49					
11. REI	0.81	0.47	-0.57	-0.57	-0.81	-0.47	-0.25	0.85	0.78	0.05				
12. REI_{maint}	0.80	0.44	-0.56	-0.56	-0.56	-0.38	-0.20	0.81	0.74	0.05	0.86			
13. REP	-0.42	-0.56	0.62	0.62	0.38	0.56	0.60	-0.40	0.001	0.52	-0.53	-0.45		
14. REP_{maint}	-0.10	-0.26	0.29	0.29	0.43	0.38	0.40	-0.12	0.13	0.34	-0.33	0.12	0.63	
15. RIEP	-0.70	-0.61	0.68	0.68	0.69	0.59	0.48	-0.71	-0.44	0.28	-0.88	-0.75	0.88	0.55

[1] EB = energy balance; ECR = energy conversion ratio; ECE = energy conversion efficiency; ECE_{adj} = energy conversion efficiency adjusted; ECE_{maint} = energy conversion efficiency taking account of maintenance; PEMEP = partial efficiency of milk production; $PEMEP_{Nut}$ = partial efficiency of milk production based on nutritional tables; MEff = metabolic efficiency; FtW = feed to body-weight; KR = Kleiber ratio; REI = residual energy intake; REI_{maint} = residual energy intake taking account of maintenance; REP = residual energy production; REP_{maint} = residual energy production taking account of maintenance; RIEP = residual intake and energy production.

Correlations < |0.03| were not different from zero.

Correlations between efficiency and production traits

Correlations among the various efficiency and production traits are in Table 3.6. Residual energy intake was uncorrelated with NEL; however, weak correlations ($P < 0.05$) existed between REI with milk, fat and protein yield (0.08, -0.04 and 0.09, respectively). The correlation between REI_{maint} with milk yield, $BW^{0.75}$ and BCS was 0.14, 0.18 and -0.43 respectively. Milk yield was positively correlated with almost all ratio traits that included NEL in the numerator (i.e., ECE, ECE_{adj}, ECE_{maint}, PEMEP, $PEMEP_{Nut}$, KR, and FtW) and all residual traits, but negatively correlated with ECR, MEff and EB. Moreover, RIEP was negatively correlated with NEI (-0.38). Strong correlations existed between milk fat yield and ECE (0.69), PEMEP (0.78), $PEMEP_{Nut}$ (0.91), and KR (0.91). Additionally, milk protein yield was strongly correlated with both $PEMEP_{Nut}$ (0.89) and KR (0.92). In addition, KR was strongly correlated with NEL (0.95); a strong correlation existed also between FtW and NEI (0.90). Metabolic BW and BCS were weakly correlated with the majority of the efficiency traits investigated (Table 3.6).

Table 3.6. Correlations between the various efficiency and production traits as well as energy balance (EB).

Trait[1]	NEI	NEL	Milk yield	Fat yield	Protein yield	ΔBW	ΔBCS	BCS	BW$^{0.75}$
EB	0.71	-0.16	-0.18	-0.22	-0.12	0.37	0.42	-0.07	0.26
ECR	0.15	-0.65	-0.65	-0.65	-0.62	0.33	0.40	-0.02	0.13
ECE	-0.22	0.67	0.66	0.69	0.63	-0.41	-0.50	0.06	-0.11
ECE$_{adj}$	-0.20	0.66	0.64	0.66	0.63	-0.19	-0.36	0.09	-0.09
ECE$_{maint}$	-0.63	0.07	0.10	0.10	-0.04	-0.11	-0.15	-0.40	-0.23
PEMEP	-0.04	0.78	0.73	0.78	0.73	-0.34	-0.39	0.15	0.31
PEMEP$_{Nut}$	0.23	0.93	0.89	0.91	0.89	-0.31	-0.40	0.08	0.16
MEff	0.70	-0.15	-0.16	-0.20	-0.11	0.36	0.41	-0.09	0.15
FtW	0.90	0.50	0.48	0.43	0.53	0.17	0.13	-0.09	0.12
KR	0.41	0.95	0.92	0.91	0.92	-0.23	-0.35	-0.02	-0.02
REI	0.67	0.00	0.08	-0.04	0.09	0.00	0.00	0.00	0.00
REI$_{maint}$	0.72	0.09	0.14	0.02	0.15	0.06	0.12	-0.43	0.18
REP	0.00	0.52	0.38	0.60	0.44	0.00	0.00	0.00	0.00
REP$_{maint}$	0.22	0.42	0.34	0.45	0.38	0.10	0.18	-0.64	0.27
RIEP	-0.38	0.27	0.17	0.36	0.19	0.00	0.00	0.00	0.00

[1] EB = energy balance; ECR = energy conversion ratio; ECE = energy conversion efficiency; ECE$_{adj}$ = energy conversion efficiency adjusted; ECE$_{maint}$ = energy conversion efficiency taking account of maintenance; PEMEP = partial efficiency of milk production; PEMEP$_{Nut}$ = partial efficiency of milk production based on nutritional tables; MEff = metabolic efficiency; FtW = feed to body-weight; KR = Kleiber ratio; REI = residual energy intake; REI$_{maint}$ = residual energy intake taking account of maintenance; REP = residual energy production; REP$_{maint}$ = residual energy production taking account of maintenance; RIEP = residual intake and energy production.

NEI = net energy intake; NEL = net energy for lactation; ΔBW = animals gaining and losing BW; ΔBCS = animals gaining and losing body condition score; BW$^{0.75}$ = metabolic BW.

Correlations < |0.03| were not different from zero.

Discussion

International interest in feed efficiency, and in particular NEI and REI, is intensifying due to a greater global demand for animal-derived protein and energy sources. Moreover, monitoring individual animal or herd NEI and efficiency has other uses, such as simultaneously trying to minimize the environmental footprint of an expanding global livestock sector. Future pasture-based systems of milk production will be characterized by the ability of a cow to produce the majority of milk solids from grazed pasture. A trait which could identify animals capable of producing increased milk solids from restricted levels of feed intake, independent of performance, would therefore be beneficial to a breeding program for increased production efficiency. In the present study, ample variation existed in the different efficiency traits investigated.

Residual traits

The partial regression coefficients in the REI model suggested that a 535 kg cow (i.e., the average BW of cows in the study) yielding, on average, 7.04 UFL/d NEL with no ΔBCS had a predicted NEI of 16.75 UFL/d. The partial regression coefficient of NEI on NEL (1.12 UFL/d) suggested that for every UFL increase in NEL, NEI was expected to increase by 1.12 UFL/d.

The REI definition in the present study included an interaction between $BW^{0.75}$ and BCS which is similar to McParland et al. (2014), Vallimont et al. (2011) and Veerkamp et al. (1995). This term was however not included in other REI definitions (e.g., Coleman et al., 2010; Pryce et al., 2014). Body condition score is independent of skeletal size and is a measure of depth of muscle and subcutaneous fat. Energy kinetics is associated with body lipid mass, not necessarily fat depth. For this reason a larger animal (i.e., greater $BW^{0.75}$) with the same BCS (i.e., subcutaneous fat depth) is expected to have greater lipid mass compared to a smaller animal. An interaction between BCS and $BW^{0.75}$ was required to capture this (Savietto et al., 2014).

The energy sinks (e.g., NEL, $BW^{0.75}$) and additional contributors to energy kinetics (e.g., ΔBW^{-}) combined, explained 59% of the variability in NEI, implying that REI represented only 41% of the total variance in NEI; the likely contribution of errors in the estimation of, for example grass DMI using the n-alkane technique, suggests that this 41% may actually be the upper limit. Systematic environmental effects such as parity, herd, year, and season are also likely to contribute to this variability. This variability in NEI explained by the REI model was nonetheless less than documented in previous studies in lactating Holstein-Friesian dairy cows. The REI model of Coleman et al. (2010) explained 86% of the variation in feed intake. For comparative purposes, the more traditional definition of residual feed intake (i.e., RFI = DMI minus year, fat, protein and lactose yield, $BW^{0.75}$, ΔBW and BCS; Coleman et al., 2010) was calculated on the current data set. The correlation between the traditional RFI definition of Coleman et al. (2010) and our alternative REI definition was less than unity (0.72). Similarly, the correlation between our REI definition and that of Connor et al. (2013) (REI = energy intake minus parity effect, $BW^{0.75}$, average daily gain and energy corrected milk yield) was also less than unity (0.73). The REI model of Connor et al. (2013) explained 72% of the variation in energy intake. Consequently, we believe that the alternative definition of REI in the present study should be considered for future studies on RFI, as our definition better accounts for lipid mass (change).

Residual energy intake was, as expected, uncorrelated with NEL, $BW^{0.75}$, and BCS since REI was estimated using multiple regression which included these traits. Despite the milk production traits (i.e., milk, fat and protein) comprising the definition of NEL in the REI model, relatively weak correlations ($P < 0.05$) still existed between REI and milk, fat and protein yield. Consequently, milk, fat and protein yield should be included individually in the

REI model to guarantee total independence of fat, and protein yield from REI. When NEL in the REI model was substituted with milk, fat and protein yield, then REI was uncorrelated with these yield traits. The partial regression coefficient of NEI on milk, fat and protein yield was 0.008 kg, 1.14 kg and 8.85 kg, respectively. The correlation between the REI definition using NEL as a measure of energy required for milk production, and REI using milk yield, fat yield and protein yield as measures of energy required for milk production was 0.95.

The strong correlation between REI and EB (0.81) signifies that negative REI (i.e., deemed more efficient animals) animals were also, on average, in more negative energy balance. Negative energy balance is known to be unfavourably associated with reproductive performance (Beam and Butler, 1998; Collard et al., 2000). The similarity between EB and REI across lactation is further illustrated in Figure 3.1. This strong association between REI and EB is not unexpected given their mathematical similarity (Savietto et al., 2014). The correlation between REI and EB was strongest (0.96) in mid-lactation (90-180 DIM) when average BW change was close to zero (mean ΔLW of 0.22 kg/d). When BW change is zero, then BW change does not contribute to the REI model, and thus REI is mathematically equivalent to energy balance (Veerkamp, 2002). Although antagonistic genetic correlations (e.g., REI and fertility) can be overcome within a balanced breeding goal, the appropriate weightings within a selection index require precise estimates of the necessary genetic correlations. This means that if REI is to be considered in a breeding goal, precise estimates of the genetic correlations with health and fertility traits (and others) are required. An alternative would simply be to include DMI itself in a breeding goal with the appropriate weighting; this would be mathematically similar to including REI in the breeding goal if all other traits in the REI model were also in the breeding goal. The relative weighting on all other traits in the breeding goal would then be independent of their associated energy cost which may vary by time of the year (Wall et al., 2008) thus impacting the complexity of the calculations.

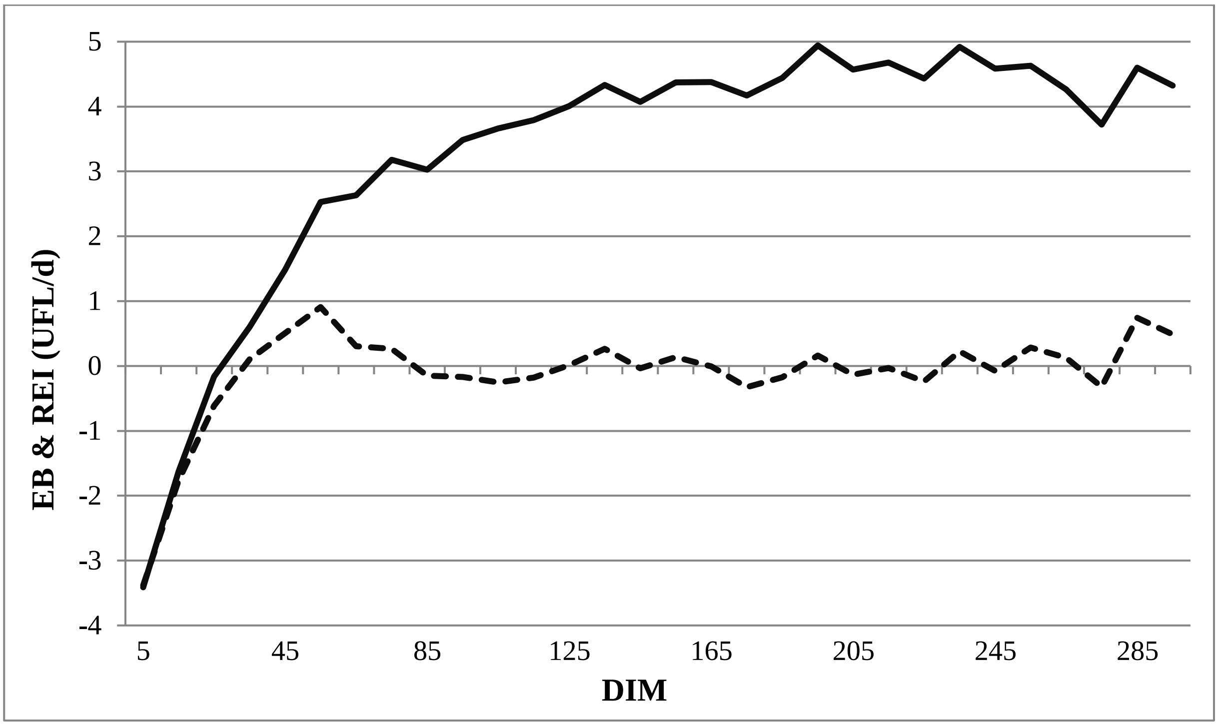

Figure 3.1. Mean energy balance (── EB) and residual energy intake (---- REI) of the population across lactation.

The definition of REI in the present study, and elsewhere, on average, penalises a smaller animal (i.e., reduced BW) compared to a larger animal all else being equal. This is because the energy required to maintain the extra BW is used to derive predicted NEI which, when subtracted from actual NEI, gives REI. Therefore, an alternative definition of REI, REI_{maint}, was defined in the present study where the energy demand of BW (i.e., $BW^{0.75}$ times the regression coefficient on $BW^{0.75}$) and lipid mass (i.e., $BW^{0.75}$ x BCS) was added back to REI. The correlation between REI and REI_{maint} was less than unity (0.86; $P < 0.05$). Although REI_{maint} is not independent of $BW^{0.75}$, which is a reported advantage of REI, this is of little consequence if REI is used in a holistic breeding goal which also includes BW (Berry and

Crowley, 2013). The negative correlation between $\mathrm{REI}_{\mathrm{maint}}$ and BCS nonetheless indicates that this approach to select for greater efficiency through both reduced NEI and body size (i.e., $\mathrm{REI}_{\mathrm{maint}}$) will not be detrimental to BCS. This is important because BCS is related to animal performance (Roche et al., 2009). The comparison of REI and $\mathrm{REI}_{\mathrm{maint}}$ can be further illustrated by evaluating two cows from the dataset. Both cows had identical REI (-3.07 UFL/d) and NEL (4.08 UFL/d) values but had different BW (480 kg v 610 kg). The lighter cow consumed less (average of 9.01 UFL/d) and had a greater ECE value (0.45); in contrast, the heavier cow consumed more (average of 13.67 UFL/d) and had a lesser ECE value (0.29). The $\mathrm{REI}_{\mathrm{maint}}$ was lower (i.e., superior) (15.85 UFL/d) for the lighter cow compared to the heavier cow (20.86 UFL/d). Thus, the $\mathrm{REI}_{\mathrm{maint}}$ trait considers the greater energy costs associated with a heavier cow although this is of little consequence for breeding programs if BW is also included in the breeding goal.

Analogous to residual gain as defined in growing cattle (Koch et al., 1963), REP may be defined as actual milk energy produced relative to expected milk energy produced based on the NEL of an animal and other energy sinks and sources (Coleman et al., 2010). In contrast to REI, positive REP values are indicative of more energy efficient animals. The moderate correlation between REP and REI (-0.53) suggests they are indeed different traits. The more negative REI animals (i.e., deemed more efficient) are expected to, on average, have a greater NEI but have the same milk. In contrast, the more positive REP animals (i.e., deemed more efficient) are expected to, on average, consume the same NEI, but produce, on average, more milk energy output. The benefits of both REI and REP were combined to generate RIEP which is analogous to RIG as defined in growing cattle (Berry and Crowley, 2012). The results substantiate the benefits of RIEP, when accessing the performance of the top 10% of test-day records ranked on REI, REP and RIEP (Table 3.4). The top ranked 10% of RIEP test-day records were associated with more milk when compared to the top ranked

REI test-day records. Additionally, the top RIEP test-day records had the greatest ECE in comparison to both the REP and REI test-day records; therefore, RIEP might be a trait more favoured by the producer because it simultaneously increases NEL and reduces NEI.

Ratio traits

Many of the correlations among the ratio traits in the present study differed from unity implying that each trait is depicting a somewhat different aspect of efficiency. Almost all traits which explicitly included NEL in the numerator (ECE, $ECE_{adj,}$ PEMEP, and KR) were strongly correlated with milk yield, indicating these traits were predominately influenced by NEL.

Energy conversion efficiency, and its reciprocal ECR, are most commonly used internationally across species (Tolkamp et al., 2010). Selection on the former has, however, been shown to be associated with greater BW loss and reduced BCS throughout lactation (Vallimont et al., 2011). The correlations from the present study substantiate this. The correlation between ECE and ΔBCS (-0.50) suggests that 25% of the variation in ECE was due to BCS mobilization, which indicates that loss of BCS throughout lactation contributes to higher ECE values thereby questioning the suitability of ECE as a measure of efficiency. Energy conversion efficiency was therefore redefined in the present study where the contribution of body tissue mobilization to energetic efficiency was accounted for in both ECE_{adj} and ECE_{maint}. Nonetheless, the ECE_{adj} trait was not completely effective in achieving the desired outcome as greater ECE_{adj} was still associated with loss in BW and body condition although the correlations had weakened. The correlations with BCS and BW change were further weakened with the ECE_{maint} trait but the correlations remained negative implying that both BCS and BW loss were still contributing to variability in ECE_{maint}.

Both definitions of PEMEP in the present study were novel and represented the proportion of NEI used for milk production having accounted for maintenance energy requirements. Both PEMEP and $\text{PEMEP}_{\text{Nut}}$ were defined similarly, except for the calculation of maintenance energy, which resulted in a strong correlation between them. The moderately negative correlation of PEMEP and $\text{PEMEP}_{\text{Nut}}$ with BCS and BW change, suggested the loss of BW and BCS throughout lactation contributed to high PEMEP and $\text{PEMEP}_{\text{Nut}}$ values as was the case for ECE.

Similar to PEMEP, although KR is not a feed efficiency measure *per se*, it can be used as a measure of feed efficiency if all animals are fed the same restricted diet, as could be argued to exist in grazing production systems (e.g., the present study). Nonetheless, KR was strongly correlated with $\text{PEMEP}_{\text{Nut}}$ suggesting these traits were nearly identical. The main advantage of KR is that it does not require any measure of feed intake.

The FtW trait defined in the present study and elsewhere (Coleman et al., 2010) provides an indication of cow intake capacity, which is important as successful grazing systems require dairy cows that are adapted to achieving large intakes of high-quality forage. Like KR, FtW does not require feed intake observations and can thus be calculated using data which is routinely available on some farms. In the present study, FtW was further modified where NEL was subtracted from NEI in the numerator to generate the MEff trait. Energy balance is close to a linearization of MEff because EB is formulated when the dominator (i.e., BW) is interchanged to the numerator; thus, a very strong correlation between both is expected. Also, because of this strong correlation, both MEff and EB had similar correlations with the production traits. Nonetheless, the statistical properties of ratio traits suggest that for breeding programmes at least, linearized traits are more favourable (Berry and Crowley, 2013).

Conclusion

This is the first study to comprehensively describe the inter-relationships among alternative definitions of energy efficiency in intensive pasture-based lactating Holstein-Friesian dairy cows. Given the potential of REI to reduce feed intake and therefore variable costs associated with milk production, our findings suggest REI could be a valuable tool for future genetic improvement. However, the existence of genetic variation in such a trait as well as the estimation of precise correlations between REI and both reproduction and health traits (as well as other traits) need to be quantified. Several alternative efficiency definitions were developed in the present study each with their own respective strengths and weaknesses. For example the ratio traits are easy to calculate and understand particularly by producers; however, they are correlated with the component traits and do not fully account for the contribution of, for example BCS change, to energy available. Residual energy intake is more difficult to explain and therefore understand by producers (Wulfhorst et al., 2010) but it is independent of the components of energy kenetics included in its derivation. The eventual decision on which feed intake or efficiency measure to use is of course dependent on the end use. For example a ratio trait may be more suitable for management purposes at a herd level, an REI type trait may be more useful in research experiments attempting to elucidate the factors associated with inter-animal variability in efficiency, while an REI-type trait or DMI itself may be more applicable in a breeding program. Many of the correlations among the various measures of feed efficiency differed from unity implying that each trait is measuring a different aspect of efficiency.

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Chapter 4

Characteristics of feed efficiency within and across lactation in dairy cows and the impact of genetic selection

A.M. Hurley[1, 2], N. López-Villalobos[2], S. McParland[1], E. Kennedy[1], E. Lewis[1],
M. O'Donovan[1], J.L. Burke[2], and D.P. Berry[1]

[1]Teagasc, Animal & Grassland Research and Innovation Centre, Moorepark, Fermoy, Co. Cork, Ireland

[2]Institute of Veterinary, Animal and Biomedical Sciences, Massey University, Private Bag 11-222, Palmerston North, New Zealand

Journal of Dairy Science (2018) 101:1267-1280.

doi.org/10.3168/jds.2017-12841.

Abstract

The objective of the present study was to investigate the phenotypic inter- and intra-relationships within and among alternative feed efficiency metrics across different stages of lactation and parities; the expected impact of genetic selection for feed efficiency on the resulting phenotypic lactation profiles was also quantified. A total of 8,199 net energy intake (NEI) test-day records from 2,505 lactations on 1,290 cows were used. Derived efficiency traits were either ratio-based or residual-based; the latter were derived from least squares regression models. Residual energy intake (REI) was defined as NEI minus predicted energy requirements based on lactation performance; residual energy production (REP) was defined as net energy for lactation (NEL) minus predicted energy requirements based on lactation performance. Energy conversion efficiency (ECE) was defined as NEL divided by NEI. Pearson phenotypic correlations among traits were computed across lactation stages and parities, and the significance of the differences was determined using the Fisher r-to-z transformation. Sources of variation in the feed efficiency metrics were investigated using linear mixed models which included the fixed effects of contemporary group, breed, parity, stage of lactation, and the two-way interaction of parity-by-stage of lactation. With the exception of REI, parity was associated with all efficiency and production traits. Stage of lactation, as well as the two-way interaction parity-by-stage of lactation, were associated with all efficiency and production traits. Phenotypic correlations among the efficiency and production traits differed not only by stage of lactation but also by parity. For example, the strong phenotypic correlation between REI and energy balance (EB) (0.89) for cows in parity-three or greater and early lactation was weaker ($P < 0.05$) for parity-one cows at the same lactation stage (0.81), suggesting primiparous cows use the ingested energy for both milk production and growth. Nonetheless, these strong phenotypic correlations between REI and EB suggested negative REI animals (i.e., more efficient) are also in more-negative EB. These correlations were further supported when assessing the impact on phenotypic performance of animals genetically divergent for feed intake and efficiency based on parental average. Animals genetically selected to have lower REI resulted in cows who consumed less NEI but were also in negative EB throughout the entire lactation. Nonetheless, such repercussions of negative EB do not imply that selection for negative REI (as defined here) should not be practiced, but instead should be undertaken within the framework of a balanced breeding objective which includes traits like reproduction and health.

Keywords: estimated breeding value, feed intake, residual energy intake, energy balance, heritability.

Introduction

Improving feed efficiency is a well-established goal in many species and is highly relevant given current international concerns regarding greenhouse gas emissions, nutrient losses, and water quality (Leip et al., 2015). Therefore, identifying more efficient animals that produce the same quantity of product using fewer resources is highly desirable. Feed efficiency in some species has improved substantially in recent decades although this trend has not been as rapid in other species, especially ruminants. The ratio of energy ingested versus energy output in usable product for dairy cows is much worse than both pigs and poultry (Losinger, 1998; Havenstein et al., 1994). Therefore, improving feed efficiency in ruminants is particularly important. It is also important to unravel the correlation structure of feed efficiency across the productive life of the cow and to understand the repercussions of genetic selection for the feed intake complex on the resulting lactation profiles of feed efficiency and related traits (e.g., energy balance).

The contribution of breeding to improvements in feed efficiency is well recognized (Cahaner and Siegel, 1986; Havenstein et al., 1994; Havenstein et al., 2003). In poultry, the kilograms of feed required to produce a kilogram of meat (i.e., feed conversion ratio) was predicted to have reduced by 50% and growth rate increased by over 400%, between the years 1960 and 2005 (Zuidhof et al., 2014). Also, in broilers, Havenstein et al. (2003) and Sherwood (1977) showed that approximately 85% to 90% of the improvements in feed efficiency are due to genetics. Although response to selection for a trait can be predicted using selection index theory (Smith, 1936), accurate predictions require a large population of phenotyped animals to accurately estimate the necessary genetic parameters. Nonetheless, in the absence of precise estimates of genetic parameters, especially the necessary genetic (co)variances, it is possible to elucidate the response to selection through examination of phenotypic performance of animals divergent in genetic merit for the trait of interest (which does not include their own phenotypic information). Such a strategy could be useful in lactating dairy cows where data to estimate precise genetic parameters are limited.

The focus of the present study was, therefore, to accurately quantify the phenotypic inter- and intra-relationships among alternative feed efficiency metrics and other performance traits across parities and lactation stages in lactating dairy cows; the expected impact of genetic selection for efficiency on the resulting phenotypic lactation profiles was also quantified.

Materials and methods

Data

Data were collected from the Animal and Grassland Research and Innovation Centre, Teagasc Moorepark, Fermoy, Co. Cork, Ireland, between the years 1995 to 2014, inclusive.

Cows that participated in the current study originated from several controlled experiments which evaluated alternative grazing strategies, nutritional experiments, or strains of Holstein-Friesian animals; see O'Neill et al. (2013) for a full description of database. The Holstein-Friesian animals consisted of differing genotypes originating from different populations (Kennedy et al., 2003; Buckley et al., 2007; McCarthy et al., 2007; Coleman et al., 2010). All experiments were performed on two adjacent research farms in southern Ireland (latitude 52°9N; longitude 8°16W); Grass dry matter intake (DMI) for each cow at pasture was periodically estimated using the n-alkane technique (Mayes et al., 1986). Procedures used to gather and analyse fecal samples are described in Kennedy et al. (2008). All cows were offered a basal diet of grazed grass. Swards constituted primarily of perennial ryegrass (*Lolium perenne*) were managed under a rotational grazing system comparable to that detailed by Dillon et al. (1995). Some animals were supplemented with concentrate feed (depending on feeding protocol), varying from 0.89 to 4.0 kg DM per cow daily, offered in equal feeds during each milking.

Cows were milked twice daily. Individual cow milk yield was recorded daily while milk fat, protein and lactose concentration was determined from successive morning and evening milk samples once per week using mid-infrared spectroscopy (FT6000, FOSS, Hillerod, Denmark). Net energy requirement for lactation (NEL) was calculated using the following formula according to Agabriel (2007):

$$\mathrm{NEL} = ((0.054 \times \mathrm{FC}) + (0.031 \times \mathrm{PC}) + (0.028 \times \mathrm{LC}) - 0.015) \times \mathrm{milk\,kg}$$

where FC is fat concentration (%), PC is protein concentration (%), and LC is lactose concentration (%).

Individual animal body-weight (BW) was largely measured weekly following morning milking using electronic scales (Tru-Test Limited, Auckland, New Zealand). The scales were calibrated weekly against known loads. Body condition score (BCS) on a scale of 1 (emaciated) to 5 (obese) was assessed by trained scorers every two to three weeks in increments of 0.25 (Edmonson et al., 1989). Cubic splines were fitted through individual BW and BCS test-day records as described elsewhere (Hurley et al., 2016).

Individual cow daily total DMI (i.e., grazed pasture DMI plus concentrate DMI) was available up to eight times (average of 4.5 times) per lactation. Energy values of the pasture and concentrate were based on the French Net Energy system where 1 unité fourragère du lait (UFL) is the net energy requirements for lactation equivalent of 1 kg standard air-dried barley (Jarrige et al., 1986) equivalent to 7.11 MJ net energy or 11.85 MJ metabolisable energy. The offered herbage UFL concentration was calculated using the acid detergent fibre and crude protein concentration which were quantified in the laboratory (Jarrige, 1989). Concentrate UFL value was determined from the chemical composition of the feed. Where the net energy content of the offered herbage (UFL/kg dry matter) was not available (i.e., 10% of test-day records), the year-month average was assumed. Where the net energy content of the offered concentrate (UFL/kg dry matter) was not available (i.e., 20% of test-day records), the year-month average was assumed. The sum of pasture and concentrate NEI were used to define total net energy intake (NEI).

Data editing

Obvious data errors for BW, BCS, and the milk production traits (e.g., milk yield (kg), fat concentration (%), protein concentration (%), and lactose concentration (%) lower than 2 kg, 2%, 2%, and 2%, respectively) were discarded. Only data between 8 and 280 DIM were retained as limited data existed after 280 DIM. Parity was categorized as 1, 2, and ≥ 3. Contemporary group of experimental treatment by test-date was defined for NEL, NEI, BW, and BCS. Contemporary groups with less than 5 observations were discarded. Following edits, the final dataset consisted of 95,455 test-day records from 2,505 lactations on 1,290 Holstein-Friesian cows; 8,199 individual feed intake measurements remained.

Estimates of energy efficiency and energy balance

Definitions of all traits have been previously described in detail by Hurley et al. (2016). Energy balance (EB) for each test day was calculated in accordance with the net energy system outlined by Jarrige (1989) and modified for Irish dairy systems by O'Mara (1996):

$$\mathrm{EB} = \mathrm{NEI} - \Delta\mathrm{NE} - \mathrm{NEL} - \mathrm{NEM} - \mathrm{NEP}$$

where NEI is daily net energy intake, ΔNE is an adjustment of daily net energy intake for the proportion of concentrates in the diet, NEL is daily net energy requirements for lactation, NEM is daily net energy requirements for maintenance calculated as $((1.4 + (0.6 \times (\mathrm{BW}/100))) \times 1.2)$, and NEP is daily net energy requirements for pregnancy where UFL requirement for the 6th, 7th, and 8th month of pregnancy were 0.9, 1.6, and 2.6 UFL/d, respectively (O'Mara, 1996).

Residual-based efficiency traits. Residual energy intake **(REI)** was defined as the residuals from the regression of NEI on energy sinks and other energy sources as:

$$\mathrm{REI} = \mathrm{NEI} - [\mathrm{NEL} + \mathrm{parity} + \textstyle\sum_{i=1}^{2} \mathrm{DIM}^{\mathrm{i}} + \mathrm{BW}^{0.75} + \mathrm{BCS} + \mathrm{BW}^{0.75} \times \mathrm{BCS} +$$
$$\Delta\mathrm{BW}^{+} + \Delta\mathrm{BW}^{-} + \Delta\mathrm{BCS}^{+} + \Delta\mathrm{BCS}^{-} + \Delta\mathrm{BW}^{+} \times \mathrm{BCS} + \Delta\mathrm{BW}^{-} \times \mathrm{BCS}]$$

where REI is daily residual energy intake, NEI is daily net energy intake, NEL is daily net energy requirements for lactation, parity (1, 2, and ≥ 3), $\sum_{i=1}^{2} \mathrm{DIM}^{\mathrm{i}}$ is days in milk included as a continuous variable with a linear $(\mathrm{i} = 1)$ and quadratic effect $(\mathrm{i} = 2)$, $\mathrm{BW}^{0.75}$ is metabolic BW, and BCS is body condition score. The energy generated from a 1 kg loss in BW is less than the energy required for a 1 kg gain in BW (O'Mara, 1996); therefore, piecewise regression was applied to BW and BCS in the REI model where $\Delta\mathrm{BW}^{+}$ describes animals gaining BW, $\Delta\mathrm{BW}^{-}$ describes animals losing BW, while $\Delta\mathrm{BCS}^{+}$ describes animals gaining BCS, and $\Delta\mathrm{BCS}^{-}$ describes animals losing BCS. No multicollinearity existed in the multiple regression model. The partial regression coefficients of the REI model are outlined in Hurley et al. (2016).

Analogous to residual gain in growing cattle (Koch et al., 1963), residual energy production (REP) for each day of lactation was derived from the residuals of a least squares regression model regressing net energy for lactation on NEI plus energy sinks and other energy sources, similar to that described by Coleman et al. (2010).

$$\mathrm{REP} = \mathrm{NEL} - [\mathrm{NEI} + \mathrm{parity} + \textstyle\sum_{\mathrm{i}=1}^{2} \mathrm{DIM}^{\mathrm{i}} + \mathrm{BW}^{0.75} + \mathrm{BCS} + \mathrm{BW}^{0.75} \times \mathrm{BCS} + \Delta\mathrm{BW}^{+} + \Delta\mathrm{BW}^{-} + \Delta\mathrm{BCS}^{+} + \Delta\mathrm{BCS}^{-} + \Delta\mathrm{BW}^{+} \times \mathrm{BCS} + \Delta\mathrm{BW}^{-} \times \mathrm{BCS}]$$

where REP is daily residual energy production, NEL is daily net energy requirements for lactation, NEI is daily net energy intake, parity (1, 2, and ≥ 3), $\sum_{i=1}^{2} \mathrm{DIM}^{\mathrm{i}}$ is days in milk included as a continuous variable with a linear and quadratic effect, $\mathrm{BW}^{0.75}$ is metabolic BW, BCS is body condition score, $\Delta\mathrm{BW}^{+}$ describes animals gaining BW, $\Delta\mathrm{BW}^{-}$ describes animals losing BW, $\Delta\mathrm{BCS}^{+}$ describes animals gaining BCS, and $\Delta\mathrm{BCS}^{-}$ describes animals losing BCS. No multicollinearity existed in the multiple regression model.

Analogous to residual intake and gain as defined by Berry and Crowley (2012) in growing cattle, residual intake and energy production (RIEP) was defined using both REI and REP, each standardized to have a variance of one:

$$\mathrm{RIEP} = \widetilde{\mathrm{REP}} - \widetilde{\mathrm{REI}}$$

where $\widetilde{\mathrm{REP}}$ is residual energy production standardized to a variance of one, and $\widetilde{\mathrm{REI}}$ is residual energy intake standardized to a variance of one.

Ratio-based efficiency traits. Energy conversion efficiency (ECE) for each day of lactation was defined as:

$$\mathrm{ECE} = \frac{\mathrm{NEL}}{\mathrm{NEI}}$$

where NEL is the daily net energy requirements for lactation, and NEI is the daily net energy intake.

Metabolic efficiency (MEff) was defined as:

$$\mathrm{MEff} = \frac{\mathrm{NEI} - \mathrm{NEL}}{\mathrm{BW}^{0.75}}$$

where NEI is daily net energy intake, NEL is net energy requirements for lactation, and $\mathrm{BW}^{0.75}$ is metabolic BW.

Feed to body-weight (FtW) was defined as:

$$\mathrm{FtW} = \frac{\mathrm{NEI}}{\mathrm{BW}^{0.75}}$$

where NEI is daily net energy intake, and $\mathrm{BW}^{0.75}$ is metabolic BW.

Kleiber ratio (KR) (Kleiber, 1961) in growing animals is defined as average daily gain divided by metabolic BW. An analogous Kleiber ratio trait in dairy cows was defined as:

$$\mathrm{KR} = \frac{\mathrm{NEL}}{\mathrm{BW}^{0.75}}$$

where NEL is the net energy requirements for lactation and $\mathrm{BW}^{0.75}$is metabolic BW.

Statistical analysis

Pearson correlation coefficients among traits were computed within each lactation stage, and the significance of the differences in the same pairwise correlations between parities and between lactation stages was determined using the Fisher r-to-z transformation. For the purpose of calculating the effect of stage of lactation and parity on the correlation among traits, stage of lactation was stratified into stages (8 to 90 DIM, from 91 to 180 DIM, and > 180 DIM) and parity was defined as 1, 2, and ≥ 3.

Linear mixed models in ASReml (Gilmour et al., 2009) were used to quantify the factors associated with each of the efficiency and production traits. Fixed effects treated as categorical variables were contemporary group, parity (1, 2, and ≥ 3), stage of lactation (9 classes: 8-30, 31-60, …, 241-280 DIM), and the interaction between stage of lactation and parity. The proportion of Friesian and “other breeds, excluding Holstein” (Holstein was not included to avoid linear dependency in the model) were both treated as continuous variables. Within- and across-lactation animal permanent environmental effects were considered as random effects.

Supplementary analyses were undertaken to characterize the profiles of lactations divergent for mean lactation REI. Lactations were stratified into high and low (i.e., high or low 10%) mean lactation REI but a restriction was imposed that only lactations with a minimum of three REI values where one record had to be < 60 DIM and another had to be > 150 DIM; after edits, the dataset contained 3,315 records from 622 lactations on 512 cows. A mixed model in ASReml (Gilmour et al., 2009) was then fitted with REI as the dependent variable and the same fixed effects as previously described; however, a within-lactation animal permanent environmental effect was the only random effect considered. The cow-lactation solutions for REI were stratified into two categories (i.e., high or low 10%); in this instance “low” means closer to minus infinity (more efficient) and “high” means closer to plus infinity (less efficient). A mixed model with the fixed effects of contemporary group, parity (1, 2, and ≥ 3), stage of lactation (9 classes: 8-30, 31-60, …, 241-280 DIM), and REI category (n = 3; high, low, in between) was then used where the dependent variable was all of performance and efficiency traits; an interaction between the REI category and lactation stage was also considered in the model as a fixed effect. Cow lactation was fitted as a random effect. Least squares means of the dependent variable for the high and low REI strata were compared.

Genetic evaluation

A genetic evaluation was undertaken for NEI, ECE, REI, REP, and RIEP with the purpose of characterizing animals divergent in genetic merit for each of the five measures. All data used in the genetic evaluation were across an entire lactation (i.e., 8 to 280 DIM). A validation dataset was generated which included animals with phenotypic records masked in the genetic evaluation. Cows in the validation dataset were those that had phenotypic records in the years 2012 to 2014; all of their records were masked in the genetic evaluation including if the cow appeared in years earlier than 2012. A restriction was also imposed that cows in the validation dataset had to have at least three paternal half-sibs with the respective phenotype in the years prior to 2012 and thus included in the genetic evaluation; the validation dataset contained 947 test-day records from 249 cows. Data in the genetic evaluation consisted of 7,291 test-day records from 2,006 lactations on 1,094 cows. A pedigree file, of at least 4 generations (where available), was produced for all animals included in the study; eight animals with no recorded sire were discarded. The average number of daughters per sire was 5.78.

Breeding values for NEI, ECE, REI, REP, and RIEP were predicted for the 249 validation cows via their pedigree relationships using a mixed model in ASReml (Gilmour et al., 2009). The model fitted was the same as previously described; however, an animal additive genetic effect was added as a random term. The estimated breeding values (EBVs) for all of NEI, ECE, REI, REP, and RIEP were stratified, within trait, into 3 groups of low, medium, and high; in this instance “low” means closer to minus infinity and “high” means closer to plus infinity. Subsequent to this, a mixed model with the fixed effects of contemporary group, parity (1, 2, and ≥ 3), stage of lactation (9 classes: 8-30, 31-60, …, 241-280 DIM), and the stratum (i.e., high, average, low) of EBV for each of the five traits singly was used to determine the association between EBV for NEI, ECE, REI, REP, and RIEP and phenotypic performance; an interaction between EBV stratum and lactation stage was also considered in the model as a fixed effect to determine if the association between EBV and phenotypic performance differed across stages of lactation. Animal lactation was fitted as a random effect. Least squares means of the high and low EBVs for NEI, ECE, REI, REP, and RIEP were compared.

Results

Factors associated with the efficiency and production traits

The least squares means for EB, the efficiency and production traits for parity 1, parity 2, and parity ≥ 3 cows are in Table 4.1. Least squares means for NEI, NEL, and $BW^{0.75}$ across lactations are in Figure 4.1. Least squares means for EB and some efficiency traits across stages of lactation are in Figure 4.2. The mean, genetic standard deviation (σ_g), heritability, and repeatability, for EB, the efficiency traits and the production traits are in Table 4.2. Heritability estimates for the efficiency traits ranged from 0.05 (REI) to 0.21 (REP and KR). With the exception of REI, parity was associated ($P < 0.05$) with all efficiency and production traits. Stage of lactation, as well as the two-way interaction parity-by-stage of lactation, were associated ($P < 0.001$) with all efficiency and production traits. The observed impact of the two-way interaction parity-by-stage of lactation on the efficiency traits as well as the production traits, was however, biologically small (Figure 4.3). The proportion of Friesian in the cow was not associated ($P > 0.05$) with ECE, RIEP, MWT, and NEL.

Table 4.1. Number of observations (N), least squares means (standard error in parenthesis) for EB, the efficiency and production traits for parity 1, parity 2, and parity ≥ 3 cows.

	Parity 1		Parity 2		Parity ≥ 3	
Trait[1]	N	Mean	N	Mean	N	Mean
EB (UFL/d)	2,856	-0.38 (0.10)^{a}	2,522	0.10 (0.10)^{b}	2,314	-0.01 (0.10)^{b}
ECE	2,881	0.60 (0.01)^{a}	2,572	0.61 (0.01)^{ab}	2,376	0.62 (0.01)^{b}
MEff (UFL/kg$^{0.75}$)	2,856	0.06 (0.001)^{a}	2,522	0.06 (0.001)^{b}	2,314	0.004 (0.001)^{b}
FtW (UFL/kg$^{0.75}$)	2,948	0.14 (0.001)^{a}	2,632	0.15 (0.001)^{b}	2,401	0.15 (0.001)^{b}
KR (UFL/kg$^{0.75}$)	31,237	0.08 (0.001)^{a}	27,571	0.09 (0.001)^{b}	25,124	0.09 (0.001)^{c}
REI (UFL/d)	2,852	-0.23 (0.09)^{a}	2,519	-0.37 (0.09)^{a}	2,308	-0.33 (0.10)^{a}
REP (UFL/d)	2,852	-0.03 (0.07)^{a}	2,519	-0.05 (0.07)^{ab}	2,308	-0.33 (0.07)^{bc}
RIEP (UFL/d)	2,852	0.10 (0.07)^{a}	2,519	0.15 (0.07)^{a}	2,308	-0.03 (0.07)^{a}
NEI (UFL/d)	2,975	14.02 (0.11)^{a}	2,689	16.76 (0.11)^{b}	2,470	17.88 (0.12)^{c}
NEL (UFL/d)	32,844	8.16 (0.07)^{a}	29,298	9.86 (0.08)^{b}	26,628	10.72 (0.08)^{c}
BW (kg$^{0.75}$/d)	33,477	102.93 (0.37)^{a}	29,472	110.80 (0.38)^{b}	26,973	117.29 (0.38)^{c}
BCS (scale 1 to 5)	33,483	2.79 (0.01)^{a}	29,608	2.74 (0.01)^{b}	26,978	2.76 (0.01)^{ab}

[1] EB = energy balance; ECE = energy conversion efficiency; MEff = metabolic efficiency; FtW = feed to body-weight; KR = Kleiber ratio; REI = residual energy intake; REP = residual energy production; RIEP = residual intake and energy production; NEI = net energy intake; NEL = net energy for lactation; BW = metabolic BW; BCS = body condition score.

$^{a\text{-}c}$Values within rows differing in superscript are different ($P < 0.05$).

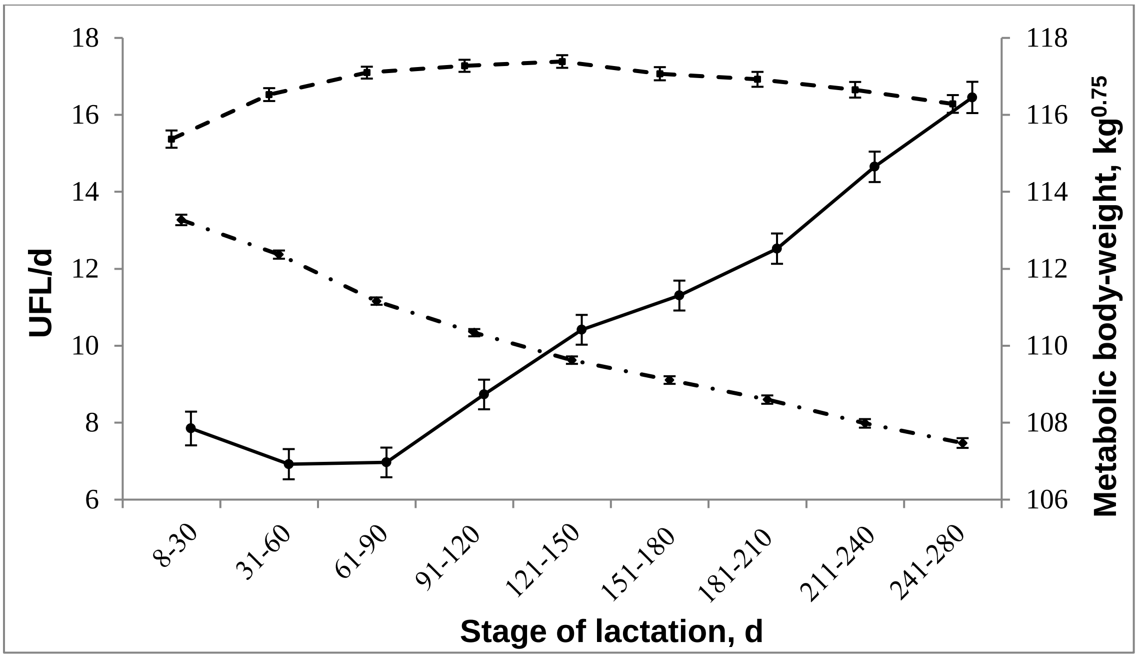

Figure 4.1. Least squares means for net energy intake (UFL/d; ---■---), net energy for lactation (UFL/d; -·-♦-·-), and metabolic BW (kg$^{0.75}$; —●—) across lactations. The error bars represent the SE per stage of lactation.

Table 4.2. Number of records (n), mean, genetic standard deviation (σ_g), heritability (standard error), and repeatability (standard error) for EB, the efficiency and production traits.

Trait[1]	N	Mean	σ_g	Heritability	Repeatability
EB (UFL/d)	7,692	0.54	0.44	0.05 (0.02)	0.10 (0.01)
ECE	7,829	0.60	0.02	0.11 (0.02)	0.16 (0.01)
MEff (UFL/kg$^{0.75}$)	7,692	0.06	0.004	0.06 (0.02)	0.12 (0.01)
FtW (UFL/kg$^{0.75}$)	7,981	0.15	0.01	0.09 (0.02)	0.23 (0.02)
KR (UFL/kg$^{0.75}$)	83,932	0.09	0.01	0.21 (0.04)	0.45 (0.01)
REI (UFL/d)	7,679	0.00	0.44	0.07 (0.02)	0.13 (0.02)
REP (UFL/d)	7,679	0.001	0.45	0.21 (0.04)	0.34 (0.01)
RIEP (UFL/d)	7,679	0.001	0.34	0.09 (0.02)	0.16 (0.02)
NEI (UFL/d)	8,134	16.55	0.80	0.10 (0.03)	0.28 (0.02)
NEL (UFL/d)	88,770	9.59	0.65	0.20 (0.04)	0.42 (0.001)
BW (kg$^{0.75}$/d)	89,922	110.21	6.92	0.17 (0.05)	0.92 (0.01)
BCS (scale 1 to 5)	90,069	2.85	0.16	0.32 (0.05)	0.76 (0.01)

[1] EB = energy balance; ECE = energy conversion efficiency; MEff = metabolic efficiency; FtW = feed to body-weight; KR = Kleiber ratio; REI = residual energy intake; REP = residual energy production; RIEP = residual intake and energy production; NEI = net energy intake; NEL = net energy for lactation; BW = metabolic BW; BCS = body condition score.

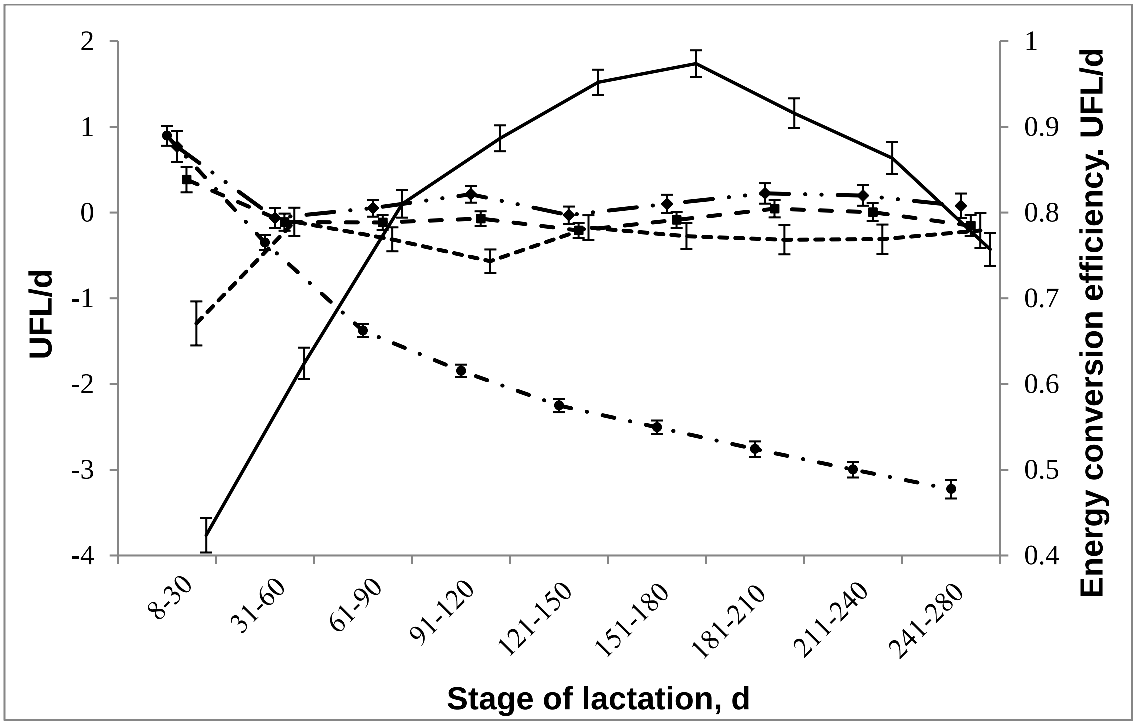

Figure 4.2. Least squares means for energy balance (UFL/d; ——), energy conversion efficiency (-·-●-·-), residual energy intake (UFL/d; ------), residual energy production (UFL/d; ---■---), and residual intake and energy production (UFL/d; -··-♦-··-) across lactations. The error bars represent the SE per stage of lactation.

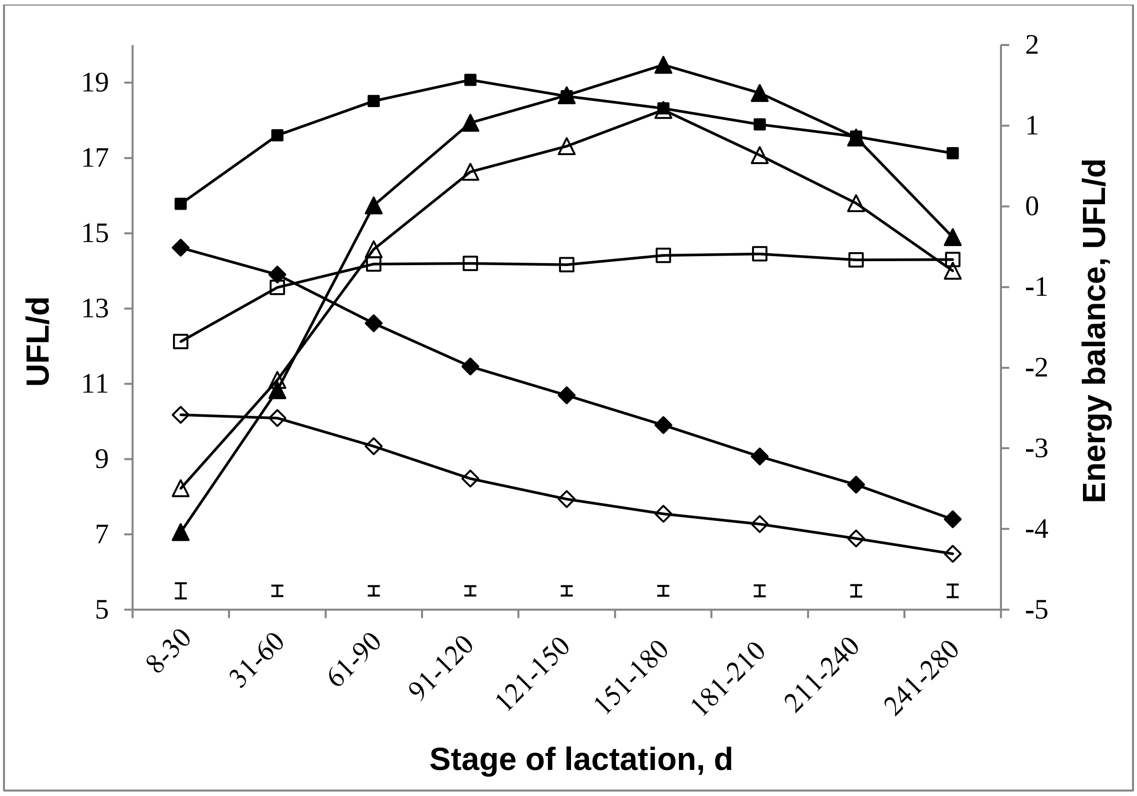

Figure 4.3. Least squares means across stage of lactation for net energy intake for parity 1 (UFL/d; —□—) and parity 3 (UFL/d; —■—) cows, net energy for lactation for parity 1 (UFL/d; —◊—) and parity 3 (UFL/d; —♦—) cows and energy balance for parity 1 (UFL/d; —Δ—) and parity 3 (UFL/d; —▲—) cows across lactation. The error bars represent the mean SE per stage of lactation.

Correlations

Pearson correlations among the efficiency traits, the production traits, and EB for the entire dataset are in Table 4.3. Residual energy intake was positively phenotypically correlated with NEI (0.72) and negatively phenotypically correlated with ECE (-0.56). Residual intake and energy production was positively phenotypically correlated with REP (0.84) but negatively phenotypically correlated with REI (-0.84). Phenotypic correlations between a given trait in one lactation stage with the same trait in another lactation stage are in Table 4.4; phenotypic correlations between a given trait in one parity with the same trait in another parity are in Table 4.5. With the exception of KR, correlations were all weak for the efficiency traits; in contrast, all production traits were moderately to strongly phenotypically correlated. Strong phenotypic correlations between BW in one lactation stage with BW in another lactation stage existed; strong phenotypic correlations also existed between BW in one parity with BW in another parity with phenotypic correlations never less than 0.82.

Table 4.3. Phenotypic correlations among the efficiency traits, the production traits, and EB for the entire dataset.

Trait[1]	EB	ECE	MEff	FtW	KR	REI	REP	RIEP	NEI	NEL
ECE	-0.82									
MEff	0.97	-0.81								
FtW	0.68	-0.23	0.68							
KR	-0.31	0.71	-0.33	0.46						
REI	0.82	-0.56	0.82	0.82	0.01^{NS}					
REP	-0.55	0.55	-0.50	0.01^{NS}	0.55	-0.41				
RIEP	-0.82	0.66	-0.75	-0.45	0.31	-0.84	0.84			
NEI	0.60	-0.27	0.59	0.89	0.38	0.72	0.00^{NS}	-0.43		
NEL	-0.33	0.66	-0.25	0.45	0.96	0.00^{NS}	0.56	0.33	0.52	
BW	0.08^{NS}	-0.11	0.09	0.10	-0.06	0.00^{NS}	0.00^{NS}	0.00^{NS}	0.53	0.19

[1] EB = energy balance; ECE = energy conversion efficiency; MEff = metabolic efficiency; FtW = feed to body-weight; KR = Kleiber ratio; REI = residual energy intake; REP = residual energy production; RIEP = residual intake and energy production; NEI = net energy intake; NEL = net energy for lactation; BW = body-weight.

^{NS}Correlation estimates do not differ ($P > 0.05$) from zero.

The pairwise phenotypic correlations among the efficiency traits, EB, and NEI within each stage of lactation (i.e., 8 to 90 DIM, 91 to 180 DIM, and ≥ 180 DIM) by parity (i.e., 1, 2, and ≥ 3) are in Table 4.6. The phenotypic correlation between REI and EB strengthened ($P < 0.05$) from early to mid-lactation and was near unity from mid to late lactation irrespective of parity. A strong phenotypic correlation existed between REI and EB (0.89) for parity 3 or greater animals in early lactation yet, the same correlation was weaker ($P < 0.05$) at the same stage of lactation in parity one animals

(0.81). The phenotypic correlation between REP and ECE (0.59) in parity one early lactation animals was stronger ($P < 0.05$) at the same stage than animals in parity two (0.65) and parity 3 or greater (0.66) animals.

Table 4.4. Phenotypic correlations* between observations within lactation stages for the efficiency traits, EB, NEI, and NEL.

		Within lactation	
Trait[1]	DIM stage	91–180 DIM	>180 DIM
EB	8–90 DIM	0.11	0.22
	91–180 DIM		0.09
ECE	8–90 DIM	0.16	0.13
	91–180 DIM		0.04
MEff	8–90 DIM	0.08	0.17
	91–180 DIM		0.07
FtW	8–90 DIM	0.29	0.34
	91–180 DIM		0.43
KR	8–90 DIM	0.57	0.57
	91–180 DIM		0.73
REI	8–90 DIM	0.19	0.23
	91–180 DIM		0.12
REP	8–90 DIM	0.42	0.49
	91–180 DIM		0.46
NEI	8–90 DIM	0.28	0.34
	91–180 DIM		0.59
NEL	8–90 DIM	0.45	0.62
	91–180 DIM		0.77

[1] EB = energy balance; ECE = energy conversion efficiency; MEff = metabolic efficiency; FtW = feed to body-weight; KR = Kleiber ratio; REI = residual energy intake; REP = residual energy production; NEI = net energy intake; NEL = net energy for lactation.

[*] All correlation estimates differed ($P < 0.001$) from 1.

Table 4.5. Phenotypic correlations* between observations across parity for the efficiency traits, EB, NEI, and NEL.

		Across parity	
Trait[1]	Parity	Parity 2	Parity ≥ 3
EB	Parity 1	0.22	0.07
	Parity 2		0.06
ECE	Parity 2	0.18	0.02
	Parity 3		0.03
MEff	Parity 2	0.23	0.04
	Parity 3		0.02
FtW	Parity 2	0.35	0.27
	Parity 3		0.47
KR	Parity 2	0.73	0.44
	Parity 3		0.59
REI	Parity 1	0.23	0.13
	Parity 2		0.23
REP	Parity 1	0.55	0.40
	Parity 2		0.42
NEI	Parity 1	0.49	0.34
	Parity 2		0.44
NEL	Parity 1	0.78	0.51
	Parity 2		0.63

[1] EB = energy balance; ECE = energy conversion efficiency; MEff = metabolic efficiency; FtW = feed to body-weight; KR = Kleiber ratio; REI = residual energy intake; REP = residual energy production; NEI = net energy intake; NEL = net energy for lactation.

[*] All correlation estimates differed ($P < 0.001$) from 1.

Table 4.6. Phenotypic correlations among the efficiency traits, EB, and NEI across lactation stages and parities.

	8–90 DIM				91–180 DIM				>180 DIM			
					Parity 1							
Trait[1]	ECE	EB	REI	REP	ECE	EB	REI	REP	ECE	EB	REI	REP
EB	-0.91^{a}				-0.90^{a}				-0.66^{a}			
REI	-0.72^{a}	0.81^{a}			-0.74^{a}	0.93^{a}			-0.60^{a}	0.90^{a}		
REP	0.59^{a}	-0.45^{a}	-0.52^{a}		0.78^{a}	-0.60^{a}	-0.41^{a}		0.82^{a}	-0.50^{a}	-0.33^{a}	
NEI	-0.66^{a}	0.80^{a}	0.82^{a}	-0.03^{a}	-0.38^{a}	0.66^{a}	0.83^{a}	-0.01^{a}	-0.25^{a}	0.71^{a}	0.89^{a}	-0.01^{a}
					Parity 2							
EB	-0.92^{a}				-0.91^{a}				-0.68^{a}			
REI	-0.77^{b}	0.88^{b}			-0.73^{a}	0.93^{a}			-0.59^{a}	0.91^{a}		
REP	0.65^{a}	-0.61^{b}	-0.48^{a}		0.82^{b}	-0.63^{a}	-0.39^{a}		0.85^{a}	-0.45^{a}	-0.26^{a}	
NEI	-0.66^{a}	0.72^{a}	0.87^{b}	-0.09^{a}	-0.30^{b}	0.61^{b}	0.83^{a}	0.03^{a}	-0.23^{a}	0.76^{b}	0.90^{a}	0.05^{a}
					Parity ≥ 3							
EB	-0.96^{b}				-0.90^{a}				-0.71^{b}			
REI	-0.75^{b}	0.89^{b}			-0.74^{a}	0.94^{a}			-0.59^{a}	0.90^{a}		
REP	0.66^{a}	-0.59^{b}	-0.40^{a}		0.82^{b}	-0.64^{a}	-0.44^{a}		0.88^{b}	-0.57^{b}	-0.34^{a}	
NEI	-0.65^{a}	0.68^{a}	0.81^{a}	-0.03^{a}	-0.39^{a}	0.69^{a}	0.86^{b}	-0.03^{a}	-0.18^{b}	0.66^{c}	0.87^{a}	0.04^{a}

[1] ECE = energy conversion efficiency; EB = energy balance; REI = residual energy intake; REP = residual energy production; NEI = net energy intake.

[a,c] Correlation estimates within parity across stage differ ($P < 0.05$) from each other.

Lactations ranked on residual energy intake and energy conversion efficiency

The association between EB, ECE, REI, and NEI and the REI category (i.e., high and low 10%) was dependent on lactation stage. Figure 4 depicts the least squares means of EB, ECE, and REI of either the low 10% of lactations (n = 62; most efficient) and high 10% of lactations (n = 62; least efficient) ranked on REI. Lactations from animals ranked in the lowest (i.e., most negative) 10% on REI were consistently in negative EB and REI throughout lactation which differed ($P < 0.05$) from the highest 10% of lactations ranked on REI where EB and REI were always positive (Figure 4). The lowest ranking lactations on REI ate, on average, 14.59 UFL per day which was consistently less ($P < 0.05$) when compared to the highest ranking lactations on REI which ate, on average, 17.99 UFL per day. The lowest ranking lactations on REI produced, on average, 9.42 UFL per day (i.e., NEL) which was less when compared to the highest ranking lactations on REI which produced, on average, 9.69 UFL per day. No difference ($P > 0.05$) in NEL, BW, and BCS existed among the highest and lowest 10% of lactations ranked on REI. Where a cow is expected to remain in the herd, on average, 4 lactations over a typical 305 day lactation then total NEI saved between lactations divergent on REI was 4,148 UFL; this saving is equivalent to the average feed intake of an Irish dairy cow for a typical 305 day lactation (Berry et al. 2006).

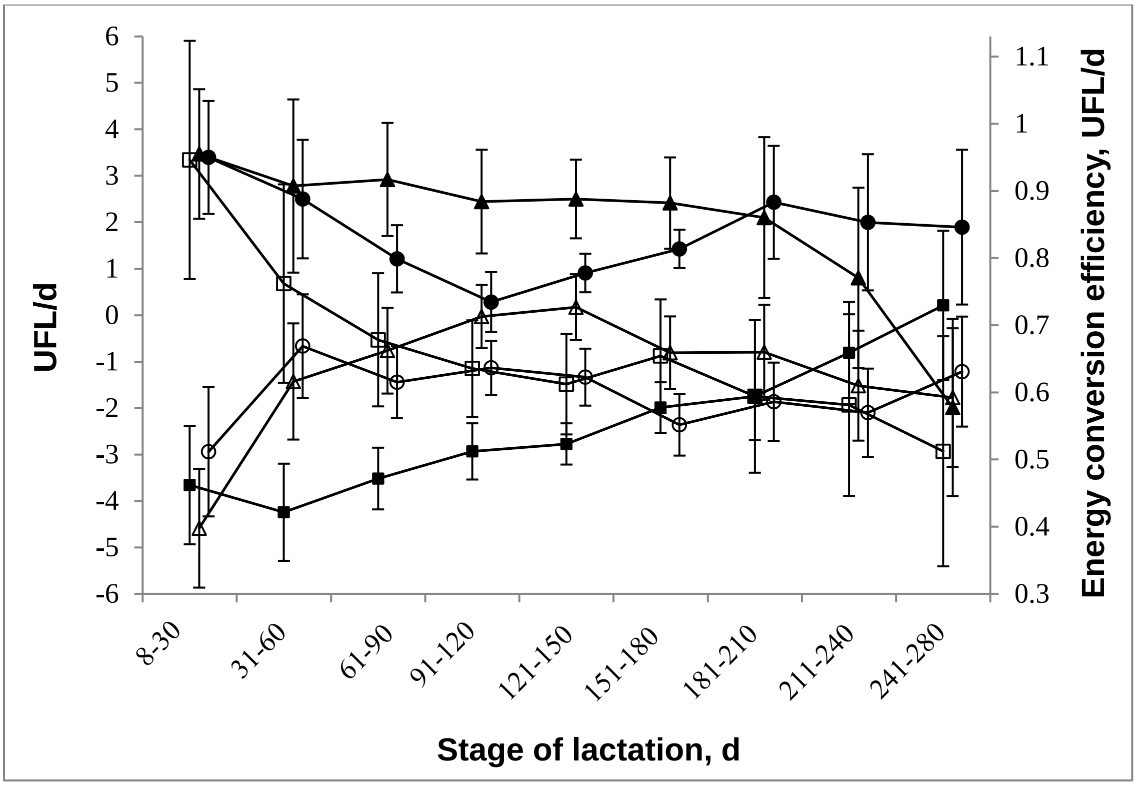

Figure 4.4. Least squares means across stage of lactation for the highest (n = 62) and lowest (n = 62) 10% of lactations for residual energy intake. Shaded symbols illustrate the highest 10% (i.e., inefficient lactations) of lactations, and un-shaded symbols illustrate the lowest 10% (i.e., efficient lactations) of lactations for energy balance (UFL/d; —▲Δ—), energy conversion efficiency (—■□—) and residual energy intake (UFL/d; —●○—).

The association between EB, ECE, REI, NEI, and BW and the ECE category (i.e., high and low 10%) was dependent on lactation stage; however, the association between NEL and the ECE category (i.e., high and low 10%) was not dependent on lactation stage. Appendix 4.2 depicts the least squares means of EB, ECE, and REI of either the lowest 10% of lactations (n = 62; least efficient) and highest 10% of lactations (n = 62; most efficient) ranked on ECE. The highest ranking lactations on ECE (i.e., most efficient) consumed, on average, 15.66 UFL/d which was less when compared to the lowest ranking lactations on ECE which, on average, consumed 16.62 UFL/d. The highest ranking lactations on ECE were, on average, in more negative EB when compared to the lowest ranking lactations on ECE (Appendix 4.5).

Impact of genetic selection for feed intake and efficiency

Least squares means, standard error of the difference (SED), and significance of the efficiency traits and the production traits for cows divergent on ECE, REI, and REP are in Table 4.7. The association between EBV stratum and each of the feed efficiency and performance metrics did not differ ($P > 0.05$) by lactation stage; therefore, only the least squares means averaged across all stages of lactation are presented (Table 4.7). The stratum of cows genetically predisposed to have lower REI (i.e., more efficient) consumed 0.59 UFL/d ($P < 0.01$) less NEI and were in more negative EB ($P < 0.001$) than their lowest ranked contemporaries (Table 4.7). The EBV difference between the top and bottom ranked stratum of cows divergent on REP was 0.31 UFL/d ($P < 0.001$). The top ranked EBV cows divergent on REP produced 0.65 UFL/d ($P < 0.0001$) more NEL compared to the lowest ranked REP cows (Table 4.7).

Table 4.7. Least squares means, standard error of the difference (SED) and significance of the efficiency and production traits for cows genetically divergent on ECE, REI, and REP.

	ECE			REI			REP		
Trait[1]	High	Low	SED[2]	High	Low	SED	High	Low	SED
EBV (UFL/d)[3]	0.01	-0.004	0.0004***	0.16	-0.10	0.01***	0.19	-0.12	0.01***
EB (UFL/d)	1.46	1.59	0.19	1.73	1.34	0.19*	1.63	1.28	0.19
ECE	0.57	0.55	0.01*	0.55	0.57	0.01	0.57	0.56	0.01
MEff (UFL/kg$^{0.75}$)	0.07	0.07	0.002	0.08	0.07	0.002	0.07	0.07	0.002
FtW (UFL/kg$^{0.75}$)	0.17	0.16	0.002*	0.16	0.16	0.002	0.17	0.16	0.002*
KR (UFL/kg$^{0.75}$)	0.09	0.09	0.001	0.09	0.09	0.001	0.09	0.08	0.001*
REI (UFL/d)	1.15	1.13	0.19	1.32	0.94	0.19*	1.36	0.75	0.19***
REP (UFL/d)	0.05	-0.47	0.11***	-0.26	-0.18	0.11	0.02	-0.64	0.10**
RIEP (UFL/d)	-0.44	-0.77	0.13*	-0.71	-0.50	0.13	-0.55	-0.73	0.13
NEI (UFL/d)	17.09	17.28	0.21	17.38	16.79	0.20*	17.44	17.08	0.20*
NEL (UFL/d)	9.59	9.34	0.12*	9.48	9.40	0.11	9.68	9.03	0.11***
BW (kg$^{0.75}$/d)	103.11	107.32	0.61**	104.25	103.89	0.60	105.68	107.74	0.59
BCS (scale 1 to 5)	2.97	2.96	0.01	2.95	2.91	0.01	3.00	2.96	0.01
Reliability (%)	11.01	12.03	0.01	9.85	8.54	0.01	8.85	7.54	0.01

[1] EBV = estimated breeding value; EB = energy balance; ECE = energy conversion efficiency; MEff = metabolic efficiency; FtW = feed to body-weight; KR = Kleiber ratio; REI = residual energy intake; REP = residual energy production; RIEP = residual intake and energy production; NEI = net energy intake; NEL = net energy for lactation; BW = metabolic BW; BCS = body condition score.

[2] SED = Standard error of the difference.

[3] EBV for animals segregated on ECE is unitless.

***Statistically significant at $P < 0.001$; **statistically significant at $P < 0.01$; * statistically significant at $P < 0.05$.

Least squares means, standard error of the difference (SED), and significance of the efficiency and production traits for cows divergent on NEI and RIEP are in Appendix 4.1. The EBV difference between the top and bottom ranked cows divergent on NEI was 0.51 UFL/d ($P < 0.001$). The stratum of cows genetically predisposed to have greater NEI consumed 0.55 UFL/d ($P < 0.01$) more and were 2.81 $kg^{0.75}$/d ($P < 0.001$) heavier than their lowest ranked contemporaries (Appendix 4.1). Animals divergent on genetic merit for NEI did not differ ($P > 0.05$) in any of the efficiency traits. The EBV difference between the top and bottom ranked stratum of cows divergent on RIEP was 0.34 UFL/d ($P < 0.001$). The top ranked EBV cows divergent on RIEP consumed 0.92 UFL/d ($P < 0.0001$) less NEI, and produced 0.57 UFL/d ($P < 0.0001$) more NEL. Additionally, the top ranked stratum of cows divergent on RIEP had both greater ECE and REP ($P < 0.0001$), and had lower REI ($P < 0.0001$) compared to the lowest ranked RIEP cows (Appendix 4.2).

Discussion

Many livestock industries including beef, swine, fish, and poultry either implicitly or explicitly include some component(s) of net feed efficiency in their breeding goals. The dairy industry, however, has been slow to explicitly include the feed intake and utilization complex in their breeding goals (Van der Werf, 2004; Berry and Crowley, 2013). This is primarily attributable to a lack of accurate feed intake data on commercial animals, but also a lack of consistency in defining the most appropriate definition of the feed intake and utilization complex. With the expected volatility in future global milk price, one approach to maintaining resilience without necessarily sacrificing milk yield output is through enhanced feed efficiency. The objective of the present study was to investigate the inter- and intra-relationships within and among alternative feed efficiency metrics across different stages of lactation and parities; the expected impact of genetic selection for efficiency on the resulting phenotypic lactation profiles was also quantified.

Results from the present study indicate that sufficient genetic variability exists in the different efficiency traits investigated as evident by the genetic coefficient of variation which ranged from 2.64% (REI) to 11.11% (KR). The fact that the (co)variation within and among the alternative efficiency metrics differ across parity and lactation stages suggests that not only are the efficiency traits all measuring different aspects of efficiency, but these relationships are not consistent across time. Nonetheless, the change in phenotypic (co)variances within and among traits for different life stages corroborate similar phenomena reported by Hurley et al., (2017) at a genetic level. This therefore suggests that the change in (co)variances across time is at least partly due to genetics. The phenotypic performance of cows genetically predisposed to have lower REI (i.e., more efficient) was that they consumed less NEI but were also in much greater negative EB, particularly in early lactation, relative to their genetically less efficient contemporaries. To the best of our knowledge, this is the first study that has illustrated the implications on phenotypic performance of selecting animals genetically divergent for efficiency; results clearly demonstrated that phenotypic differences in feed intake and efficiency can be achieved through genetic selection.

Correlations within traits

Most studies investigating REI and other measures of efficiency in dairy cows assume that feed efficiency is phenotypically the same trait across lactation (Parke et al., 1999; Zamani et al., 2008; Manafiazar et al., 2015). Results from the present study, however, question this approach. In the present study, the fact that (correlations were less than unity) weak phenotypic correlations existed within almost all efficiency traits, both across parities and lactation stages, suggests, that the efficiency traits need to be recorded across an entire lactation in order to monitor feed efficiency at a cow level. With the exception of KR, the observed weak phenotypic correlation within each efficiency trait across time is in direct contrast to the generally strong within-trait phenotypic correlation for the production traits evaluated in the present study (Table 4.4 and 4.5). The observed weaker phenotypic correlations for the composite efficiency traits could be due to the underlying physiological changes the cow is undergoing throughout lactation (e.g., underlying milk compositional changes) and its effect on the partitioning of NEI into the different components at these lactation stages.

Namkoong (1985) stated that correlations of unity within the same component trait across environments can still result in re-ranking of cows for an index trait (e.g., REI) if the variance of the component traits in the environments differs. The strong phenotypic correlations between BW across parities and lactation stages, along with the similar variance for BW across time, suggests BW is unlikely to be contributing to the change in (co)variation of the index traits (i.e., traits that are a mathematical combination of other traits) such as REI, REP, and RIEP to change across time. In the present study, the moderate to strong phenotypic correlations and the differing variances for both NEL and NEI across time suggests, therefore, that NEL and NEI are more likely contributors to the observed re-ranking of the index traits across time.

Correlations between traits

Several studies have documented the inter-relationships among different measures of feed efficiency, but such estimates were based on lactation average performance and were not undertaken by lactation stage or by parity (Connor et al., 2013; Manafiazar et al., 2015; Manzanilla-Pech et al., 2016). Results from the present study suggest that although phenotypic correlations among the efficiency traits, EB, and NEI estimated across the entire lactation (Table 4.3) are in general agreement with previous studies (Connor et al., 2013; Manafiazar et al., 2015), these pairwise correlations did in fact change both by stage of lactation and by parity. For example, the strong phenotypic correlation between REI and EB for early lactation cows in parity-three or greater (0.89) was weaker ($P < 0.05$) for parity-one cows at the same lactation stage (0.81). This phenomenon is probably due to primiparous cows also using the ingested energy for growth (Berry et al., 2004; Coffey et al., 2006).

The pairwise phenotypic correlation structure among the different traits investigated across the productive life generally varied more by stage of lactation than by parity. For example, the maximum difference in the correlation between EB and ECE across parities was never greater than 0.05, but the maximum difference in the correlation between EB and ECE was 0.25 across lactation stages. This phenomenon suggests the physiological mechanisms controlling feed efficiency across lactation stages are much greater than those across parity. The phenotypic correlations between EB and ECE weakened from early to late lactation, suggesting improved efficiency was associated with animals in more negative EB. The strong negative phenotypic correlation between EB and ECE corroborates Spurlock et al. (2012) based on data from Holstein cows where NEI was measured for only the first half of lactation. As expected, REI and REP exhibited identical phenotypic correlations with their sum (RIEP). The strong phenotypic correlation between NEL with both ECE and KR suggests these traits were predominately influenced by NEL. The strong phenotypic correlation between

MEff and EB was expected as EB is close to a linearization of MEff (Hurley et al., 2016).

Impact of genetic selection

The heritability estimates for the majority of the efficiency traits in the present study were in general agreement with several other studies on either TMR or grass fed lactating dairy cows (Ngwerume and Mao, 1992; Vallimont et al., 2011; Berry and Crowley, 2013). The heritability estimate for REI in the present study was nevertheless greater than the average of 0.04 reported by Berry and Crowley (2013) from a meta-analysis of the available literature on dairy and beef cows. Ample genetic variability existed for the different efficiency traits as evidenced in the present study by the coefficient of genetic variation which was somewhat similar to the coefficient of genetic variation which existed for NEL (i.e., 6.74%). Therefore, genetic progress in efficiency is achievable given this genetic variability as evident by the genetic gains achieved in milk production with a similar coefficient of genetic variation (Berry, 2008).

To the best of our knowledge, the present study is the first to quantify the impact on phenotypic performance of genetically selecting animals to be divergent for feed intake and efficiency based on parental average as would be the case in most breeding programs. Although response to selection for a trait can be predicted using selection index theory (Smith, 1936), accurate predictions require a large population of phenotyped animals to accurately estimate the necessary genetic parameters. Nonetheless, in the absence of precise estimates of the necessary genetic (co)variances, it is also possible to elucidate the response to selection through examination of phenotypic performance of animals divergent in genetic merit for the trait(s) of interest. Such a strategy could potentially be useful in lactating dairy cows where data are limited on some traits such as NEI, and this strategy is often adopted in controlled studies for different performance traits (Coffey et al., 2003; Coleman et al., 2010).

Although, on average, the reliability of the lowest ranked cows (n = 79) divergent on REI (i.e., most efficient) was low the reliability of the mean of their EBV was 99%. The phenotypic difference in REI between the high and low ranked cows divergent on REI was 0.38 UFL/d which is slightly larger than the expectation of 0.26 UFL/d based on their mean EBV difference for REI. The difference in REI between the high and low ranked cows divergent on REI represented 2.30% of mean NEI (i.e., 16.55 UFL/d), while the difference in EBV between the high and low ranked cows divergent on REI was less represented 1.57% of mean NEI. This clearly illustrates that the variability in REI is small, even though the cows on trial were an unselected population but represented considerable genetic diversity with the Holstein-Friesians used originating from many different countries (Coleman et al., 2010; McCarthy et al., 2007). Nonetheless, there is scope for selecting on REI as evidenced by the genetic standard deviation (0.44 UFL/d) and the observed response to selection.

The phenotypic difference in NEI between the high and low ranked cows divergent on REI was 0.59 UFL/d. Therefore, assuming a cow remains in the herd for, on average, 4 lactations, over 365 days, this translates to an estimated saving of €67.19 (assuming a cost of €0.078/UFL; Finneran et al., 2010). The potential extra revenue generated is close to €17 million over a 365 day period per million dairy cows. The value of REI has previously been quantified in Australia using selection index theory; results illustrate that RFI (residual feed intake) contributed approximately 3% per year of the genetic gain for extra profit which was documented to be worth an estimated AUS$0.55M to the industry per year (Gonzalez-Recio et al., 2014). Cows ranked divergent on REI were also more efficient with higher ECE compared to their less efficient counterparts, although no differences in MEff, FtW, and KR existed between both groups.

While many studies (Herd and Arthur, 2009; Crowley et al., 2010) proposed selecting for more negative REI (i.e., more efficient), results from the present study suggest that selection on negative REI alone will result in cows that are in greater negative EB, especially in early lactation. The implication of negative EB on health and fitness traits, including fertility, has been well documented (Beam and Butler, 1998; Collard et al., 2000; De Vries and Veerkamp, 2000). Nonetheless, such repercussions of negative EB do not imply that selection for negative REI should not be practiced, but instead should be undertaken within the framework of a balanced breeding objective which includes traits like reproduction and health (Berry and Crowley, 2013). Moreover, (some of) the strong relationship observed in the present study between REI and EB could simply be a statistical artefact of the mathematical definition of both REI and EB in the present study; the use of many of same parameters in the definition of both traits imply a part-whole relationship thus contributing to a statistical relationship. Whether the heretofore relationships reported between EB with both health and fertility (Beam and Butler, 1998; Collard et al., 2000; De Vries and Veerkamp, 2000) also exist for REI remains largely unknown.

The phenotypic difference in REP between the high and low ranked cows divergent on REP was 0.66 UFL/d which is double the expectation of 0.31 UFL/d based on the mean difference in EBV for REP between the divergent cows. The difference in REP between the high and low ranked cows divergent on REP represented 6.78% of mean NEL (i.e., 9.59 UFL/d), while the difference in EBV between the high and low ranked cows divergent on REP represented 3.23% of mean NEL. These results suggest considerably greater variability exists in REP compared with REI which was substantiated by the coefficient of genetic variation for REP (i.e., 4.73%) being almost twice as large as the coefficient of genetic variation for REI (i.e., 2.64%).

Conclusion

Results from the present study suggest that caution should be demonstrated when accessing the inter- and intra-relationships among alternative feed efficiency metrics on a per lactation basis since these do vary both across parities and across lactation stages or at the very least when presenting such correlations, from where the data originates should be made clear. This is the first study to comprehensively describe the implications on phenotypic performance from lactating dairy cows genetically diverse for efficiency measures. Results clearly show that phenotypic differences in feed intake and efficiency can be achieved through genetic selection; of course the results reported within are only applicable to the population utilized in the present study which was based on an extensive production system where the basal cow diet consisted predominantly of *in situ* grazed grass. Given the need to increase the production of several important agricultural commodities, including milk, REI or REP could offer possible effective solutions to increase production efficiency. Nonetheless, genetic correlations with the feed intake and utilisation complex with both reproduction and health traits need to be estimated prior to possible consideration in any breeding program.

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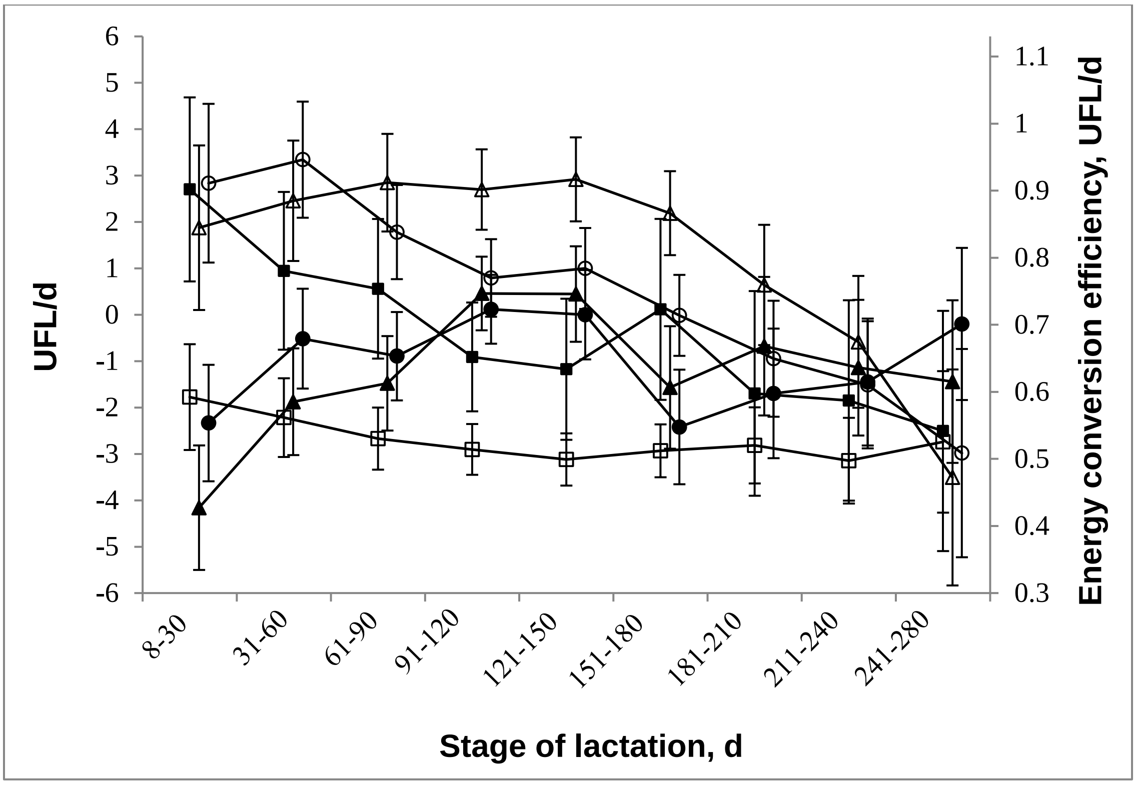
Appendix 4.1. Least squares means, standard error of the difference (SED) and significance of the efficiency and production traits for cows divergent on NEI and RIEP.

	NEI			RIEP		
Traits[1]	High	Low	SED[2]	High	Low	SED
EBV (UFL/d)	0.36	-0.15	0.01***	0.22	-0.12	0.01***
EB (UFL/d)	1.56	1.33	0.20	1.11	2.29	0.19***
ECE	0.56	0.57	0.01	0.58	0.52	0.01***
MEff (UFL/kg$^{0.75}$)	0.07	0.07	0.002	0.07	0.08	0.002***
FtW (UFL/kg$^{0.75}$)	0.16	0.16	0.20	0.164	0.163	0.002
KR (UFL/kg$^{0.75}$)	0.09	0.09	0.001	0.09	0.08	0.001***
REI (UFL/d)	1.25	0.93	0.19	0.79	1.71	0.18***
REP (UFL/d)	-0.24	-0.11	0.11	0.23	-1.06	0.10***
RIEP (UFL/d)	-0.65	-0.45	0.13	-0.18	-1.40	0.12***
NEI (UFL/d)	17.46	16.91	0.21*	16.67	17.59	0.20**
NEL (UFL/d)	9.65	9.47	0.12	9.52	8.95	0.11**
BW (kg$^{0.75}$/d)	106.85	104.04	0.61**	106.35	108.17	0.56
BCS (scale 1 to 5)	2.96	2.95	0.01	2.94	2.98	0.01
Reliability (%)	0.11	0.11	0.005	0.26	0.24	0.004**

[1] EBV = estimated breeding value; EB = energy balance; ECE = energy conversion efficiency; MEff = metabolic efficiency; FtW = feed to body-weight; KR = Kleiber ratio; REI = residual energy intake; REP = residual energy production; RIEP = residual intake and energy production; NEI = net energy intake; NEL = net energy for lactation; BW = metabolic BW; BCS = body condition score.

[2] SED = Standard error of the difference.

***Statistically significant at $P < 0.001$; **statistically significant at $P < 0.01$; * statistically significant at $P < 0.05$.



Appendix 4.2. Least squares means across stage of lactation for the highest (n = 62) and lowest (n = 62) 10% of lactations for energy conversion efficiency. Shaded symbols illustrate the highest 10% (i.e., efficient lactations) of lactations, and un-shaded symbols illustrate the lowest 10% (i.e., inefficient lactations) of lactations for energy balance (UFL/d; —▲∆—), energy conversion efficiency (—■□—) and residual energy intake (UFL/d; —●○—).

Chapter 5

Genetics of alternative definitions of feed efficiency in grazing lactating dairy cows

A.M. Hurley[1, 2], N. López-Villalobos[2], S. McParland[1], E. Kennedy[1], E. Lewis[1],
M. O'Donovan[1], J.L. Burke[2], and D.P. Berry[1]

[1]*Teagasc, Animal & Grassland Research and Innovation Centre, Moorepark, Fermoy, Co. Cork, Ireland*

2Institute of Veterinary, Animal and Biomedical Sciences, Massey University, Private Bag 11-222, Palmerston North, New Zealand

Journal of Dairy Science (2017) 100:5501-5514.

doi: https://doi.org/10.3168/jds.2016-12314.

Abstract

The objective of the present study was to estimate genetic parameters across lactation for measures of energy balance (EB) and a range of feed efficiency variables as well as to quantify the genetic inter-relationships between them. Net energy intake (NEI) from pasture and concentrate intake was estimated up to eight times per lactation for 2,481 lactations from 1,274 Holstein-Friesian cows. A total of 8,199 individual feed intake measurements were available. Efficiency traits were either ratio-based or residual-based; the latter were derived from least squares regression models. Residual energy intake (REI) was defined as NEI minus predicted energy requirements (e.g., net energy for lactation (NEL), maintenance, and body tissue anabolism) or supplied from body tissue mobilization; residual energy production (REP) was defined as the difference between actual NEL and predicted NEL based on NEI, maintenance, and body tissue anabolism/catabolism. Energy conversion efficiency (ECE) was defined as NEL divided by NEI. Random regression animal models were used to estimate residual, additive genetic and permanent environmental (co)variances across lactation. Heritability across lactation stages varied from 0.03 to 0.36 for all efficiency traits. Within-trait genetic correlations tended to weaken as the interval between lactation stages compared lengthened for EB, REI, REP, and NEI. Analysis of eigenvalues and associated eigenfunctions for EB and the efficiency traits indicate the ability to genetically alter the profile of these lactation curves to potentially improve dairy cow efficiency differently at different stages of lactation. Residual energy intake and EB were moderate to strongly genetically correlated with each other across lactation (genetic correlations ranged from 0.45 to 0.90) indicating selection for lower REI alone (i.e., deemed efficient cows) would favour cows with a compromized energy status; nevertheless, selection for REI within a holistic breeding goal could be used to overcome such antagonisms. The smallest (8.90% of genetic variance) and middle (11.22% of genetic variance) eigenfunctions for REI changed sign during lactation indicating the potential to alter the shape of the REI lactation profile. Results from the present study suggest exploitable genetic variation exists for a range of efficiency traits, and the magnitude of this variation is sufficiently large to justify consideration of the feed efficiency complex in future dairy breeding goals. Moreover, it is possible to alter the trajectories of the efficiency traits to suit a particular breeding objective, although this relies on very precise across-parity genetic parameter estimates, including genetic correlations with health and fertility traits (as well as other traits).

Keywords: feed intake, residual energy intake, fertility, energy balance, heritability.

Introduction

The gross efficiency of converting feed energy to milk in dairy cows has more than doubled over the past century, largely as the indirect consequence of increased milk output per cow (Oltenacu and Broom, 2010). Reducing feed intake, without repercussions for the other performance traits, is important to maintain dairy sector competitiveness while also meeting projected consumer demands for animal protein within the realm of constrained resources. Improving feed efficiency is also desirable because of its potential benefits towards reducing both nutrient and greenhouse gas emissions per animal. The importance of feed efficiency to the dairy industry is well recognized and has led to a large-scale global effort to improve this animal characteristic (Berry et al., 2014; de Haas et al., 2015).

Genetic selection for feed efficiency is common in pigs and poultry (Emmerson, 1997; Lonergan et al., 2001), but it is not explicitly considered in most dairy cow breeding objectives. Its omission from the dairy cow breeding objective is due to both a lack of available feed intake data from which to estimate net feed efficiency, but also the lack of a consensus on the most appropriate definition of net feed efficiency in dairy cows. Several feed efficiency definitions have been proposed and have been the subject of extensive discussion. Hurley et al. (2016) described the phenotypic (co)variances among a range of different definitions of feed efficiency in grazing lactating dairy cows. Less well known, however, is the genetic (co)variance among these alternative definitions of feed efficiency. Most of the studies on the genetics of the feed intake complex have been derived from dairy cows in confined production systems, and assumed feed efficiency was genetically the same trait throughout lactation (Manzanilla-Pech et al., 2014; Manafiazar et al., 2015). The existence of genetic variation in alternative definitions of feed efficiency, as well as the estimation of precise intra- and inter-trait genetic correlations, needs to be quantified prior to consideration in genetic evaluations and subsequent inclusion in breeding objectives. The objective of the present study was to estimate genetic parameters across lactation for a range of alternative measures of feed efficiency in grazing lactating Holstein-Friesian dairy cows, and quantify the genetic intra- and inter-relationships among these alternative definitions.

Materials and methods

Data

Data were collected from the Animal and Grassland Research and Innovation Centre, Teagasc Moorepark, Fermoy, Co. Cork, Ireland, between the years 1995 to 2014, inclusive. All studies were undertaken on two adjacent research farms, namely

Curtin's Research Farm and the Moorepark Research Farm located in southern Ireland (latitude 52°9N; longitude 8°16W). The majority of cows used in the present study originated from several controlled experiments which evaluated alternative grazing strategies, nutritional strategies, or strains of Holstein-Friesian animals; a description of the database is provided by Hurley et al. (2016). Individual animal grass dry matter intake (DMI) at pasture was periodically estimated using the n-alkane technique (Mayes et al., 1986). Details on the procedures used to collect and analyze fecal grab samples have been provided elsewhere (Kennedy et al., 2008). The procedure provides a measure of DMI averaged across 6 days of sampling. All cows were offered a basal diet of grazed grass. Perennial ryegrass (*Lolium perenne*) was the predominant pasture species at both research farms and pastures were managed under a rotational grazing system comparable to that detailed by Dillon et al. (1995). Some animals were supplemented with concentrates (depending on feeding protocol), varying from 0.89 to 3.9 kg DM per cow daily, offered in equal feeds during each milking.

Cows were milked twice daily at 0700 and 1500 h and individual cow milk yield was recorded daily; milk fat, protein and lactose concentration was determined from successive evening and morning milk samples once per week using mid-infrared spectroscopy (FT6000, FOSS, Hillerod, Denmark). Net energy requirement for lactation (NEL) was calculated as (Agabriel, 2007):

$$\mathrm{NEL} = ((0.054 \times \mathrm{FC}) + (0.031 \times \mathrm{PC}) + (0.028 \times \mathrm{LC}) - 0.015) \times \mathrm{milk\,kg}$$

where FC is fat concentration (%), PC is protein concentration (%), and LC is lactose concentration (%).

Individual animal body-weight (BW) was generally measured weekly following morning milking using an electronic scale (Tru-Test Limited, Auckland, New Zealand). The scales were calibrated weekly against known weights. Body condition score (BCS) on a scale of 1 (emaciated) to 5 (obese) was assessed by trained scorers every two to three weeks in increments of 0.25 (Edmonson et al., 1989). Cubic splines with 6 knot points at 20, 70, 120, 170, 220, and 270 days in milk (DIM), with a covariance structure fitted among knot points, were fitted through individual BW and BCS records. Body-weight and BCS at each DIM were interpolated from the fitted splines. Forward differencing was used to estimate daily BW and BCS change at each DIM. Individual cow daily total DMI (i.e., grazed pasture DMI plus concentrate DMI) was available up to eight times (average of 4.5 times) per lactation.

Energy values of the pasture and concentrate were based on the French Net Energy system where 1 unité fourragère du lait (UFL) is the net energy requirements for lactation equivalent of 1 kg standard air-dry barley (Jarrige, 1989) equivalent to 7.11 MJ net energy or 11.85 MJ metabolizable energy. The UFL concentration of the offered herbage was calculated using the acid detergent fibre and crude protein concentration which were measured in the laboratory (Jarrige, 1989). Concentrate UFL value was also calculated from the chemical composition of the feed. The net energy content of the concentrate offered was calculated for each day; where UFL content of concentrate was not available (i.e., 26% of test-day records) the year-month average was assumed. Where the net energy content of the offered herbage (UFL/kg dry matter) was not available (i.e., 8% of test-day records), the year-month average was assumed. Total net energy intake (NEI) was defined as the sum of pasture and concentrate NEI.

Data editing

Obvious data errors for BW, BCS, and the milk production traits (i.e., milk yield, fat yield, protein yield, lactose yield) were discarded. Only data between 8 and 280 days in milk (DIM) were retained. Parity was categorized as 1, 2, and ≥ 3.

Contemporary group of experimental treatment by test-date was defined for NEI, BW, BCS, milk yield and composition. Contemporary groups with less than 5 observations were discarded. Following edits, the final dataset contained 97,376 test-day records from 2,481 lactations on 1,274 cows; 8,134 individual feed intake measurements remained.

The pedigree of all cows was traced back at least 4 generations, where available. Animals with no recorded sire or dam (n = 16) were excluded from the analysis. The average number of daughters per sire was 5.87.

Definitions of energy efficiency and energy balance

Definitions of all traits have been previously described in detail by Hurley et al. (2016). Energy balance (EB) for each test-day was calculated in accordance with the net energy system outlined by Jarrige (1989) and modified for Irish dairy systems by O'Mara (1996):

$$\mathrm{EB} = \mathrm{NEI} - \Delta\mathrm{NE} - \mathrm{NEL} - \mathrm{NEM} - \mathrm{NEP}$$

where NEI is daily net energy intake, ΔNE is an adjustment of daily net energy intake for the proportion of concentrates in the diet, NEL is daily net energy requirements for lactation, NEM is daily net energy requirements for maintenance calculated as $((1.4 + (0.6 \times (\mathrm{BW}/100))) \times 1.2)$, and NEP is daily net energy requirements for pregnancy where UFL requirement for the 6th, 7th, and 8th month of pregnancy were 0.9, 1.6, and 2.6 UFL/d, respectively (O'Mara, 1996).

Residual-based efficiency traits. Residual energy intake **(REI)** for each day of lactation was defined as the residuals from the regression of NEI on energy sinks and other energy sources as:

$$\text{REI} = \text{NEI} - [\text{NEL} + \text{Parity} + \sum_{i=1}^{2} \text{DIM}^{i} + \text{BW}^{0.75} + \text{BCS} + \text{BW}^{0.75} \times \text{BCS} + \Delta\text{BW}^{+} + \Delta\text{BW}^{-} + \Delta\text{BCS}^{+} + \Delta\text{BCS}^{-} + \Delta\text{BW}^{+} \times \text{BCS} + \Delta\text{BW}^{-} \times \text{BCS}]$$

where REI is daily residual energy intake, NEI is daily net energy intake, NEL is daily net energy requirements for lactation, parity (1, 2, $\geq$ 3), $\sum_{i=1}^{2} \text{DIM}^{i}$ is days in milk included as a continuous variable with a linear ($i = 1$) and quadratic effect ($i = 2$), $\text{BW}^{0.75}$ is metabolic BW, and BCS is body condition score. The energy generated from a 1 kg loss in BW is less than the energy required for a 1 kg gain in BW (O'Mara, 1996); therefore, piecewise regression was applied to BW and BCS in the REI model where ΔBW^{+} describes animals gaining BW, ΔBW^{-} describes animals losing BW, while ΔBCS^{+} describes animals gaining BCS, and ΔBCS^{-} describes animals losing BCS. No multicollinearity existed in the multiple regression model.

Analogous to residual gain in growing cattle (Koch et al., 1963), residual energy production (REP) for each day of lactation was defined from the residuals of a least squares regression model regressing net energy for lactation on NEI plus energy sinks and other energy sources, similar to that described by Coleman et al. (2010):

$$\text{REP} = \text{NEL} - [\text{NEI} + \text{Parity} + \sum_{i=1}^{2} \text{DIM}^{i} + \text{BW}^{0.75} + \text{BCS} + \text{BW}^{0.75} \times \text{BCS} + \Delta\text{BW}^{+} + \Delta\text{BW}^{-} + \Delta\text{BCS}^{+} + \Delta\text{BCS}^{-} + \Delta\text{BW}^{+} \times \text{BCS} + \Delta\text{BW}^{-} \times \text{BCS}]$$

where REP is daily residual energy production, NEL is daily net energy requirements for lactation, NEI is daily net energy intake, parity (1, 2, 3+), $\sum_{i=1}^{2} \mathrm{DIM}^{i}$ is days in milk included as a continuous variable with a linear and quadratic effect, $\mathrm{BW}^{0.75}$ is metabolic BW, BCS is body condition score, $\Delta\mathrm{BW}^{+}$ describes animals gaining BW, $\Delta\mathrm{BW}^{-}$ describes animals losing BW, $\Delta\mathrm{BCS}^{+}$ describes animals gaining BCS, and $\Delta\mathrm{BCS}^{-}$ describes animals losing BCS. No multicollinearity existed in the multiple regression model.

Ratio-based efficiency traits. Energy conversion efficiency (ECE) for each day of lactation was defined as:

$$\mathrm{ECE} = \frac{\mathrm{NEL}}{\mathrm{NEI}}$$

where NEL is the daily net energy requirements for lactation, and NEI is the daily net energy intake.

Metabolic efficiency (MEff) was defined as:

$$\mathrm{MEff} = \frac{\mathrm{NEI} - \mathrm{NEL}}{\mathrm{BW}^{0.75}}$$

where NEI is daily net energy intake, NEL is net energy requirements for lactation, and $\mathrm{BW}^{0.75}$ is metabolic live-weight.

Feed to live-weight (FtW) was defined as:

$$\mathrm{FtW} = \frac{\mathrm{NEI}}{\mathrm{BW}^{0.75}}$$

where NEI is daily net energy intake, and $\mathrm{BW}^{0.75}$ is metabolic live-weight.

Kleiber ratio (KR) (Kleiber, 1961) in growing animals is defined as average daily gain divided by metabolic live-weight. An analogous Kleiber ratio trait in dairy cattle was defined as:

$$\mathrm{KR} = \frac{\mathrm{NEL}}{\mathrm{BW}^{0.75}}$$

where NEL is the net energy requirements for lactation and $\mathrm{BW}^{0.75}$ is metabolic live-weight.

Data analysis

All energy efficiency traits and EB followed a Gaussian distribution. Components of (co)variances for the efficiency traits and EB were quantified using random regression animal models (RRM) across DIM in ASReml (Gilmour et al., 2009). Fixed effects included in the models were contemporary group, parity (1, 2, and ≥ 3), as well as a two-way interaction between parity and DIM. The most parsimonious fixed effect Legendre polynomial regression was based on visual inspection of the resulting lactation profile for each polynomial order. Although higher order polynomials for fixed effects fit the data better ($P < 0.05$), the lactation profiles of the quadratic and higher order polynomials were graphically almost identical for all traits. Random regressions using Legendre polynomials were used to model the additive genetic variance and within-lactation permanent environmental variance. A single across lactation permanent environment effect was also fitted.

Residual variances were estimated within 6 stages of lactation: 8 to 50 DIM, 51 to 100 DIM, 101 to 150 DIM, 151 to 200 DIM, 201 to 250 DIM, and > 250 DIM. Within stage, residual variances were assumed to be homogenous, while heterogeneity in residual variances was modelled across stages of lactation. No residual (co)variance was assumed among stages of lactation. The most parsimonious random regression model was determined by constantly increasing the order of the random regression coefficients for both the additive genetic component and permanent environmental component within-lactation. The lowest Akaike information criterion (AIC) of converged models was the main statistical test to determine the most parsimonious model.

The genetic (co)variances across all DIM were estimated as:

$$\boldsymbol{\delta} = \boldsymbol{\Phi}'\mathbf{K}\boldsymbol{\Phi}$$

in which $\boldsymbol{\delta}$ is the variance or (co)variance matrix for the efficiency traits and EB, $\boldsymbol{\Phi}$ is the matrix of Legendre polynomial regression coefficients, and $\mathbf{K}$ is the matrix of the additive genetic (co)variance matrix of the random polynomial coefficient. Standard errors of the heritability estimates were derived using a Taylor series expansion (Fischer et al., 2004).

Genetic correlations between the traits were estimated using a series of bivariate analyses in ASReml (Gilmour et al., 2009). Fixed and random effects included in the models were as previously described for the univariate models. The failure of some bivariate models to converge when a quadratic random regression was fitted, necessitated the order of the fitted random regression to be linear. Such amendments had to be made for the correlations between EB with ECE, MEff, FtW, KR, REI, NEI, NEL, BCS, BW; the correlations between ECE with MEff, FtW, KR, REI, REP, NEL, NEI, BW; the correlations between REI with MEff, FtW, REP, NEI, NEL, BCS, BW; the correlations between RSP with MEff, FtW, NEI, NEL, BCS, BW; the correlations between NEI with KR, MEff, BW; the correlations between NEL with MEff, FtW, KR, NEI, the correlations between BCS with MEff, FtW, NEI, NEL, and the correlations between BW with MEff, FtW, NEL. Residual variances were estimated within each of the 6 DIM stages as described previously for the univariate analysis but a residual (co)variance between traits was also estimated.

Standard errors of genetic correlations were approximated using (Falconer and MacKay, 1996):

$$SE_{r_{A_{xy}}} = \frac{1 - {r_A}^2}{\sqrt{2}} \sqrt{\frac{SE(h_x^2)\ SE\left(h_y^2\right)}{h_x^2\ h_y^2}}$$

where SE denotes the standard error, r_A is the genetic correlation between trait x and trait y, and h^2 is the heritability; the superscript x or y, represent the respective traits under investigation.

In order to quantify the potential to genetically alter lactation profiles for each of the traits investigated, the eigenvalues and associated eigenfunctions were calculated (Kirkpatrick et al., 1990). The eigenvalues and eigenvectors were calculated from the decomposition of the additive genetic (co)variance matrix, and eigenfunctions were subsequently calculated from the product of the eigenvectors and Legendre polynomial coefficients as:

$$\Psi_i(x) = \sum_{j=0}^{p-1} [k_{\Psi_i}]_j\ \emptyset_j(x)$$

where $[k\psi_i]_j$ is the j^{th} elemen*t of the i^{th} eigenvector of K, Φ is the j^{th} polynomial relating to the p^{th} order of fit, and x is DIM.

Results

Summary statistics, as well as the order of the fixed and random Legendre polynomials fitted to EB, the efficiency traits, and the production traits are in Table 5.1. Average test-day milk yield was 22.40 kg/d with a standard deviation (SD) of 6.89 kg/d. Mean milk fat yield, milk protein yield and milk lactose yield was 0.87 kg/d, 0.79 kg/d and 1.06 kg/d, respectively. A quadratic random Legendre polynomial on the additive genetic effect best fitted the data for all production and efficiency traits (Table 5.1). For 3 (REI, FtW, and EB) out of the 12 traits evaluated, a quadratic random Legendre polynomial on the within-lactation permanent environmental effect failed to converge so this effect was fitted as a linear polynomial (Table 5.1). Because a quadratic random regression was fitted to the additive genetic component for each trait, three eigenvalues existed. The percentage of variation accounted by the largest, middle, and smallest eigenvalues for the efficiency and production traits are in Table 5.2. The coefficient of genetic variation for NEL (6.74%) was greater than the coefficient of genetic variation for both REI (2.64%) and NEI (4.82%).

Table 5.1. Number of observations (N), mean, order of the fixed effect Legendre polynomial and random effect Legendre polynomial used to model the additive genetic variance and within lactation permanent environmental variance.

Trait[1]	N	Mean	Fixed	Random	
				Add. Genetic	Perm. Env.
EB, UFL/d	7,829	0.55	3	2	1
ECE	7,829	0.60	3	2	2
MEff, UFL/kg$^{0.75}$	7,829	0.06	4	2	2
FtW, UFL/kg$^{0.75}$	7,829	0.15	4	2	1
KR, UFL/kg$^{0.75}$	83,930	0.09	2	2	2
REI, UFL/d	7,829	0.00	4	2	1
REP, UFL/d	7,829	0.00	5	2	2
NEI, UFL/d	8,134	16.23	3	2	2
NEL, UFL/d	88,770	8.59	3	2	2
BW, kg	77,743	529.50	3	2	2
BCS, scale 1 to 5	37,063	2.84	3	2	2

[1] EB = energy balance; ECE = energy conversion efficiency; MEff = metabolic efficiency; FtW = feed to body-weight; KR = Kleiber ratio; REI = residual energy intake; REP = residual energy production; NEI = net energy intake; NEL = net energy for lactation; BW = test-day BW; BCS = test-day body condition score.

Table 5.2. The percentage of variation accounted by the largest, middle, and smallest eigenvalues for the efficiency and production traits.

Trait[1]	Largest (%)	Middle (%)	Smallest (%)
EB, UFL/d	67.42	20.93	11.65
ECE	71.67	24.04	4.29
MEff, UFL/kg$^{0.75}$	74.15	22.30	3.55
FtW, UFL/kg$^{0.75}$	92.13	6.85	1.01
KR, UFL/kg$^{0.75}$	82.49	15.47	2.04
REI, UFL/d	79.88	11.22	8.90
REP, UFL/d	77.17	18.09	4.74
NEI, UFL/d	93.28	6.13	0.60
NEL, UFL/d	85.09	10.63	4.28
BW, kg	95.60	3.36	1.03
BCS, scale 1 to 5	95.96	2.87	1.17

[1] EB = energy balance; ECE = energy conversion efficiency; MEff = metabolic efficiency; FtW = feed to body-weight; KR = Kleiber ratio; REI = residual energy intake; REP = residual energy production; NEI = net energy intake; NEL = net energy for lactation; BW = test-day body-weight; BCS = test-day body condition score.

Variance components

Estimated residual SD for all traits was greatest in early lactation and generally decreased as the lactation progressed. The genetic SD for NEL was greatest in very early lactation declining thereafter and varied from 0.88 UFL/d (280 DIM) to 1.13 UFL/d (8 DIM). The genetic SD for BW (1.10 kg at 39 DIM to 1.31 kg at 280 DIM), and BCS (1.93 BCS units at 29 DIM to 2.07 BCS units at 280 DIM) was greatest in late lactation (data not shown). The genetic SD for EB and a selection of the efficiency traits across lactation are in Figure 5.1. The genetic SD for REI across lactation (Figure 5.1) fluctuated from 0.64 UFL/d (34 DIM) to 0.87 UFL/d (280 DIM). Substantial genetic variation was also evident across lactation for the ratio-based efficiency traits. The genetic SD for MEff, FtW and KR was greatest in early lactation decreasing across DIM and varied from 0.39 UFL/kg$^{0.75}$ to 0.64 UFL/kg$^{0.75}$ for MEff, from 0.67 UFL/kg$^{0.75}$ to 0.82 UFL/kg$^{0.75}$ for FtW, and from 0.74 UFL/kg$^{0.75}$ to 1.01 UFL/kg$^{0.75}$ for KR (data not shown).

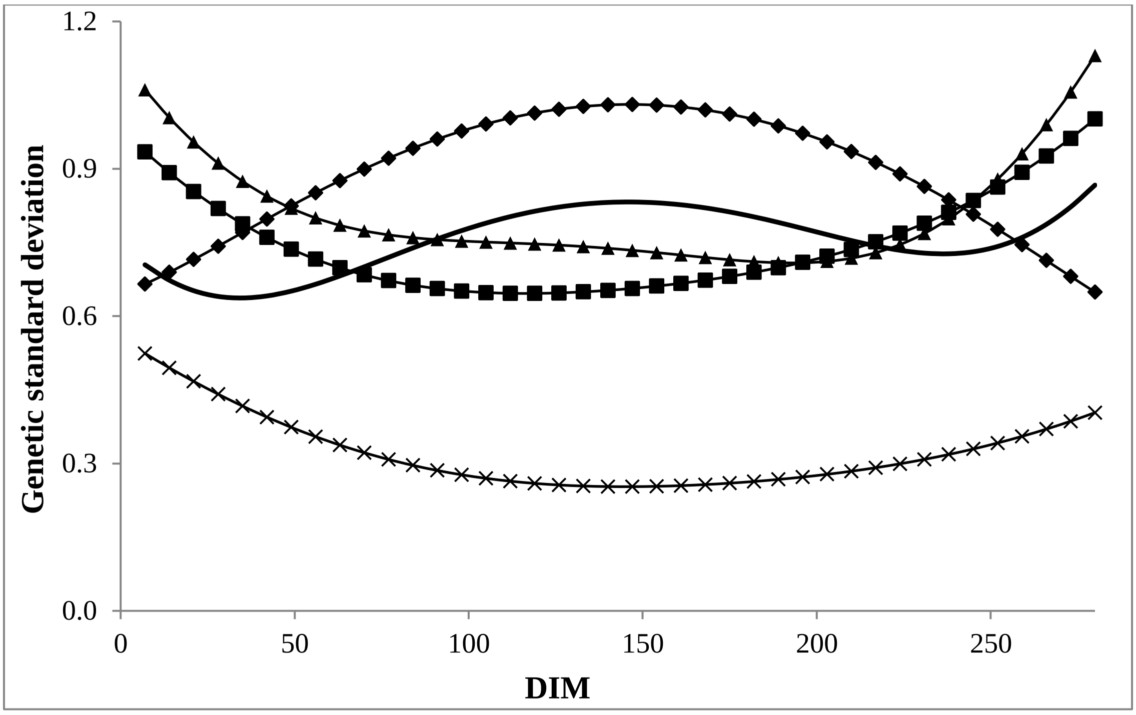


Figure 5.1. Genetic standard deviation for energy balance (UFL/d; —▲—), energy conversion efficiency (—x—), residual energy intake (UFL/d; ——), residual energy production (UFL/d; —■—), and net energy intake (UFL/d; —♦—). The genetic standard deviation for residual energy intake and residual energy production were both rescaled, in that residual energy intake was divided by a factor of 2 and residual energy production was divided by a factor of 5.

The eigenfunction associated with the largest eigenvalue for ECE was almost linear and positive across all DIM (Figure 5.2). The eigenfunction associated with the largest eigenvalue for REI was slightly curvilinear but nonetheless positive throughout-lactation. Similar to ECE, the eigenfunction associated with the largest eigenvalue for REP was relatively linear and positive across all DIM.

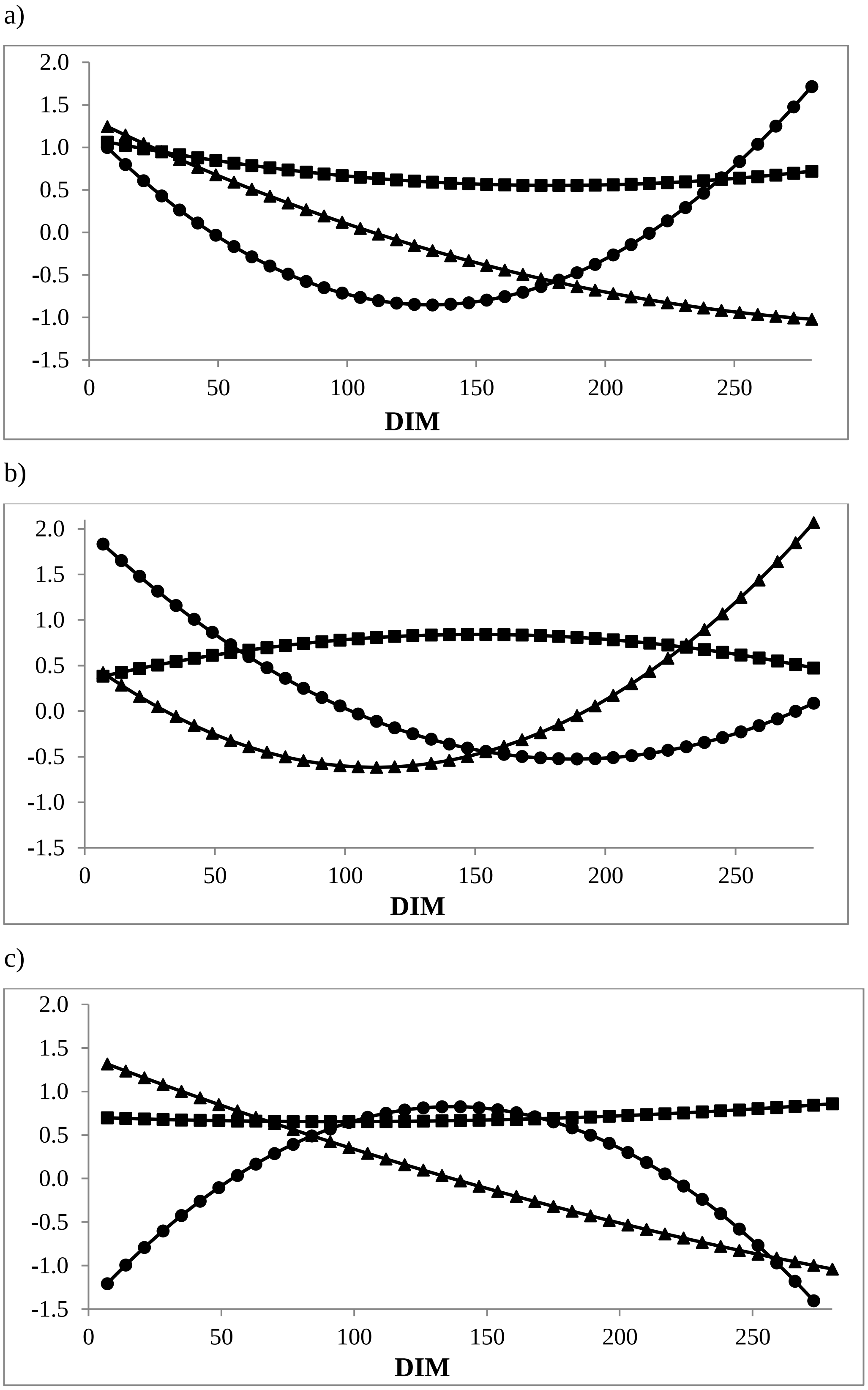


Figure 5.2. Eigenfunctions (y-axis) associated with the largest (■), middle (▲), and smallest (●) eigenvalue for a) energy conversion efficiency, b) residual energy intake, and c) residual energy production.

Heritability estimates for EB, ECE, REI, REP and NEI are in Figure 5.3. Heritability ranged from 0.06 (50 DIM) to 0.18 (280 DIM) for EB, from 0.06 (50 DIM) to 0.28 (250 DIM) for ECE, from 0.04 (34 DIM) to 0.11 (280 DIM) for REI, from 0.12 (50 DIM) to 0.36 (250 DIM) for REP, and from 0.06 (8 DIM) to 0.28 (151 DIM) for NEI. The standard error (SE) for all heritability estimates for these traits was never greater than 0.08 (Figure 5.3). Summary statistics of the daily heritability estimates for the other efficiency and production traits are in Appendix 5.1.

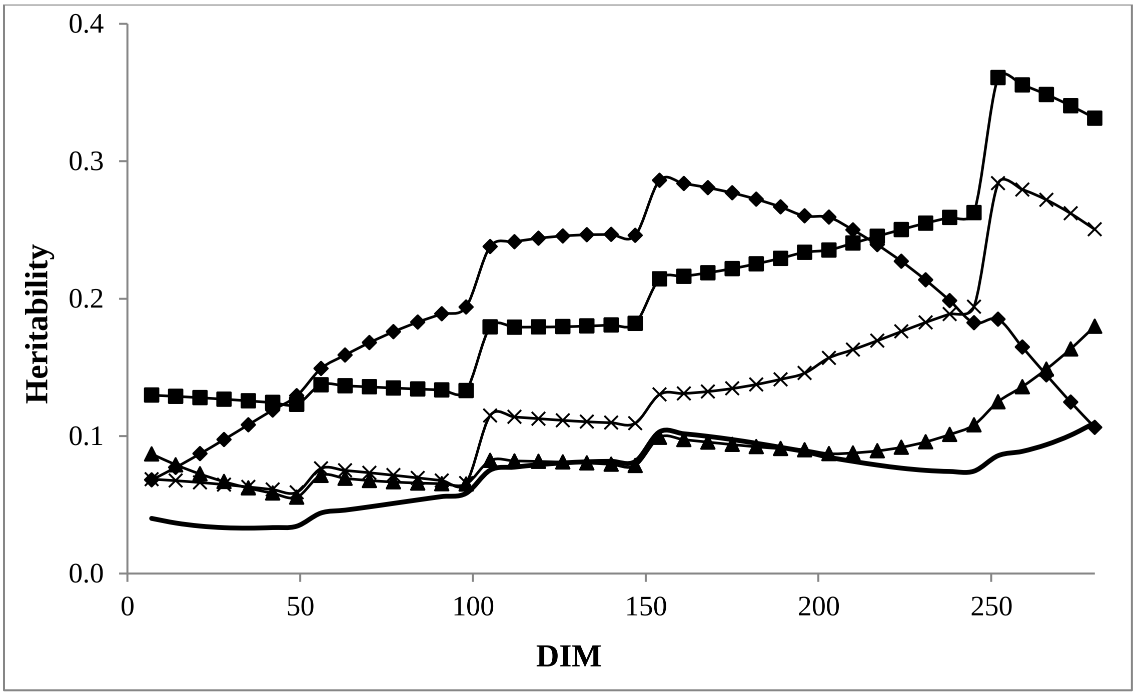


Figure 5.3. Heritability estimates (SE in parenthesis) for energy balance (—▲—; 0.04 to 0.07), energy conversion efficiency (—x—; 0.02 to 0.08), residual energy intake (——; 0.03 to 0.06), residual energy production (—■—; 0.03 to 0.07), and net energy intake (—♦—; 0.03 to 0.06).

Genetic correlations within-trait in different stages of lactation

Within-trait, genetic correlations at 8 DIM, 150 DIM and 280 DIM with all other DIM for EB, ECE, REI, REP and NEI are in Figure 5.4. Within-trait genetic correlations for MEff, FtW and KR, at different DIM ranged from -0.12 (± 0.02) to 1.00 (± 0.001), 0.64 (± 0.01) to 1.00 (± 0.001), and 0.50 (± 0.01) to 1.00 (± 0.001), respectively. The strength of the genetic correlations was inversely related to the interval between compared DIM; the weakest genetic correlations existed between 8 DIM and 280 DIM. Within trait genetic correlations for the production traits at different DIM ranged from 0.48 (± 0.01) to 1.00 (± 0.00) for NEL, from 0.82 (± 0.02) to 1.00 (± 0.00) for BW, and from 0.78 (± 0.01) to 1.00 (± 0.00) for BCS; the correlations weakened as the distance between time intervals compared increased.

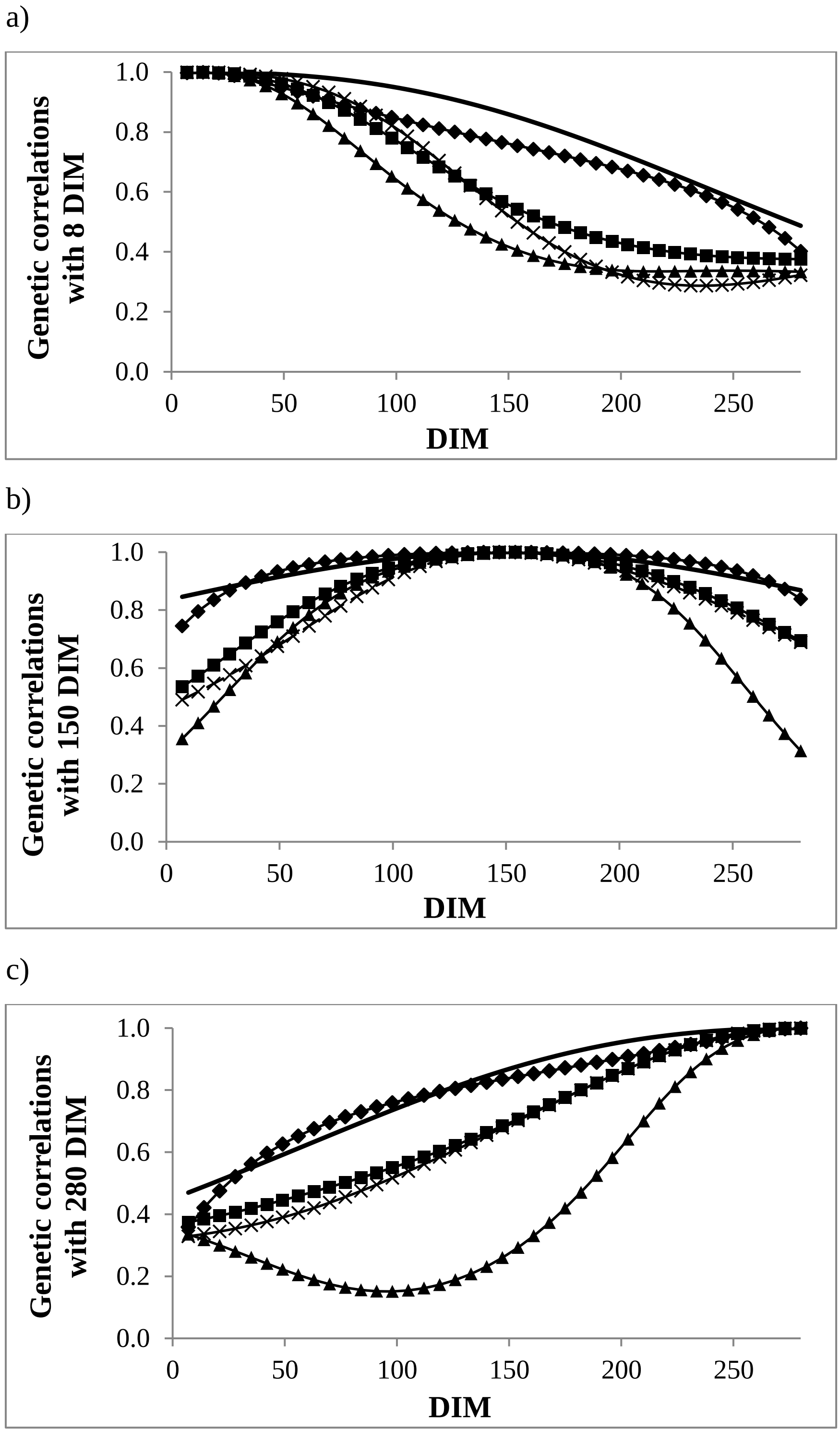


Figure 5.4. Genetic correlations (SE in parenthesis) between observations at a) 8 DIM b) 150 DIM and c) 280 DIM for energy balance (—▲—; 0.00 to 0.02), energy conversion efficiency (—x—; 0.00 to 0.01), residual energy intake (——; 0.00 to 0.01), residual energy production (—■—; 0.00 to 0.02), and net energy intake (—♦—; 0.00 to 0.01).

Genetic correlations between the efficiency and production traits

Genetic correlations across lactation between EB with ECE, MEff, REI, REP, NEI, NEL, and BCS are in Figure 5.5. Energy balance was moderately genetically correlated with REI in early lactation (0.45 ± 0.18 at 8 DIM), while near unity correlations existed in mid and late lactation stages. Energy balance and BCS were negatively genetically correlated in early lactation (-0.34 ± 0.24 at 8 DIM), but changed sign in very late lactation (0.23 ± 0.17 at 220 DIM).

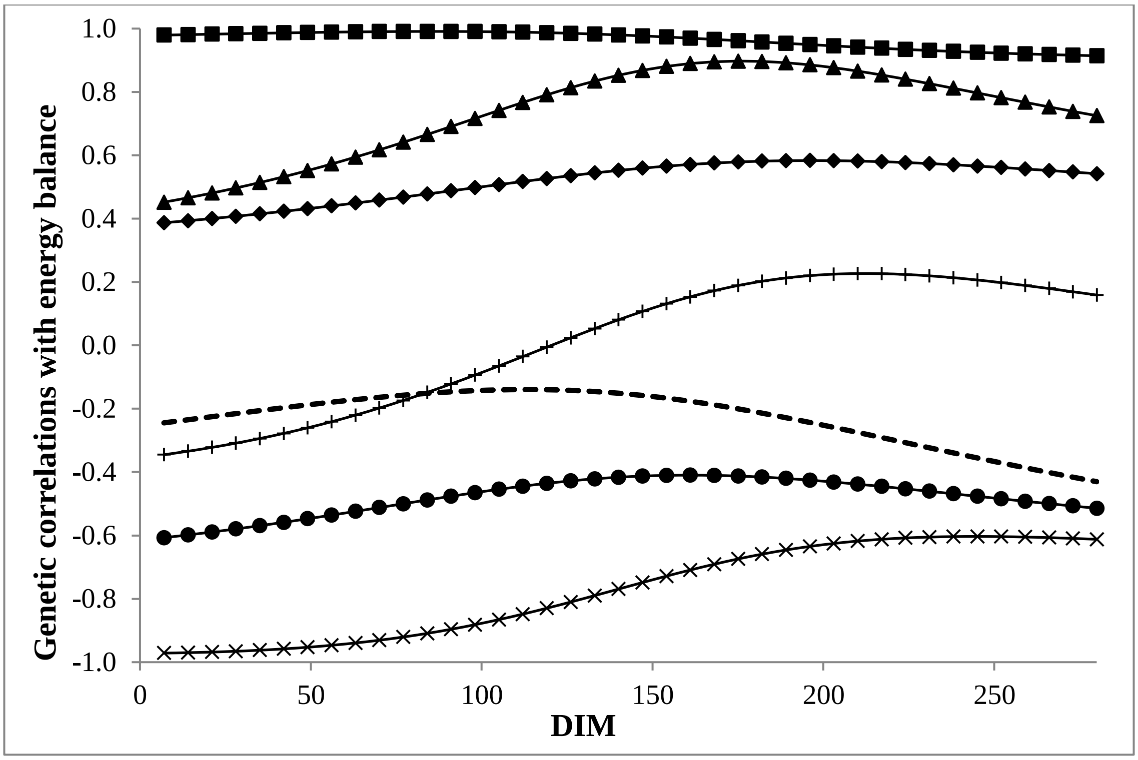


Figure 5.5. Genetic correlations (SE in parenthesis) between energy balance with energy conversion efficiency (—x—; 0.17 to 0.21), metabolic efficiency (—■—; 0.21 to 0.27), residual energy intake (—▲—; 0.06 to 0.18), residual energy production (—●—; 0.07 to 0.14), net energy intake (—♦—; 0.14 to 0.24), net energy for lactation (-----; 0.08 to 0.21) and body condition score (—+—; 0.16 to 0.29).

Genetic correlations across lactation between ECE with REI, REP, NEI, NEL, BW and BCS are in Figure 5.6. Energy conversion efficiency was strongly correlated with REP throughout all lactation stages. The genetic correlations between ECE with both NEI and NEL followed a similar trend across DIM but correlations differed in magnitude (Figure 5.6). Energy conversion efficiency was strongly correlated with MEff at the onset of lactation (-0.98 ± 0.26 at 8 DIM) weakening to a moderate correlation at the end of lactation (-0.49 ± 0.24 at 280 DIM). The genetic correlations between ECE and KR strengthened from early to late lactation (0.53 ± 0.16 at 8 DIM to 0.91 ± 0.14 at 280 DIM).

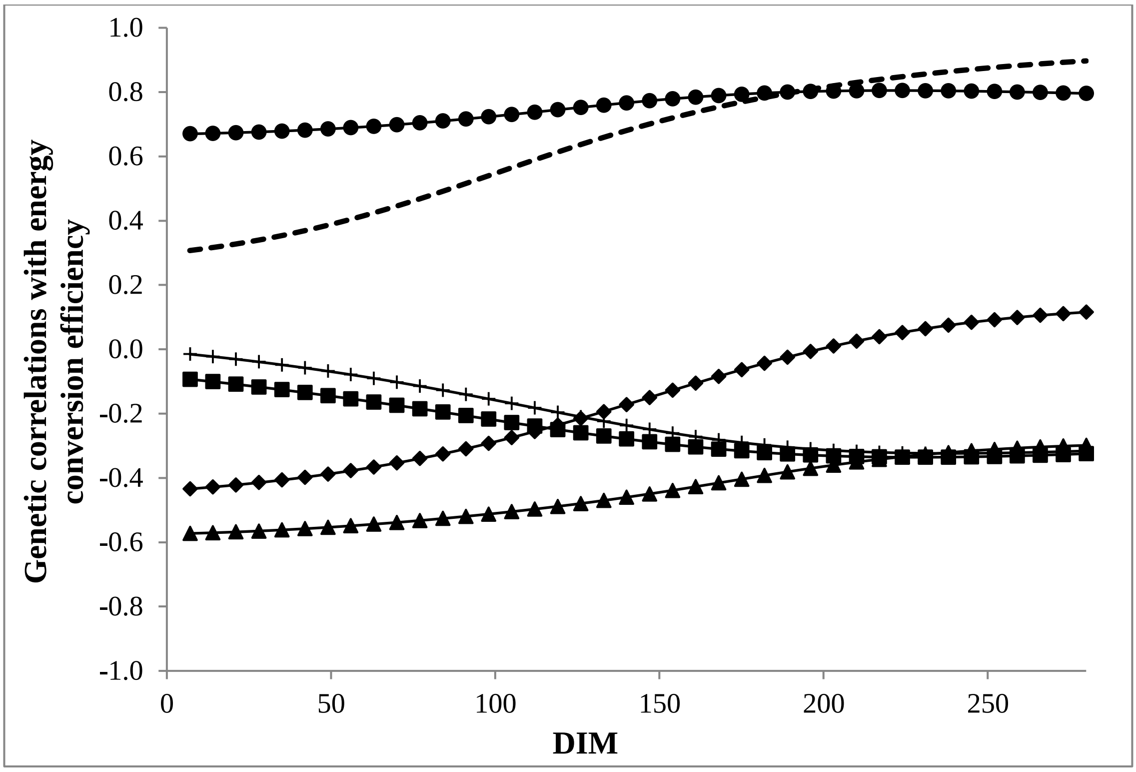


Figure 5.6. Genetic correlations (SE in parenthesis) between energy conversion efficiency with residual energy intake (—▲—; 0.21 to 0.30), residual energy production (—●—; 0.09 to 0.14), net energy intake (—♦—; 0.18 to 0.21), net energy for lactation (-----; 0.06 to 0.19), body-weight (—■—; 0.17 to 0.24), and body condition score (—+—; 0.16 to 0.21).

Genetic correlations between REI with KR, REP, NEI, NEL, BW and BCS are in Figure 5.7. Residual energy intake and REP were not correlated in very early lactation (0.004 ± 0.34 at 8 DIM), but a moderately negative genetic correlation existed in late lactation (-0.35 ± 0.14 at 280 DIM). Residual energy intake was strongly genetically correlated with NEI in mid lactation (0.89 ± 0.24 at 209 DIM), although, the same correlations at the onset of lactation were moderate (0.42 ± 0.15 at 8 DIM). The correlation between REI and NEL followed a curvilinear trend with the strongest correlation (0.61 ± 0.14) existing in mid lactation (145 DIM).

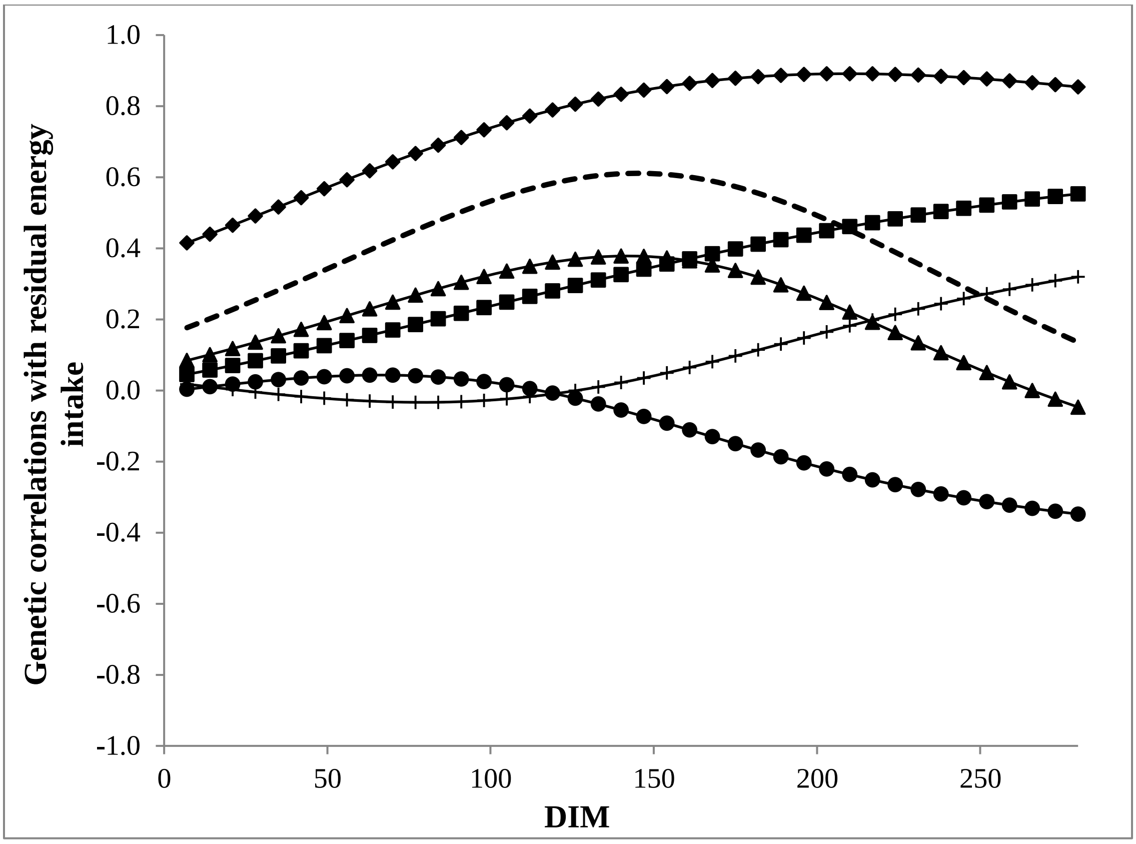


Figure 5.7. Genetic correlations (SE in prentices) between residual energy intake with Kleiber ratio (—▲—; 0.06 to 0.14), residual energy production (—●—; 0.14 to 0.36), net energy intake (—♦—; 0.15 to 0.29), net energy for lactation (-----; 0.12 to 0.24), body-weight (—■—; 0.15 to 0.32), and body condition score (—+—; 0.13 to 0.25).

Genetic correlations between REP with MEff, KR, NEI, NEL, BW, and BCS are in Figure 5.8. Strong genetic correlations existed between REP with KR (varying from 0.92 ± 0.15 at 280 DIM to 0.98 ± 0.22 at 8 DIM), and with NEL (varying from 0.80 ± 0.07 at 214 DIM to 0.88 ± 0.15 at 8 DIM) throughout lactation. Residual energy production was moderately genetically correlated with NEI in early-lactation (0.37 ± 0.16 at 8 DIM), but was uncorrelated in late lactation (0.01 ± 0.11 at 280 DIM).

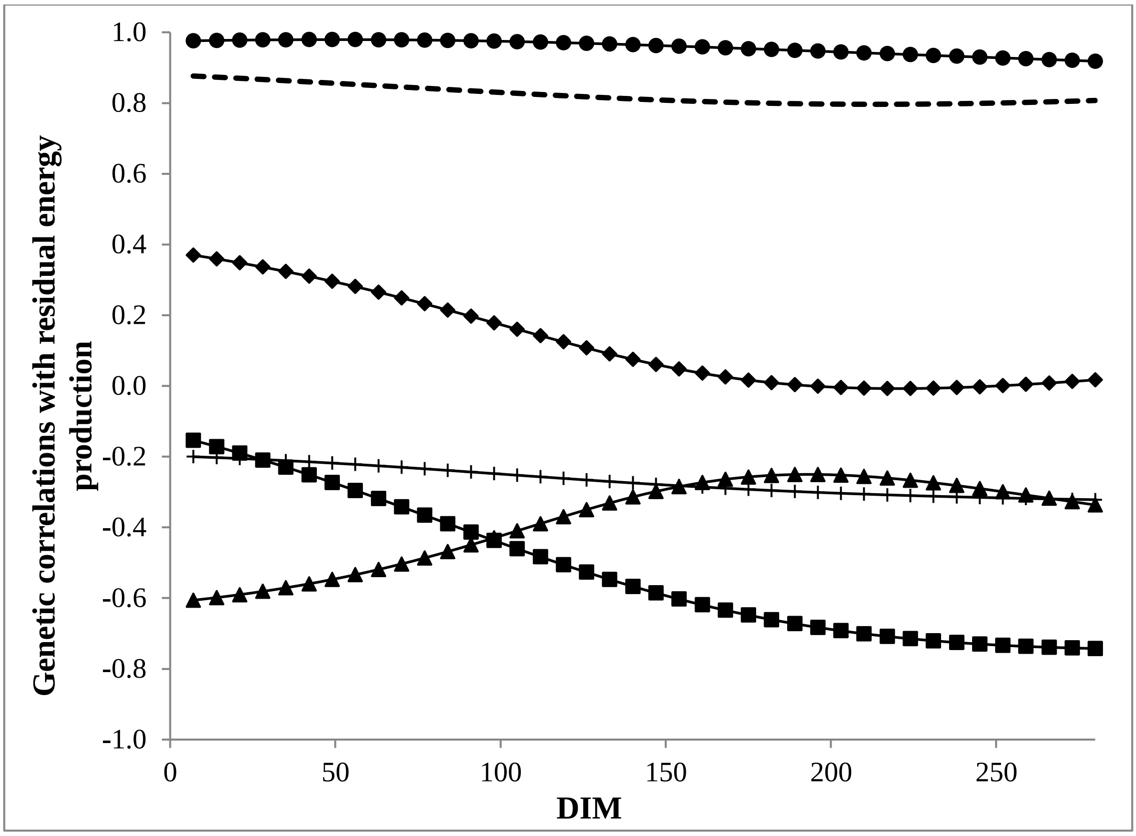


Figure 5.8. Genetic correlations (SE in prentices) between residual energy production with metabolic efficiency (—▲—; 0.11 to 0.18), Kleiber ratio (—●—; 0.11 to 0.22), net energy intake (—♦—; 0.09 to 0.16), net energy for lactation (-----; 0.07 to 0.16), body-weight (—■—; 0.08 to 0.19), and body condition score (—+—; 0.11 to 0.21).

Discussion

Major improvements in dairy cows in gross feed efficiency have been achieved in the past decades as a consequence of principally selecting for increased productivity, thereby diluting maintenance requirements (Bauman et al., 1985; VandeHaar et al., 2016). The genetic merit of current dairy cattle populations must nonetheless be further improved particularly to improve feed utilization and thereby assist the supply of global human demand for animal derived energy and protein sources. There is an on-going debate as to the best approach to select for improved feed efficiency in lactating animals including cows (Connor et al., 2013; Macdonald et al., 2014; Pryce et al., 2014; Connor, 2015). The objective of the present study was to estimate, using random regression models, the genetic (co)variances across lactation for a range of alternative measures of feed efficiency (i.e., ratio and residual traits) in grazing lactating dairy cows. The results clearly indicate that ample genetic variation exists for (net) feed efficiency in lactating dairy cows but this variability, as well as their respective heritability estimates, varied across lactation. Selection for feed efficiency in dairy cattle has historically relied upon approximations of maintenance energy requirements based on measurements of BW (Visscher et al., 1994) concurrent with selection for increased yields. Such an approach, however, is unlikely to capture all the variability in feed efficiency. In the present study, on average 41% (varied from 35% to 44%) of the genetic variation in daily NEI was associated with differences in genetic merit for BW. One approach for capturing the remaining genetic variability in feed intake is through REI (i.e., net feed efficiency; Koch, et al., 1963). Analysis of the eigenvalues and associated eigenfunctions of the additive genetic covariance matrices in the present study suggests there is scope to alter the shape of the lactation profile for the efficiency traits as some of the eigenfunctions changed sign throughout lactation; however, most of the potential from breeding lies in the ability to alter the height of the lactation profiles. To the best of our knowledge, this is the first and most comprehensive study that considers the genetics of feed efficiency across an entire lactation in grazing dairy cows.

The existence of genetic variation

The presence of genetic variation in all feed efficiency metrics investigated in the present study signify that it is indeed possible to breed for improved efficiency and is consistent with reports elsewhere in lactating and growing cattle (Berry and Crowley, 2013). The exaggerated increase in the genetic variance of the different traits on both peripheries of the lactation is likely due to the mathematical properties of a polynomial as relatively more weight is placed on observations at extremities of the parameter space (Meyer, 1998) and this is consistent with observed in other studies that used random regression models for a range of performance traits (Berry et al., 2003; Bohmanova et al., 2008). Furthermore, the larger residual variance in the stage of lactation immediately post-parturition is likely due to factors such as calving difficulty and animal health, both of which can affect subsequent performance (Berry et al., 2007; Proudfoot et al., 2009) yet were not accounted for in the statistical model used in the present study due to a lack of available data.

The estimated genetic variance for REI in the present study was consistent with previous results using random regression models applied to lactating dairy cows (Tempelman et al., 2015). The fact that the genetic variance for NEI was greatest in mid lactation agrees with the studies of both Veerkamp and Thompson (1999) using Holstein heifers, and Li et al. (2016) using different breeds of dairy cows (i.e., Holstein, Nordic Red, and Jersey).

Heritability estimates for the majority of the efficiency traits concur with most other international studies from cows offered TMR diets in confinement systems (Berry and Crowley 2013; Tempelman et al., 2015). Nonetheless, the heritability for REI in the present study was greater than the average of 0.04 reported by Berry and Crowley, (2013) from a meta-analysis of the available literature in lactating dairy cows. However, the estimated heritability for REI in the present study was less than heritability estimates of 0.22 to 0.38 reported previously in growing dairy heifers (Pryce et al., 2012; Williams et al., 2011). Furthermore, the heritability of REI estimated in the present study was generally the lowest of all the feed efficiency traits considered in the present study implying that more feed intake records would be required to achieve as high an accuracy of selection as the other feed efficiency traits. Estimated heritability of NEI in the present study was slightly lower than heritability estimates on predominately Holstein cows published elsewhere (0.15 to 0.40; Vallimont et al., 2010; Spurlock et al., 2012; Manzanilla-Pech et al., 2016); nonetheless, heritability estimates for NEI in the present study were greatest in mid lactation agreeing with other studies based on lactating Holstein cows (Spurlock et al., 2012).

Given that the greatest genetic variation (and heritability) for REI exists in mid to late lactation, first principles of genetic selection (Rendel and Robertson, 1950) would advise selection on REI at this lactation stage; a higher accuracy of selection could also be achieved given the higher heritability of REI in this period of lactation. If REI is included in the breeding goal with reproductive and health traits, however, genetic gain could still be slow (depending on its relative importance). Moreover, genetic gain in the other traits, in particular reproduction and health traits or others also antagonistically correlated with REI (or energy balance), will also reduce. As a result, the long term efficiency of the animal over its lifetime could actually be compromized in pursuit of gains in efficiency over a certain period (e.g., per lactation). Precise estimates of the genetic correlations between REI and other traits in the breeding goal are therefore crucial, and selection index theory should be used to estimate the expected responses to selection for all traits in the revised breeding goal.

An alternative approach to including REI explicitly in the breeding goal would simply be to include NEI itself as well as the energy sink traits in a breeding goal with the appropriate weighting. Such an approach is known to be mathematically equivalent to explicitly including REI in the breeding goal if all the economic and genetic parameters in the breeding goal are correct (Van der Werf, 2004). As NEI had the greatest genetic variation and heritability in mid lactation, selection at this stage of lactation could lead to the greatest genetic gain. However, estimating NEI on large numbers of animals for use in genetic evaluations is expensive, although alternatives such as predicting NEI from milk mid-infrared spectroscopy exist (McParland et al., 2014).

Correlations within and among traits

The fact that the genetic correlations among the various efficiency traits were almost all less than unity agrees with the phenotypic analysis of Hurley et al. (2016) on a subset of the data used in the present study and suggests that the efficiency traits investigated are all measuring distinctly different components of efficiency. Moreover, the strength of the genetic correlations within each efficiency trait at different DIM sometimes deviated from one suggesting the same efficiency traits could be governed by different genetic mechanisms throughout lactation. This is not unexpected given that most of the efficiency traits are a function of at least two performance traits (i.e., milk production and BW), and the contribution of these traits to the feed efficiency definition will vary as the respective variances changes during lactation. Such phenomena need consideration when contemplating including feed efficiency traits in a breeding program. Nonetheless, in general the weakest genetic correlation among records for the same trait were rarely less than 0.80 for REI, KR, and FtW; Robertson (1959) stated that if correlations between the same trait in two environments was > 0.80 then they could be considered the same trait. Therefore, although the genetic correlations for the same trait in different stages of lactation differed from unity, for some efficiency traits, they could be considered the same during the lactation with minimal repercussions. Of greater concern, however, was the relatively weak genetic correlation that existed between REI at the extreme DIMs. Such a weak correlation for REI could be due to the physiological changes of lactation and its effect on the partition of NEI into the different components across lactation. The strength of the genetic correlations between NEI at different DIM was very similar to the genetic correlations between REI at different stages of lactation.

Hurley et al. (2016), using a subset of the data used in the present study, reported strong phenotypic correlations between REI and EB and justified this correlation based on the mathematical equations underlying both REI and EB. The strong positive genetic correlation between REI and EB in the present study indicates selection on lower REI (i.e., deemed efficient cows) would favour cows with a lower energy status, and this correlation was strongest in mid-lactation when BW change was least (Hurley et al., 2016). Although unfavourable genetic correlations have been reported between greater negative energy balance and both reproductive performance (Beam and Butler, 1998) and health (Collard et al., 2000), selection for REI within a balanced breeding goal could be used to overcome such antagonisms (Berry and Crowley, 2013). In the present study, positive genetic correlations existed between REI and NEI which is supported by ealier studies also on dairy cows (Van Arendonk et al., 1991; Vallimont et al., 2011; Manafiazar et al., 2015). Possible reasons for genetic correlations between REI and its component traits have been discussed in beef (Crews, 2005) and dairy cattle (Kennedy et al., 1993).

In the present study, strong genetic correlations existed among some of the ratio traits, EB, and production traits. The observed stronger genetic correlation between ECE with NEL was predominately caused by the larger coefficient of genetic variation for NEL (6.74%) compared to the coefficient of genetic variation for NEI (4.82%). The generally strong genetic correlations between ECE and NEL were in agreement with previous studies on dairy cows (Prendiville et al., 2009; Spurlock et al., 2012).

Moreover, the moderately negative genetic correlations between ECE with both BCS and BW could potentially indicate that the loss of both BCS and BW throughout lactation contributes to higher (i.e., superior) ECE values. The strong genetic correlation which existed between ECE and EB signify that cows with a higher ECE (i.e., more efficient cows) were also in more negative EB. The unfavourable implications of negative EB on health and fitness traits have been well documented (Beam and Butler, 1998; Collard et al., 2000). Of particular interest in the present study was the change in sign of the genetic correlation between EB and BCS. The moderately negative genetic correlation between EB and BCS in early lactation indicates that fatter cows, on average, are genetically predisposed to mobilizing more body condition in early lacation as concluded by Berry et al. (2002). However, the change in sign of the genetic correlation between EB and BCS in mid lactation (i.e., at 121 DIM) suggests that cows in greater positive EB put on more body condition.

Potential to alter lactation profiles

The use of RRMs facilitates the calculation of breeding values for the particular trait of interest across each DIM but also enables the quantification of the potential to genetically alter the lactation profile (Kirkpatrick et al., 1990). The structure of the eigenfunctions and size of the associated eigenvalues give an indication into the extent to which the lactation curve can be altered (Kirkpatrick et al., 1990). The sign of the eigenfunctions is irrevalent, but instead what matters is the consistency, or lack thereof, of the sign of the eigenfunctions over the trajectory (Van Der Werf, 1997). The eigenfunctions associated with 11.22% (middle) and 8.90% (smallest) of the genetic variance for REI changed sign across lactation implying that REI is indeed under different genetic control across different stages of lactation but also indicates the potential to alter the shape of the REI lactation profile. However, as the intercept term of the covariance function explained the largest proportion (i.e., > 70%) of the genetic variation, strategies to alter the shape of the lactation profile, would require greater selection pressure on the relevant eigenfunction.

Conclusion

This is the first study to comprehensively describe the genetic inter-relationships among alternative definitions of energy efficiency in lactating dairy cows. Results clearly indicate that ample genetic variation exists for all feed efficiency traits in lactating dairy cows but this variability, as well as their respective heritability estimates, varies across lactation. Of particular interest is that the results suggest that selection for decreased REI should result in genetically superior animals for energy efficiency without any compromize in productivity. Moreover potential exists to select on the trajectories of the efficiency traits (i.e., ECE, REI, and REP) to alter the shape of the lactation profile to suit a particular breeding objective. The moderate to strong genetic correlations estimated between REI and EB are worrying for the impact of selection of REI on lifetime efficiency. Nonetheless, precise genetic correlations between the feed efficiency complex with both reproduction and health traits need to be quantified.

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Appendix 5.1. Number of records (n), mean, maximum (standard error) and minimum (standard error) heritability estimates for the efficiency and production traits.

Trait[1]	N	Mean	Minimum (SE)	Maximum (SE)
MEff, UFL/kg$^{0.75}$	7,829	0.06	0.06±0.02 at 47 DIM	0.12±0.08 at 151 DIM
FtW, UFL/kg$^{0.75}$	7,829	0.15	0.12±0.04 at 50 DIM	0.18±0.06 at 280 DIM
KR, UFL/kg$^{0.75}$	83,930	0.09	0.21±0.03 at 50 DIM	0.33±0.04 at 151 DIM
NEL, UFL/d	88,770	8.59	0.21±0.02 at 8 DIM	0.41±0.04 at 151 DIM
BW, kg	77,743	529.5	0.45±0.04 at 8 DIM	0.60±0.05 at 200 DIM
BCS, scale 1 to 5	37,063	2.84	0.27±0.03 at 8 DIM	0.39±0.05 at 280 DIM

[1] MEff = metabolic efficiency; FtW = feed to body-weight; KR = Kleiber ratio; NEL = net energy for lactation; BW = body-weight; BCS = body condition score.

Chapter 6

Genetic relationships between feed efficiency and reproductive performance in grazing lactating dairy cows

A.M. Hurley[1, 2], N. López-Villalobos[2], S. McParland[1], E. Kennedy[1], E. Lewis[1],
M. O'Donovan[1], A. Geoghegan[1], J.L. Burke[2], and D.P. Berry[1]

[1]*Teagasc, Animal & Grassland Research and Innovation Centre, Moorepark, Fermoy,*
Co. Cork, Ireland
[2]*Institute of Veterinary, Animal and Biomedical Sciences, Massey University,*
Private Bag 11-222, Palmerston North, New Zealand

Submitted to the Journal of Dairy Science.

Abstract

Due primarily to a lack of phenotypic data, little research has been undertaken on the genetic inter-relationships between feed efficiency and reproductive performance in lactating dairy cows. The objective of the present study was to quantify, using data from seasonal-calving grazing lactating Holstein-Friesian dairy cows, the genetic inter-relationships between alternative efficiency metrics and reproductive traits. A total of 4,062 parity records from 1,185 animals were used to estimate variance components for a range of reproductive traits using animal linear mixed models; 8,085 individual net energy intake (NEI) test-day records were available. Co-variance components within and between the efficiency and reproductive traits were estimated using a series of univariate and bivariate repeatability animal linear mixed models. Eight reproductive traits were generated representing interval (n=3), count (n=1) and binary traits (n=4). Efficiency traits were either ratio-based (n=4) or residual-based (n=3) and mean efficiency throughout the entire lactation, or just within early lactation, was considered. Residual energy intake (REI) was defined as NEI minus predicted energy requirements based on lactation performance; residual energy production (REP) was defined as net energy for lactation (NEL) minus predicted energy requirements based on lactation performance. Although associated with large standard errors, the genetic correlations between the efficiency traits and reproductive performance were either neutral or favourable. For example, REI was positively genetically correlated with calving interval (0.10 ± 0.28) suggesting that negative REI (i.e., more efficient) animals appear to have a shorter calving interval. Results from the present study suggest greater genetic merit for feed efficiency does not appear to be antagonistically genetically correlated with reproductive performance.

Keywords: feed intake, residual energy intake, fertility, energy balance, heritability.

Introduction

Genetic improvements in feed efficiency is both of economic (Gonzalez-Recio et al., 2014) and environmental value (Basarab et al., 2013; Leip et al., 2015) to the dairy cow sector. Feed efficiency is currently not directly included in most dairy cow breeding objectives. The Australian dairy cattle breeding program was the first to implement direct genetic selection for improved net feed efficiency (Pryce et al., 2015) by combining residual feed intake (RFI) and feed required for maintenance which was predicted from body-weight (BW). Residual feed intake is defined as the difference between actual and predicted feed intake independent of body size and production (Koch et al., 1963; Berry and Crowley, 2013; Connor et al., 2013). However, to properly derive the selection index weights in a breeding program, as well as infer the expected responses to selection, estimates of the genetic correlations among the index and goal traits are required. Estimates of genetic correlations in seasonal calving, lactating dairy cows between feed efficiency and, in particular, reproductive performance, are non-existent in the scientific literature. This is despite the inclusion of reproductive traits in almost all dairy cow breeding goals internationally (Miglior et al., 2005). In fact, the genetic correlations between efficiency and reproduction in dairy cows in general are lacking, and those that do exist are associated with substantial standard errors.

Hurley et al. (2017b) illustrated that lactating dairy cows genetically predisposed to have low REI (i.e., more efficient) across lactation, while consuming less NEI, were also in negative energy balance (EB) throughout the entire lactation. Negative EB in dairy cows is known to be unfavourably associated with both health and fitness traits, including reproductive performance (Beam and Butler, 1998; Collard et al., 2000; De Vries and Veerkamp, 2000). Consequently, enhanced feed efficiency over a given time period could actually be offset by a deterioration in the productive lifespan of the cow owing to poorer reproductive performance. We therefore hypothesize that reproductive performance will be unfavourably genetically correlated with feed efficiency and in particular REI. The objective of the present study was to quantify, using data from seasonal-calving grazing lactating Holstein-Friesian dairy cows, the genetic inter-relationships between alternative efficiency metrics and reproductive traits. The present study will be the first, to our knowledge, to quantify the genetic correlations between efficiency traits and reproductive performance in seasonal calving, grazing, lactating dairy cows. Results from the present study will be helpful in deriving selection index weights for different breeding goals as well as aiding in quantifying the expected response to selection in a breeding goal when feed efficiency is explicitly considered.

Materials and methods

Data

The data used in the present study originated from the Animal and Grassland Research and Innovation Centre, Teagasc Moorepark, Fermoy, Co. Cork, Ireland; all calving events were collected between the years 1995 to 2014, inclusive. The feed intake data has been described in detail elsewhere (Hurley et al., 2016, 2017). Data used in the present study originated from cows that participated in several controlled experiments which evaluated alternative grazing strategies, different stocking rates, nutritional experiments, or strains of Holstein-Friesian animals. All experiments were performed on two adjacent research farms in southern Ireland (latitude 52°9N; longitude 8°16W). Data available included animal pedigree, breed composition, milk yield and composition (concentration of fat, protein, and lactose), reproductive phenotypes (i.e., calving dates, pregnancy diagnosis, and service dates) as well as total dry matter intake (DMI) for each cow. All Holstein-Friesian cows included in the present study calved in spring.

Grass DMI for each cow at pasture was periodically estimated using the n-alkane technique (Mayes et al., 1986). Procedures used to gather and analyse fecal samples are outlined in detail by Kennedy et al. (2008). All cows were offered a basal diet of grazed grass. Swards constituted primarily of perennial ryegrass (*Lolium perenne*) and were managed under a rotational grazing system comparable to that detailed by Dillon et al. (1995). Some animals were supplemented with concentrates (depending on experimental treatment), varying from 0.89 to 4.0 kg DM per cow daily, offered in equal feeds during each milking.

Animals were milked twice per day with milk yield recorded at each milking; milk fat, protein, and lactose concentration was determined from successive evening and morning milk samples once per week using mid-infrared spectroscopy (FT6000, FOSS, Hillerod, Denmark). Net energy requirement for lactation (NEL) was calculated using the following formula according to Agabriel (2007):

$$\mathrm{NEL} = ((0.054 \times \mathrm{FC}) + (0.031 \times \mathrm{PC}) + (0.028 \times \mathrm{LC}) - \ 0.015) \times \mathrm{milk\,kg}$$

where FC is fat concentration (%), PC is protein concentration (%), and LC is lactose concentration (%).

Individual animal BW was generally measured weekly following morning milking using electronic scales (Tru-Test Limited, Auckland, New Zealand); scales were calibrated weekly against known loads. Body condition score (BCS) on a scale of 1 (thin) to 5 (fat) was assessed and recorded by trained technicians every two to three weeks in increments of 0.25 (Edmonson et al., 1989). For the purpose of the present study, cubic splines were fitted through individual BW and BCS test-day records as described elsewhere (Hurley et al., 2016).

Individual cow daily total DMI (i.e., grazed pasture DMI plus concentrate DMI) was available up to eight times (average of 4.5 times) per lactation. Energy values of the pasture and concentrate were based on the French Net Energy system where 1 unité fourragère du lait (UFL) is the NEL equivalent of 1 kg standard air-dry barley (Jarrige et al., 1986) equivalent to 7.11 MJ net energy or 11.85 MJ metabolizable energy. The offered herbage UFL concentration was calculated using the acid detergent fibre and crude protein concentration which were quantified in the laboratory (Jarrige, 1989). Concentrate UFL value was determined from the chemical composition of the feed. The net energy content of the concentrate offered was calculated for each day; where UFL content of concentrate was not available (i.e., 20% of test-day records) the year-month average was assumed. Where the net energy content of the offered herbage (UFL/kg dry matter) was not available (i.e., 10% of test-day records) the year-month average was assumed. The sum of pasture and concentrate NEI were used to define total net energy intake (NEI).

Reproductive traits

The reproductive traits defined in the present study were based on the available data and each trait is described in detail elsewhere (Berry et al., 2013; Berry and Evans, 2014). Eight reproductive traits were generated and included age at first calving (**AFC**), calving interval (**CIV**), calving to first service interval (**CFS**), number of services (**NS**), submission rate in the first 21 d of a herd's breeding season (**SR21**), pregnancy rate in the first 42 d of a herd's breeding season (**PR42**), pregnancy rate in the first 84 d of a herd's breeding season (**PR84**), and pregnancy rate to first service (**PRFS**).

Age at first calving was defined as the age, in days, at which a heifer calved for the first time; age at first calving records less than 660 d were discarded. Calving interval was defined as the number of days between two consecutive calving events; only CIV records between 300 and 700 d were considered. Calving to first service interval was defined for all cows as the number of days from calving to the first service event; only CFS records greater than 10 d were considered. Number of services was defined as the number of times a cow was served per lactation.

The start of the breeding season was defined, within herd, on a set date during the year (usually the 16th of April); the end of the breeding season was also defined, within herd, on a set date during the year (usually the 10th of July). The defined breeding season was used to derive submission rate and pregnancy rate. Submission rate was calculated as whether or not a cow was served for the first time within the first 21 d of the breeding season (SR21), irrespective of calving date. Submission rate for cows not served for the first time during a predefined breeding season were set to missing.

Pregnancy rate in the first 42 d of the breeding season and PR84 were not defined in heifers; as cows in the present study were from seasonal calving herds, PR84 was used to infer survival. Cows were coded PR42 and PR84 if they were served in the first 42 d and the first 84 d of the breeding season, provided their calving date was within 265 and 295 d of the initial service date (i.e., mean gestation length in Holstein cows is reported to be 279 d with a standard deviation of 5.5 to 5.7 d; Norman et al., 2009); therefore, gestation lengths between 265 and 295 d were used in the present study. Cows with a service date recorded after 42 d from the start of the breeding season were coded as not PR42; similarly, cows with a service date recorded after 84 d from the start of the breeding season were coded as not PR84. Cows served in the first 42 d or the first 84 d of the breeding season, which were still not defined pregnant after the aforementioned edits, were defined pregnant or not pregnant, on the basis of their pregnancy diagnoses.

Pregnancy rate to first service was defined as whether or not a cow was pregnant to their first service. If a cow had greater than one service recorded then she was coded as not PRFS. Subsequent calving dates and pregnancy diagnoses were used to determine PRFS for cows with only one service record.

Data editing

Only feed efficiency records between 8 and 280 DIM were retained as limited data existed beyond 280 DIM. Cow parities were categorized as 1, 2, and ≥ 3; cow parities > 10 were discarded. Cow breed composition was obtained from the national database and, for the purpose of the present study, was defined as the proportion of Holstein, Friesian, and “Other”.

Contemporary group of experimental treatment by test-date was defined for NEL, NEI, BW, and BCS; contemporary groups with less than 5 observations were discarded. Contemporary group for CIV, CFS, NS, SR21, PR42, PR84, and PRFS was defined as herd-year-season of calving, while the contemporary group for AFC was defined as herd-year-season of birth. All herd-year-season contemporary groups were generated for each of the reproductive traits separately using an algorithm described by Schmitz et al. (1991) and Crump et al. (1997) and used previously on Irish data (Berry and Evans, 2014). Specifically, the algorithm grouped animals, within herd, which calved in close proximity (i.e., within 10 d of each other). Contemporary groups that contained less than five animals were discarded from the reproductive dataset. All lactations of cows were included in the final dataset even if the cow lactation had no NEI phenotype available. Following edits, the final dataset consisted of 4,062 lactations from 1,185 Holstein-Friesian cows; of these 2,435 lactations had an NEI phenotype while 4,017 lactations had a reproductive phenotype. A pedigree file, of at least 4 generations (where available), was produced for all animals included in the study; eight animals with no recorded sire were discarded. The average number of daughters per sire was 5.12.

Estimates of energy efficiency and energy balance

Definitions of all traits have been previously described in detail by Hurley et al. (2016). Energy balance (EB) for each test day was calculated in accordance with the net energy system outlined by Jarrige (1989) and modified for Irish dairy systems by O'Mara (1996):

$$\mathrm{EB} = \mathrm{NEI} - \Delta\mathrm{NE} - \mathrm{NEL} - \mathrm{NEM} - \mathrm{NEP}$$

where NEI is daily net energy intake, $\Delta\mathrm{NE}$ is an adjustment of daily net energy intake for the proportion of concentrates in the diet, NEL is daily net energy requirements for lactation, NEM is daily net energy requirements for maintenance calculated as $((1.4 + (0.6 \times (\mathrm{BW}/100))) \times 1.2)$, and NEP is daily net energy requirements for pregnancy where UFL requirement for the 6th, 7th, and 8th month of pregnancy were 0.9, 1.6, and 2.6 UFL/d, respectively (O'Mara, 1996).

Residual-based efficiency traits. Residual energy intake **(REI)** for each day of lactation was defined as the residuals from the regression of NEI on energy sinks and other energy sources as:

$$\mathrm{REI} = \mathrm{NEI} - [\mathrm{NEL} + \mathrm{parity} + \textstyle\sum_{i=1}^{2} \mathrm{DIM}^{\mathrm{i}} + \mathrm{BW}^{0.75} + \mathrm{BCS} + \mathrm{BW}^{0.75} \times \mathrm{BCS} +$$
$$\Delta\mathrm{BW}^{+} + \Delta\mathrm{BW}^{-} + \Delta\mathrm{BCS}^{+} + \Delta\mathrm{BCS}^{-} + \Delta\mathrm{BW}^{+} \times \mathrm{BCS} + \Delta\mathrm{BW}^{-} \times \mathrm{BCS}]$$

where REI is daily residual energy intake, NEI is daily net energy intake, NEL is daily net energy requirements for lactation, parity (1, 2, and ≥ 3), $\sum_{i=1}^{2} \mathrm{DIM}^{\mathrm{i}}$ is days in milk included as a continuous variable with a linear $(\mathrm{i} = 1)$ and quadratic effect $(\mathrm{i} = 2)$, $\mathrm{BW}^{0.75}$ is metabolic BW, and BCS is body condition score. The energy generated from a 1 kg loss in BW is less than the energy required for a 1 kg gain in BW (O'Mara, 1996); therefore, piecewise regression was applied to BW and BCS in the REI model where $\Delta\mathrm{BW}^{+}$ describes animals gaining BW, $\Delta\mathrm{BW}^{-}$ describes animals losing BW, while ΔBCS^{+} describes animals gaining BCS, and $\Delta\mathrm{BCS}^{-}$ describes animals losing BCS. No multicollinearity existed in the multiple regression model.

Analogous to residual gain in growing cattle (Koch et al., 1963), residual energy production (REP) for each day of lactation was derived from the residuals of a least squares regression model regressing NEL on NEI plus energy sinks and other energy sources, similar to that described by Coleman et al. (2010).

$$\mathrm{REP} = \mathrm{NEL} - [\mathrm{NEI} + \mathrm{parity} + \textstyle\sum_{\mathrm{i}=1}^{2} \mathrm{DIM}^{\mathrm{i}} + \mathrm{BW}^{0.75} + \mathrm{BCS} + \mathrm{BW}^{0.75} \times \mathrm{BCS} + \Delta\mathrm{BW}^{+} + \Delta\mathrm{BW}^{-} + \Delta\mathrm{BCS}^{+} + \Delta\mathrm{BCS}^{-} + \Delta\mathrm{BW}^{+} \times \mathrm{BCS} + \Delta\mathrm{BW}^{-} \times \mathrm{BCS}]$$

where REP is daily residual energy production, NEL is daily net energy requirements for lactation, NEI is daily net energy intake, parity (1, 2, and ≥ 3), $\sum_{i=1}^{2} \mathrm{DIM}^{\mathrm{i}}$ is days in milk included as a continuous variable with a linear and quadratic effect, $\mathrm{BW}^{0.75}$ is metabolic BW, BCS is body condition score, $\Delta\mathrm{BW}^{+}$ describes animals gaining BW, $\Delta\mathrm{BW}^{-}$ describes animals losing BW, $\Delta\mathrm{BCS}^{+}$ describes animals gaining BCS, and $\Delta\mathrm{BC}S^{-}$ describes animals losing BCS. No multicollinearity existed in the multiple regression model.

Analogous to residual intake and gain as defined by Berry and Crowley (2012) in growing cattle, residual intake and energy production (RIEP) was defined using both REI and REP, each standardized to have a variance of one:

$$\mathrm{RIEP} = \widetilde{\mathrm{REP}} - \widetilde{\mathrm{REI}}$$

where $\widetilde{\mathrm{REP}}$ is residual energy production standardized to a variance of one, and $\widetilde{\mathrm{REI}}$ is residual energy intake standardized to a variance of one.

Ratio-based efficiency traits. Energy conversion efficiency (ECE) for each day of lactation was defined as:

$$\mathrm{ECE} = \frac{\mathrm{NEL}}{\mathrm{NEI}}$$

where NEL is the daily net energy requirements for lactation, and NEI is the daily net energy intake.

Metabolic efficiency (MEff) for each day of lactation was defined as:

$$\mathrm{MEff} = \frac{\mathrm{NEI} - \mathrm{NEL}}{\mathrm{BW}^{0.75}}$$

where NEI is daily net energy intake, NEL is net energy requirements for lactation, and $\mathrm{BW}^{0.75}$ is metabolic BW.

Feed to body-weight (FtW) for each day of lactation was defined as:

$$\mathrm{FtW} = \frac{\mathrm{NEI}}{\mathrm{BW}^{0.75}}$$

where NEI is daily net energy intake, and $\mathrm{BW}^{0.75}$ is metabolic BW.

Kleiber ratio (KR) for each day of lactation was defined as (Hurley et al., 2016):

$$\mathrm{KR} = \frac{\mathrm{NEL}}{\mathrm{BW}^{0.75}}$$

where NEL is the net energy requirements for lactation and $\mathrm{BW}^{0.75}$ is metabolic BW.

Statistical analyses

Co-variance components within and among the efficiency and reproductive traits were estimated across lactation using a series of univariate and bivariate repeatability animal linear mixed models in ASReml (Gilmour et al., 2009). Fixed effects included in the model for all traits were contemporary group, parity number (1, 2, and ≥ 3), and the proportion of Friesian and “other breeds” (Holstein was not included to avoid linear dependency in the model). Stage of lactation (3 classes: 8 to 90 DIM, 91 to 180 DIM, and > 180 DIM), and the interaction between stage of lactation and parity were included as fixed effects for all efficiency traits. Calving to first service interval was fitted as a quadratic fixed effect when analyzing PRFS (Berry et al., 2011). Within and across-lactation animal permanent environmental effects were both included as random effects for all traits except AFC.

In a supplementary analysis, (co)variance components were estimated between the efficiency traits in early lactation (8 – 90 DIM) with the reproductive traits also using a series of bivariate repeatability linear mixed models in ASReml (Gilmour et al., 2009). Fixed effects and random effects fitted were the same as in the model previously described, but stages of lactation, and the interaction between stage of lactation and parity, were not included as fixed effects.

Results

A frequency distribution of the number of records available for NEI by week of lactation is in Figure 6.1. The number of observations, as well as the sample population mean, genetic standard deviation, heritability, and repeatability for the different reproductive traits investigated are in Table 6.1. Mean CFS, CIV, and AFC in the edited dataset was 76, 381, and 736, respectively (Table 6.1). Mean PRFS was 0.41, while the mean PR42 and PR84 was 0.69 and 0.86, respectively; mean NS was 1.96. Seventy five per cent of cows were served for the first time in the first 21 d of the breeding season. Heritability estimates for the reproductive traits ranged from 0.01 (CFS) to 0.05 (AFC and PRFS); repeatability estimates ranged from 0.03 (CFS and PR84) to 0.07 (PRFS) (Table 6.1). The additive genetic standard deviation of the binary reproductive traits varied from 0.05 (SR21) to 0.08 (PRFS) (Table 6.1). The coefficient of genetic variation for the continuous reproductive traits varied from 0.90 (AFC) to 9.58 (NS). The number of observations, as well as the sample population mean, genetic standard deviation, heritability, and repeatability for EB, the efficiency and production traits are in Appendix 6.1.

Table 6.1. Number of observations (N), sample population mean (µ), genetic standard deviation (σ_g), heritability (h^2; SE in parenthesis), and repeatability (t; SE in parenthesis) for the different fertility traits investigated.

Trait	N	µ	σ_g	h^2	t
Age of first calving	1,185	736	6.61	0.05 (0.02)	
Calving interval	3,386	381	8.76	0.02 (0.02)	0.04 (0.02)
Calving to first service interval	3,982	76	2.65	0.01 (0.02)	0.03 (0.01)
Number of services	4,012	1.96	0.19	0.03 (0.02)	0.06 (0.02)
Submission rate in 21 d	3,924	0.75	0.05	0.04 (0.02)	0.05 (0.02)
Pregnancy rate in first 42 d	3,760	0.69	0.06	0.03 (0.02)	0.04 (0.02)
Pregnancy rate in first 84 d	3,806	0.86	0.06	0.02 (0.02)	0.03 (0.01)
Pregnancy rate to first service	3,618	0.41	0.08	0.05 (0.02)	0.07 (0.02)

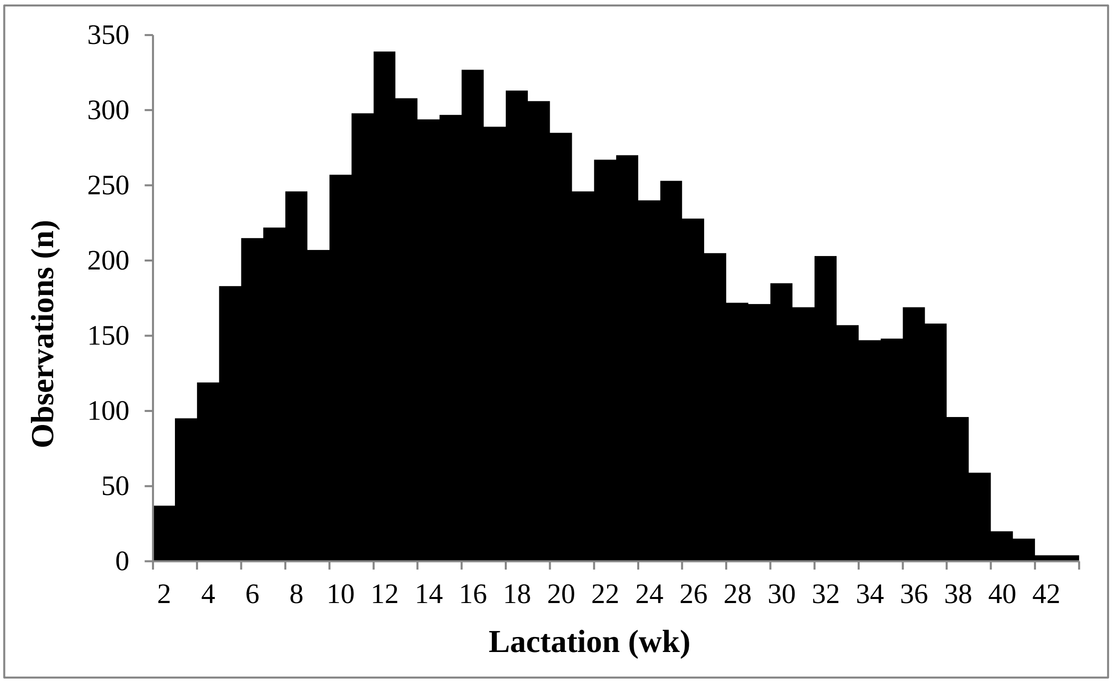

Figure 6.1. The number of observations for net energy intake for each week of lactation.

Correlations between the efficiency traits and reproductive traits across lactation

Genetic correlations between both EB and the efficiency traits measured across the entire lactation with the various reproductive traits are in Table 6.2; all genetic correlation estimates were associated with large standard errors. Energy balance, NEI, NEL, $BW^{0.75}$, and BCS were all positively (0.04 to 0.61) genetically correlated with AFC. Net energy intake, NEL, and $BW^{0.75}$ were all moderate to strongly positively (0.52 to 0.73) genetically correlated with CIV, while EB and BCS were negatively (-0.21 to -0.20) genetically correlated with CIV. Energy balance, NEI, and NEL were all negatively (-0.45 to -0.31) genetically correlated with SR21, but $BW^{0.75}$ and BCS were both positively (0.55 to 0.64) genetically correlated with SR21. Phenotypic correlations between both EB and the efficiency traits measured across the entire lactation with the various reproductive traits were all close to zero and are therefore not presented.

Energy conversion efficiency and KR were positively, albeit weakly (0.13 to 0.22) genetically correlated with AFC, while MEff and FtW were weakly negatively (-0.17 to -0.14) genetically correlated with AFC. Metabolic efficiency, FtW, and KR were all positively but weakly (0.09 to 0.16) genetically correlated with CFS, while ECE was negatively genetically correlated with CFS (-0.55 ± 0.29).

Although associated with large standard errors, REP and RIEP were weakly negatively (-0.22 to -0.13) genetically correlated with CIV, while a weak positive genetic correlation existed between REI and CIV (0.10 ± 0.28). All residual traits were positively genetically associated with CFS and PRFS, but negatively genetically associated with NS, although the correlations were weak (Table 6.2).

Table 6.2. Genetic correlations (SE in parenthesis) between both EB and the efficiency traits measured across the entire lactation with the various reproductive traits.

Trait[1]	AFC	CIV	CFS	NS	SR21	PR42	PR84	PRFS
EB	0.04 (0.28)	-0.20 (0.41)	0.12 (0.32)	-0.13 (0.28)	-0.45 (0.51)	0.08 (0.31)	0.11 (0.24)	-0.16 (0.27)
NEI	0.47 (0.22)*	0.52 (0.31)	-0.09 (0.29)	0.12 (0.25)	-0.42 (0.36)	-0.38 (0.26)	-0.01 (0.19)	0.03 (0.25)
NEL	0.58 (0.22)*	0.73 (0.34)*	-0.13 (0.30)	0.21 (0.26)	-0.31 (0.42)	-0.56 (0.34)	-0.15 (0.31)	0.11 (0.26)
$BW^{0.75}$	0.61 (0.17)*	0.52 (0.33)	-0.36 (0.27)	0.38 (0.19)*	0.64 (0.36)	-0.35 (0.25)	-0.10 (0.17)	-0.18 (0.26)
BCS	0.18 (0.19)	-0.21 (0.27)	-0.28 (0.25)	-0.18 (0.23)	0.55 (0.32)	0.70 (0.31)*	0.56 (0.38)	0.41 (0.29)
ECE	0.22 (0.28)	0.15 (0.42)	-0.55 (0.29)	0.03 (0.30)	0.07 (0.48)	-0.44 (0.32)	-0.09 (0.35)	-0.42 (0.28)
MEff	-0.17 (0.27)	-0.31 (0.42)	0.09 (0.31)	-0.19 (0.28)	-0.25 (0.42)	0.20 (0.30)	0.11 (0.24)	-0.02 (0.27)
FtW	-0.14 (0.23)	-0.13 (0.31)	0.16 (0.30)	-0.18 (0.25)	-0.32 (0.35)	-0.08 (0.26)	0.06 (0.21)	0.19 (0.27)
KR	0.13 (0.22)	0.20 (0.34)	0.12 (0.29)	-0.03 (0.26)	-0.44 (0.42)	-0.51 (0.37)	-0.09 (0.20)	0.19 (0.26)
REI	0.36 (0.24)	0.10 (0.28)	0.12 (0.34)	-0.04 (0.28)	-0.30 (0.40)	-0.11 (0.31)	-0.08 (0.49)	0.04 (0.21)
REP	-0.57 (0.23)*	-0.13 (0.37)	0.10 (0.33)	-0.26 (0.28)	-0.25 (0.45)	-0.05 (0.29)	0.14 (0.31)	0.41 (0.28)
RIEP	-0.61 (0.23)*	-0.22 (0.41)	0.05 (0.36)	-0.21 (0.31)	0.12 (0.38)	0.13 (0.34)	0.06 (0.35)	0.36 (0.30)

[1] EB = energy balance; NEI = net energy intake; NEL = net energy for lactation; $BW^{0.75}$ = metabolic body-weight, BCS = body condition score; ECE = energy conversion efficiency; MEff = metabolic efficiency; FtW = feed to body-weight; KR = Kleiber ratio; REI = residual energy intake; REP = residual energy production; RIEP = residual intake and energy production; AFC = age at first calving; CIV = calving interval; CFS = calving to first service interval; NS = number of services; SR21 = submission rate in the first 21 d of the breeding season; PR42 = pregnancy in first 42 d of breeding season; PR84 = pregnancy in first 84 d of breeding season; PRFS = pregnancy rate to first service.

**P* < 0.05.

Correlations between the efficiency traits in early lactation and reproductive traits

Genetic correlations between both EB and the efficiency traits measured in early lactation with the various reproductive traits are in Table 6.3; all genetic correlation estimates were associated with large standard errors. Net energy intake, NEL, and $BW^{0.75}$ were all positively (0.55 to 0.84) genetically correlated with CIV, while EB and BCS were negatively but weakly (-0.28 to -0.23) genetically correlated with CIV. Net energy intake, NEL, $BW^{0.75}$, and BCS were all negatively (-0.60 to -0.22) genetically correlated with CFS, while EB was positively but weakly (0.15 ± 0.37) genetically correlated with CFS. Net energy intake, NEL, and $BW^{0.75}$ were all negatively genetically correlated with PR42 and PR84, yet EB and BCS were positively genetically correlated with PR42 and PR84. Phenotypic correlations between both EB and the efficiency traits measured in early lactation with the various reproductive traits were all close to zero and are therefore not presented.

Albeit associated with large standard errors, ECE and KR were positively but weakly (0.22 to 0.30) genetically correlated with CIV, while MEff and FtW were negatively (-0.49 to -0.24) genetically correlated with CIV. Weak to moderate positive (0.13 to 0.40) genetic correlations existed between MEff, FtW, and KR with CFS, while MEff, FtW, and KR were all negatively but weakly (-0.36 to -0.18) genetically correlated with NS.

Although associated with large standard errors, REI was positively but weakly (0.22 ± 0.41) genetically correlated with CIV, while REP and RIEP were negatively but weakly (-0.25 to -0.15) genetically correlated with CIV. Similar to the genetic correlations across lactation, all residual traits were positively genetically correlated with CFS.

Table 6.3. Genetic correlations (SE in parenthesis) between both EB and the efficiency traits measured in early lactation with the various reproductive traits.

Trait[1]	AFC	CIV	CFS	NS	SR21	PR42	PR84	PRFS
EB	-0.28 (0.38)	-0.23 (0.47)	0.15 (0.37)	-0.08 (0.32)	-0.08 (0.51)	0.12 (0.36)	0.10 (0.29)	-0.20 (0.32)
NEI	0.15 (0.27)	0.55 (0.41)	-0.22 (0.37)	0.13 (0.31)	-0.27 (0.44)	-0.21 (0.26)	-0.10 (0.26)	-0.15 (0.32)
NEL	0.58 (0.36)	0.84 (0.33)*	-0.22 (0.36)	0.22 (0.31)	-0.23 (0.18)	-0.54 (0.35)	-0.17 (0.29)	0.03 (0.32)
$BW^{0.75}$	0.70 (0.13)*	0.66 (0.39)	-0.60 (0.41)	0.52 (0.28)	0.24 (0.38)	-0.46 (0.30)	-0.37 (0.31)	-0.27 (0.27)
BCS	0.47 (0.24)*	-0.28 (0.41)	-0.49 (0.30)	-0.03 (0.28)	0.58 (0.34)	0.62 (0.38)	0.36 (0.21)	0.66 (0.31)*
ECE	0.74 (0.51)	0.22 (0.32)	-0.50 (0.31)	0.40 (0.18)*	0.03 (0.56)	-0.32 (0.26)	0.16 (0.29)	-0.46 (0.38)
MEff	-0.39 (0.37)	-0.49 (0.49)	0.40 (0.35)	-0.36 (0.34)	-0.07 (0.44)	0.17 (0.35)	0.02 (0.46)	0.49 (0.48)
FtW	-0.33 (0.32)	-0.24 (0.46)	0.13 (0.37)	-0.31 (0.31)	-0.27 (0.43)	0.23 (0.22)	0.33 (0.25)	0.47 (0.38)
KR	0.07 (0.29)	0.30 (0.38)	0.14 (0.37)	-0.18 (0.31)	-0.36 (0.47)	-0.31 (0.29)	-0.32 (0.30)	0.21 (0.31)
REI	0.16 (0.28)	0.22 (0.41)	0.18 (0.54)	0.06 (0.45)	-0.06 (0.42)	-0.35 (0.26)	-0.14 (0.40)	-0.35 (0.47)
REP	-0.44 (0.35)	-0.15 (0.44)	0.03 (0.39)	-0.42 (0.35)	-0.30 (0.46)	0.31 (0.28)	0.38 (0.36)	0.45 (0.34)
RIEP	-0.40 (0.34)	-0.25 (0.51)	0.04 (0.45)	-0.43 (0.48)	-0.35 (0.36)	0.34 (0.34)	0.37 (0.41)	0.41 (0.45)

[1] EB = energy balance; NEI = net energy intake; NEL = net energy for lactation; $BW^{0.75}$ = metabolic body-weight, BCS = body condition score; ECE = energy conversion efficiency; MEff = metabolic efficiency; FtW = feed to body-weight; KR = Kleiber ratio; REI = residual energy intake; REP = residual energy production; RIEP = residual intake and energy production; AFC = age at first calving; CIV = calving interval; CFS = calving to first service interval; NS = number of services; SR21 = submission rate in the first 21 d of the breeding season; PR42 = pregnancy in first 42 d of breeding season; PR84 = pregnancy in first 84 d of breeding season; PRFS = pregnancy rate to first service.

*$P < 0.05$.

Discussion

Poor reproductive performance directly affects profitability. Any compromise in reproductive performance will likely reduce cow longevity (Veerkamp et al., 2002) and increase involuntary culling within the herd (Hadley et al., 2006). This is particularly important for seasonal calving herds which predominate in Ireland (Berry et al., 2014b), and elsewhere (e.g., New Zealand). In such herds, calving must coincide with the initiation of grass growth, thereby maximizing the exploitation of low-cost, grazed grass in the cow’s diet (Horan et al., 2006). It is therefore desirable that selection for enhanced feed efficiency will not have any unfavourable repercussions on genetic trends in reproductive performance other than through a reduction of selection intensity from the inclusion of a new trait in the breeding objective (Berry, 2015). The objective of the present study was to quantify, using data from seasonal-calving grazing lactating Holstein-Friesian dairy cows, the genetic inter-relationships between alternative efficiency metrics and reproductive traits. Heritability estimates of the reproductive traits in the present study were low (≤ 0.05), but consistent with the low heritability estimates reported internationally for reproductive traits in dairy cows (for review see Berry et al., 2014b). Heritability estimates of the efficiency traits from the dataset have been discussed at length elsewhere (Hurley et al., 2017). Although associated with large standard errors, the genetic correlations between the eight reproductive traits with the seven efficiency traits evaluated in the present study were either neutral or favourable suggesting that greater genetic merit for feed efficiency does not at least appear to be antagonistically genetically correlated with reproductive performance. To the best of our knowledge, this is the first study that quantifies the genetic correlations between efficiency traits and reproductive performance in seasonal calving lactating dairy cows and the most comprehensive for any population of lactating dairy cows.

Genetic associations between feed efficiency and reproductive performance

A concern often muted with selection for negative REI (i.e., more efficient) is the possible repercussions on reproductive performance (Berry and Crowley, 2013; Connor, 2015). In dairy cows, Veerkamp (2002) hypothesized that REI and EB are strongly correlated, while, based on empirical data, Hurley et al. (2016, 2017a, and 2017b) documented that REI and EB are indeed both strongly phenotypically and genetically correlated across the entire lactation in Holstein-Friesian dairy cows. In dairy cows, negative EB in early lactation is well-proven to be both unfavourably phenotypically (Beam and Butler, 1998; Collard et al., 2000; Roche et al., 2007) and genetically (Veerkamp et al., 2000) associated with health and reproductive performance. Consequently, in the present study it was hypothesized that REI, in particular, would be unfavourably genetically correlated with reproductive performance, especially when REI was measured in early lactation. The genetic correlations between REI and reproductive performance documented in the present study, however, were either favourable or neutral thus refuting our hypothesis. These somewhat unexpected associations between REI and reproductive performance are nonetheless supported by a New Zealand study by Macdonald et al. (2016) who reported the reproductive performance of seasonal-calving grazing lactating Holstein-Friesian cows divergent for residual feed intake (RFI) measured as growing calves; although the experimental design and analysis are not directly comparable with the present study, results from the three-year trial failed to detect any effect of divergence for RFI on reproductive performance. Furthermore, Coleman et al. (2010) did not find any association between RFI and reproductive performance in grazing lactating dairy cows, irrespective of whether RFI was considered in early lactation or over the full lactation. Coleman et al. (2010) defined RFI by regressing DMI on fat, protein, and lactose yield, as well as metabolic BW, daily BW change, and BCS. This definition of RFI was very similar to that used in the present study; however, the total number of cows in the study of Coleman et al. (2010) was limited (n = 175). Combined, the results from the present study with those of both Macdonald et al. (2016) and Coleman et al. (2010) suggests divergent selection for REI may not directly affect reproductive performance. Nonetheless, in an analysis of 970 US Holstein cows where feed intake and BW data was collected over 6 months, Vallimont et al. (2013) reported a negative genetic correlation between days open (i.e., days from calving to conception) and RFI (-0.50 ± 0.40), suggesting lower RFI (i.e., more efficient) resulted in greater days open (undesirable). However, the reported genetic correlation between days open and RFI by Vallimont et al. (2013) was associated with a large standard error, and in fact, was not different to the genetic correlation between REI and CIV (genetically similar to days open; Berry et al., 2014b) in the present study. In the same study, Vallimont et al. (2013) reported a favourable genetic correlation between RFI and productive life (-0.23 ± 0.29). This genetic correlation somewhat contradicts their genetic correlation between RFI and CIV, suggesting efficient animals tend to last longer within the herd, and are therefore less likely to be affected by involuntary culling due to reproductive problems. In beef cattle, Johnston et al. (2009) reported a negative genetic correlation (−0.6 ± 0.23) between age at puberty in Braham heifers and RFI measured in their growing paternal half-brothers; no genetic correlation existed in Brahman crosses (genetic correlation was 0.02 ± 0.23). All in all, the available results to-date, albeit all confined to relatively small sample population sizes, fail to conclusively determine whether REI is favourably or unfavourably (or neutrally) associated with reproductive performance. Power calculations were undertaken to determine the size of dataset required to estimate significant heritability and genetic correlation. To achieve a significant correlation between REI and CIV it is estimated that 31,000 NEI records are necessary.

All genetic correlations between the ratio traits and reproductive traits in the present study were generally favourable or near zero, albeit genetic correlations were not more than twice their respective standard error. Nonetheless, this suggests greater genetic merit for feed efficiency, based on ratio traits, will not unfavourably impact reproductive performance.

Imprecision of genetic correlation estimates

All estimated genetic correlations in the present study were associated with large standard errors. This was predominantly due to a combination of the low heritability of (some of) the efficiency and reproductive traits (Falconer and MacKay, 1996), and the relatively small sample population size. The reported genetic correlations are, nevertheless, the best estimates available as it is resource-intensive to generate sufficient sample population sizes for feed intake data to achieve precise genetic correlation estimates. One option therefore to overcome this obstacle is to undertake a meta-analysis which may entail either combining data from different sources to generate a larger dataset as has previously been undertaken for feed intake in dairy cows (Berry et al., 2014a; de Haas et al., 2015), or to undertake a true meta-analysis of reported parameters and associated sampling variability. In their meta-analysis of the available literature, Berry et al. (2014b), for example, reported some genetic correlations which in individual studies had high associated standard error but, when combined, had low standard errors. If for example, three studies each reported a genetic correlation of REI in early lactation with PRFS of -0.35 (SE=0.47; Table 6.3) then using the approach of Koots et al. (1994) to collate genetic correlation estimates, the mean and standard error from the meta-analysis would be -0.35 (SE=0.27). An alternative view is that with a favourable genetic correlation of -0.35 and associated standard error of 0.47 (genetic correlation between REI in early lactation and PRFS; Table 6.3) then there is 23% probability that the genetic correlation is truly unfavourable, or, in fact an 8% probability that the genetic correlation is actually ≥ 0.3.

Despite the relatively large standard errors associated with the genetic correlations in the present study, some of the pair-wise genetic correlations have been reported elsewhere but from larger datasets and thus with small associated standard errors; in general, the genetic correlations estimated between these traits in the present study are relatively similar to those reported from the larger populations. For example, in a review of 20 cattle populations, Berry et al. (2014b) reported genetic correlations between milk, fat, and protein yield with CIV of 0.46 (SE=0.02), 0.48 (SE=0.03), and 0.50 (SE=0.03) varying from -0.45 to 0.74, -0.30 to 0.68, and -0.39 to 0.67, respectively. The genetic correlation between NEL (i.e., similar to fat yield and protein yield) and CIV in the present study was 0.73 (SE=0.34). Similarly, in a review of six populations, Berry et al. (2014b) reported a genetic correlation between BCS and CIV of -0.44 (SE=0.02) ranging from -0.51 to -0.14; the genetic correlation between BCS and CIV in the present study (-0.36; SE=0.37) was similar to the mean. This concordance provides confidence that the other less often reported genetic correlations in the present study, although associated with large standard errors, are likely good estimates.

Conclusion

The hypothesis that reproductive performance will be unfavourably genetically correlated with efficiency traits was not proven. Results from the present study suggest the genetic relationships between the efficiency traits evaluated with the reproductive traits were either neutral or favourable suggesting greater genetic merit for feed efficiency will not negatively impact reproductive performance. This is the first study to comprehensively quantify the genetic correlations between efficiency traits and reproductive performance in (seasonal calving) lactating dairy cows. Further research is required to accurately quantify the genetic correlations between the feed intake complex with health traits but also to generate similar efficiency-reproduction correlation estimates to include in a meta-analysis thereby achieving more precise correlation estimates.

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Appendix 6.1. Number of observations (N), sample population mean (μ), genetic standard deviation (σ_g), heritability (h^2; SE in parenthesis), and repeatability (t; SE in parenthesis) estimates for EB, efficiency and production traits.

Trait[1]	N	μ	σ_g	h^2	t
EB (UFL/d)	7,692	0.54	0.44	0.05 (0.02)	0.10 (0.01)
ECE	7,829	0.60	0.02	0.11 (0.02)	0.16 (0.01)
MEff (UFL/kg$^{0.75}$)	7,692	0.06	0.004	0.06 (0.02)	0.12 (0.01)
FtW (UFL/kg$^{0.75}$)	7,981	0.15	0.01	0.09 (0.02)	0.23 (0.02)
KR (UFL/kg$^{0.75}$)	7,648	0.09	0.01	0.21 (0.04)	0.55 (0.01)
REI (UFL/d)	7,679	0.00	0.44	0.07 (0.02)	0.13 (0.02)
REP (UFL/d)	7,679	0.001	0.45	0.21 (0.04)	0.34 (0.01)
RIEP (UFL/d)	7,679	0.001	0.34	0.09 (0.02)	0.16 (0.02)
NEI (UFL/d)	8,085	16.55	0.80	0.19 (0.03)	0.28 (0.02)
NEL (UFL/d)	7,884	9.59	0.65	0.21 (0.04)	0.54 (0.01)
BW (kg$^{0.75}$/d)	7,935	110.21	6.92	0.46 (0.05)	0.92 (0.01)
BCS (scale 1 to 5)	7,940	2.85	0.16	0.44 (0.05)	0.87 (0.01)

[1] EB = energy balance; ECE = energy conversion efficiency; MEff = metabolic efficiency; FtW = feed to body-weight; KR = Kleiber ratio; REI = residual energy intake; REP = residual energy production; RIEP = residual intake and energy production; NEI = net energy intake; NEL = net energy for lactation; BW = metabolic body-weight; BCS = body condition score.

Chapter 7

Breeding for Improved Net Feed Efficiency in the Irish Dairy Herd

A.M. Hurley[1, 2], N. López-Villalobos[2], S. McParland[1], E. Kennedy[1], E. Lewis[1],
M. O'Donovan[1], J.L. Burke[2], and D.P. Berry[1]

[1]*Teagasc, Animal & Grassland Research and Innovation Centre, Moorepark, Fermoy, Co. Cork, Ireland*

[2]*Institute of Veterinary, Animal and Biomedical Sciences, Massey University, Private Bag 11-222, Palmerston North, New Zealand*

Abstract

The national breeding objective in Ireland, the Economic Breeding Index (EBI), aims to identify profitable dairy animals, based on their estimated genetic merit for 19 traits. The objective of the present study was to quantify the impact of the EBI, on genetic change in residual energy intake (REI). The rate of genetic gain in the 19 EBI traits by including REI as a goal trait in the EBI with either its true economic weight or sufficient emphasis to achieve restricted gains were also investigated. Residual energy intake was defined as net energy intake (NEI) minus predicted energy requirements based on lactation performance. In the present study, all responses to selection were estimated per generation. Selection based on the status quo for the EBI using the economic weights in March 2017 and 99% accuracy of genetic evaluations for all 19 traits (base scenario) is predicted to increase yields of protein and fat, and will also increase REI (+0.01 UFL/generation). This suggests that selection based on the current EBI is predicted to generate animals with a higher REI. When the true economic weight for REI is used, but no actual phenotypic data for REI is available, the predicted genetic response for REI improved (-0.05 UFL/generation). This indicates that selection on the EBI, which includes REI with an economic weight of €0.078/UFL, will generate animals with lower REI and with limited impact on other production traits. If however, the true economic weight for REI is used, but also with 99% accuracy of genetic evaluations for all traits (including REI), then genetic gain for REI improves further (-0.06 UFL/generation). When genetic gain in REI was restricted to be zero (compared to the base scenario), genetic gain for yields of milk, fat, and protein reduced by 7.46 kg/generation, 0.09 kg/generation, and 0.15 kg/generation, respectively. As expected, genetic gain for REI was zero, but animals were predicted to consume marginally less NEI (-0.04 UFL/generation) compared to the base scenario. The EBI is currently selecting for

higher REI cows but this could be reversed if REI was included in the EBI with the appropriate economic weight.

Keywords: feed intake, residual energy intake, selection objective, correlated responses.

Introduction

The goal of a breeding objective is to select for, as far as possible, all traits that affect probability. In Ireland, the national breeding objective, the Economic Breeding Index (**EBI**), aims to identify profitable dairy animals, based on their estimated genetic merit; all genetic evaluations are performed by the Irish Cattle Breeding Federation (ICBF). The EBI constitutes seven sub-indexes, which are 1) milk production, 2) fertility, 3) calving performance, 4) beef carcass, 5) cow maintenance, 6) cow management, and 7) health. As Ireland maintains a seasonal grass based production system, cow fertility has a large influence on both milk production and subsequent profit; therefore, both cow fertility and milk production predominate the EBI comprising 68% of the total emphasis. Dry matter intake is not explicitly included in the EBI but feed efficiency is partially accounted for through the simultaneous inclusion of both milk solids and body-weight (BW). From a meta-analysis of 6 studies in dairy cows, Berry and Crowley (2013) reported that the genetic correlation between milk solids per kilogram of BW and feed conversion efficiency was 0.72. In Chapter 5, the genetic correlation between NEL per kilogram of BW and energy conversion efficiency was 0.74.

Residual feed intake (RFI), also known as net feed efficiency (Exton et al., 2000), is a commonly used measure of feed efficiency in cattle (Koch et al., 1963).

Residual feed intake is defined as observed minus expected dry matter intake (DMI), after adjusting for lipid and protein body mass changes. Regardless of whether DMI or RFI are directly included in the breeding objective, the greatest obstacle in identifying animals divergent in genetic merit for feed efficiency is sufficient records to achieve a high accuracy of selection; this requires routine access to the relevant phenotypic data. Measuring individual animal feed intake is expensive; therefore, practical and cost-effective means of quantifying individual cow feed intake in commercial populations are required. One such approach is through mid-infrared spectroscopy which is the method used globally to determine the fat, protein, and lactose concentrations in milk (McParland et al., 2012). In dairy cows, McParland et al. (2014) reported that the mid-infrared spectrum of milk samples can predict DMI and RFI with an accuracy of 80% and 60%, respectively. Genomic selection (Pryce et al., 2014a, Pryce et al., 2014b), as well as predictor traits (Berry and Crowley, 2013; Fogh et al., 2013), are both other options available to predict feed efficiency in large commercial populations. Nonetheless, should feed intake become routinely available, its inclusion in the national breeding objective may affect response to selection in other traits.

To date, no knowledge exists on the implications of selection on EBI or the implications of including cow REI directly in the breeding objective. Therefore, the objective of the present study was to quantify the impact of the EBI on genetic change in REI; the rate of genetic gain in the EBI traits by including REI as a goal trait in the EBI with either the true economic weight of the trait or sufficient emphasis to achieve restricted gains were also investigated. Results from this study may also be useful in determining the cost-benefit of recording feed intake in Ireland.

Materials and methods

Estimation of genetic correlations

Holstein-Friesian EBI bull proofs were extracted from the Irish Cattle Breeding Federation (ICBF) database in March 2017; genetic correlations among traits were inferred by correlating estimated breeding values (EBV) of high reliability bulls where a high reliability was >70% for both traits used in the pairwise correlation. Genetic correlations between EBVs for NEI, REI, and the other individual traits (except calving interval (CIV) and survival) were also estimated. To achieve this, a genetic evaluation for NEI and REI was undertaken in Chapter 4; the EBVs for both traits were correlated with the performance traits in the EBI; only sires with an EBV reliability for NEI or REI >20% were considered. The genetic correlations between both CIV and pregnancy in first 84 days of breeding season (PR84) with both NEI and REI were those estimated in Chapter 6; as cows in the present study were from seasonal calving herds, PR84 was assumed to represent the survival trait in the EBI. The genetic correlations between the EBVs are in Appendix 7.1; also included are the genetic correlations between NEI and REI with both CIV and PR84.

Genetic parameters for NEI and REI used in the selection index were those in Chapter 4. Genetic and phenotypic parameters of the traits in the EBI were those used in the national genetic evaluations.

Selection index methodology

The impact of genetic selection for either NEI or REI on the traits included in the EBI, and vice versa, was undertaken using selection index theory. The selection index (I) is a method for predicting the selection objective (H) in which several traits are selected simultaneously, such that I ≈ H. These expressions can be represented as follows (adapted from Cameron, 1997):

$$\mathrm{I} = \sum_{i=1}^{m} \mathrm{b_i X_i} = \mathbf{x}'\mathbf{b} = \mathrm{H} = \sum_{i=1}^{n} \mathrm{v_i g_i} = \mathbf{g}'\mathbf{v}$$

where $\mathbf{x}'$ is a row vector of m known and adjusted values, $\mathbf{b}'$ is a row vector of m weight coefficient to estimate, $\mathbf{g}'$ is a row vector of n unknown true breeding values and $\mathbf{v}$ is a row vector of n known relative economic weights. The measured traits in the selection index are also referred to as selection criterion (Cameron 1997).

The vector **b** was calculated from solving the equation:

$$\mathbf{b} = \mathbf{P^{-1}Gv}$$

where **G** is the genetic (co)variances matrix, $\mathbf{P^{-1}}$ is the inverse phenotypic (co)variances matrix, and $\mathbf{v}$ and $\mathbf{b}$ are vectors defined previously for H and I, respectively; the economic weight for REI (assuming a cost of €0.078/UFL; Finneran et al., 2010) was from the Moorepark Dairy Systems Model. For all the selection objectives investigated, traits included in the selection index were the same as those included in the selection objective as per the EBI.

Per generation correlated responses (R) to selection were calculated using selection index theory (Cameron 1997). This was done individually for each of the investigated scenarios (discussed later) using the equation:

$$\mathrm{R}_j = \frac{\mathbf{b}'\mathbf{C}_j}{\sqrt{\mathbf{b}'\mathbf{P}\mathbf{b}}}$$

where $\mathrm{R_j}$ is the response for the *j*th trait, and $\mathbf{C_j}$ is the *j*th column from the **C** matrix; the **C** is the genetic co-variances between all traits included in the selection index. Matrices **P** and **C** were derived from the parameters in Appendix 7.1. Matrices **P** and **C** were checked to ensure they were positive definitive and those that were not underwent bending using the procedure of Jorjani et al. (2003). Correlated response to selection on NEI was also estimated despite never been included within the EBI.

In selection index theory, true breeding values of traits included in H are weighted according to their economic weights. In the present study, those values corresponded to the March 2017 economic weights (ICBF, 2017). The economic weight, trait emphasis, genetic standard deviation, and heritability for all traits included in the EBI are in Table 7.1. The relative emphasis on trait *i* was calculated as in Van Raden (2002):

$$\mathrm{Emphasis}_i = \frac{|\mathrm{a}_i * \sigma_i|}{\sum_{j=1}^{n} |\mathrm{a}_j * \sigma_j|},$$

where a_i and a_j are the economic weight for the trait *i* and j, respectively, and σ_i and σ_j are the genetic standard deviations for trait *i* and j, respectively

Several different scenarios were investigated in the present study. The base scenario was the status quo for the EBI with the economic weights as in March 2017 (Table 7.1); 99% accuracy of genetic evaluations was assumed for all traits.

- Scenario 1 was the current EBI with a calculated economic weight for REI (assuming a cost of €0.078/UFL; Finneran et al., 2010); 99% accuracy of genetic evaluations was assumed for all traits except REI where it was assumed that no phenotypic data existed.
- Scenario 2 was the current EBI with the calculated economic weight for REI (assuming a cost of €0.078/UFL; Finneran et al., 2010); 99% accuracy of genetic evaluations was assumed for all traits including REI.
- Scenario 3 was a restricted selection index where sufficient weight was placed on REI to halt any change in genetic merit for the trait; 99% accuracy of genetic evaluations was assumed for all traits except REI where it was assumed that no phenotypic data existed.

Additional scenarios were investigated where the number of daughter records per sire for REI was changed. The first scenario (SO1) was the current EBI with the calculated economic weight for REI (assuming a cost of €0.078/UFL; Finneran et al., 2010); no progeny records per sire was assumed for REI, and records from 100 progeny per sire was assumed for all other traits. The second scenario (SO2) was the same as SO1, but sires were assumed to have REI observations on 5 progeny each but observations on 100 progeny per sire existed for all other traits. The third scenario (SO3) was the same as SO1, but sires were assumed to have REI observations on 20 progeny each but observations on 100 progeny per sire existed for all other traits. The forth scenario (SO4) was the same as SO1, but sires had 100 progeny observations for all traits including REI.

Table 7.1. Economic weight (€), trait emphasis (%), genetic standard deviation (σ_g), and heritability (h^2) for all traits currently included in the EBI.

Sub-Index	Trait	Economic weight (€)	Trait emphasis (%)	σ_g	h^2
Production	Milk yield	-€0.09	10.60 %	695.04	0.35
	Fat yield	€1.04	3.40 %	22.49	0.35
	Protein yield	€6.64	18.90 %	19.42	0.35
Fertility	Calving interval	-€12.43	24.00 %	52.02	0.03
	Survival	€12.01	10.90 %	30.43	0.02
Calving	Direct calving diff.	-€3.52	2.80 %	8.65	0.10
	Maternal calving diff.	-€1.73	1.30 %	11.50	0.04
	Gestation length	-€7.49	4.10 %	5.22	0.30
	Calf mortality	-€2.58	1.00 %	7.57	0.02
Beef	Cull cow weight	€0.15	0.70 %	28.47	0.35
	Carcass weight	€1.38	5.10 %	16.52	0.40
	Carcass conformation	-€10.32	1.70 %	1.10	0.35
	Carcass fat	€11.71	1.10 %	0.78	0.32
Maintenance	Cull cow weight	-€1.65	7.20 %	28.47	0.35
Management	Milking speed	-€0.25	2.10 %	72.28	0.13
	Milking temperature	€33.69	1.90 %	0.99	0.07
Health	Lameness	-€54.26	0.60 %	0.53	0.02
	Somatic cell count	-€43.49	1.80 %	0.55	0.13
	Mastitis	-€77.10	0.80 %	0.55	0.02

Results and discussion

There has been little success in developing and implementing breeding values to select directly for feed efficiency in dairy cattle breeding programs (Berry and Crowley, 2013). The Australian dairy cattle breeding program was the first to implement genetic selection directly for improved feed efficiency (Pryce et al., 2015) by combining RFI and feed required for maintenance which was predicted from BW. The objective of the present study was to quantify the impact of the EBI on genetic change in REI; the rate of genetic gain in the EBI traits by including REI as a goal trait in the EBI with either the true economic weight of the trait or sufficient emphasis to achieve restricted gains were also investigated. In the present study, all responses to selection were estimated per generation. However, per generation genetic responses can be translated to an approximate annual genetic response by multiplying by 0.215 (Schaeffer, 2006).

The predicted selection responses per generation for the base scenario, scenario 1, scenario 2, and scenario 3 are illustrated in Figure 7.1. Selection on the status quo for the EBI with the economic weights as in March 2017 and 99% accuracy of genetic evaluations assumed for all traits (base scenario) is predicted to increase yields of fat (4.23 kg/generation) and protein (1.85 kg/generation) and decrease cull cow weight (-4.03 kg/generation), but will also increase REI (+0.01 UFL/generation); this suggests that selection on the current EBI is predicted to generate animals with worse REI. When the true economic weight is placed on REI, despite having no direct observations for REI, (scenario 1), the predicted genetic responses for milk yield (MY), fat yield (FY), and protein yield (PY) were -125.65 kg/generation, 3.98 kg/generation, and 1.44 kg/generation, respectively (Figure 7.1); when compared to the base scenario predicted genetic responses for MY, FY, and PY decreased by 19.91 kg/generation, 0.24 kg/generation, and 0.41 kg/generation, respectively. The predicted genetic responses for

CIV and survival remained similar to the base scenario; carcass weight reduced slightly but also remained similar to the base scenario (Figure 7.1). Nonetheless, the predicted genetic response for REI improved to -0.05 UFL/generation, while the predicted genetic response for NEI was -0.44 UFL/generation. This, therefore, suggests that selection within the EBI on REI included with the appropriate economic weight will generate animals with lower REI even if no data or feed intake (i.e., REI) exists. Based on the genetic correlations from the other traits the accuracy of selection on REI from this model was 0.98 (single trait).

If however, the true economic weight on REI is used, as well as sufficient direct observations for REI to achieve 99% accuracy (i.e., scenario 2), predicted genetic gain for REI was -0.06 UFL/generation, while predicted genetic response for NEI was -0.46 UFL/generation while genetic change in all other traits remained the same or similar (Figure 7.1). Therefore, as expected, improved accuracy of selection on REI based on direct measurement itself can help achieve substantial genetic gain. Based on the heritability estimate for REI from Chapter 4 (0.07) and used in the current calculations, observations on a total of 1,600 progeny (ignoring parental contribution) for REI are required to achieve an accuracy of 0.99 (single trait). The predicted genetic response for NEI in the base scenario was 0.35 UFL/d, while the predicted genetic response for NEI in scenario 2 was 0.46 UFL/d; this gives a difference of 0.11 UFL/d. Therefore, per lactation, this translates to an estimated saving of €2.62 (assuming a cost of €0.078/UFL; Finneran et al., 2010). The potential extra revenue generated is close to €4.3 million over a 365 day period for the 1.35 million dairy cows in Ireland. When genetic gain in REI was restricted to be zero (i.e., scenario 3), relative to the base scenario, genetic gain for MY, FY, and PY reduced by 7.46 kg/generation, 0.09 kg/generation, and 0.15 kg/generation, respectively. As expected, genetic gain for REI was zero while NEI was expected to reduce by -0.04 UFL/generation compared to the base scenario.

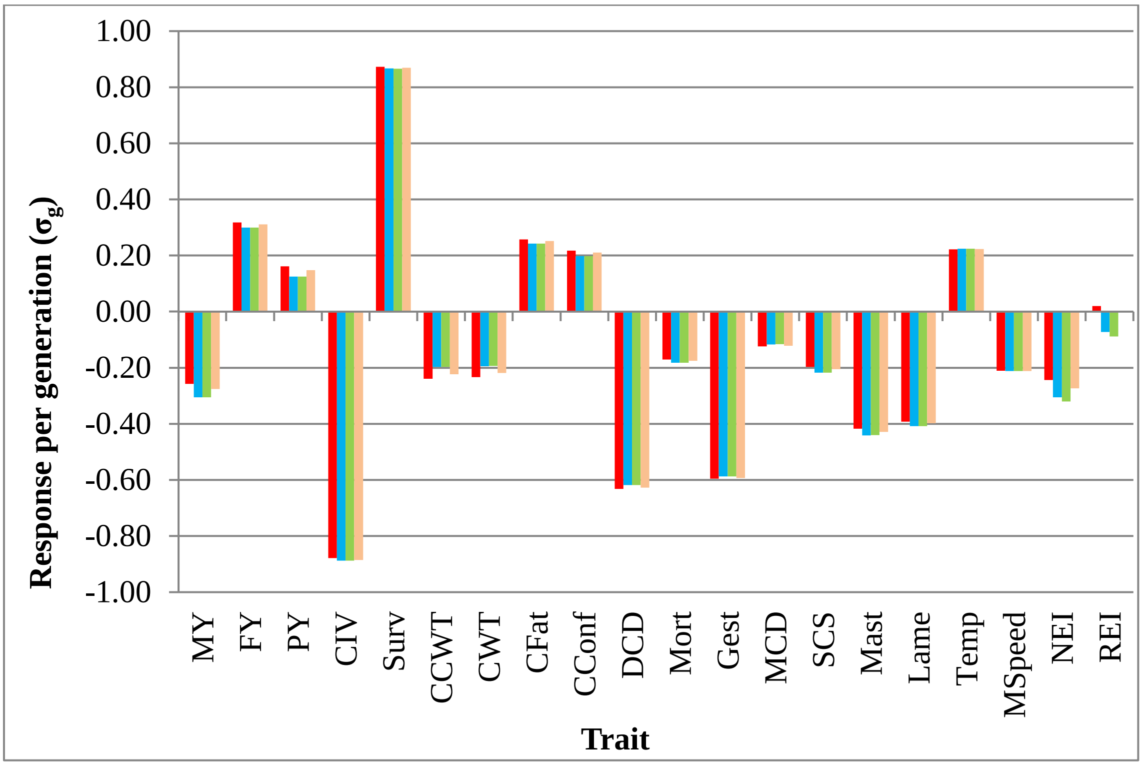

Figure 7.1. Predicted genetic responses per generation for the base scenario(🟥), scenario 1 (🟦), scenario 2 (🟩), scenario 3 (🟧); all responses were weighted by the genetic standard deviation per generation. MY = milk yield (kg); FY = fat yield (kg); PY = protein yield (kg); CIV = calving interval (%); Surv = survival (%); CCWT = cull cow weight (kg); CWT = carcass weight (kg); CFat = carcass fat (score); CConf = carcass confirmation (score); DCD = direct calving difficulty (%); Mort = mortality (%); Gest = gestation length (days); MCD = maternal calving difficulty (%); SCS = somatic cell score (cells/mL); Mast = mastitis (score); Lame = lameness (score); Temp = milking temperature (score); MSpeed = milking speed (score); NEI = net energy intake (UFL/d); REI = residual energy intake (UFL/d).

The predicted selection responses per generation for SO1, SO2, SO3, and SO4 are illustrated in Figure 7.2. If the true economic weight for REI is used in the EBI, but with no direct observations for REI, yet 100 progeny per sire for all remaining traits (i.e., SO1), the predicted genetic responses for MY, FY, and PY remained similar to the base scenario (Figure 7.2). However, relative to the base scenario the predicted genetic responses for CIV and survival decreased by -1.25%/generation and -0.62%/generation, respectively owing to an accuracy of selection based on the phenotypic data itself for the two traits being 0.66 and 0.58 (single trait), respectively. The predicted genetic response for REI improved from +0.01 UFL/generation in the base scenario to -0.021 UFL/generation in SO1. When the true economic weight is placed on REI, despite having 5 observations for REI, yet 100 progeny per sire for all remaining traits (SO2), the predicted genetic responses for REI (-0.024 UFL/generation) and NEI (-0.244 UFL/generation) remained similar to using no observations for REI (i.e., SO1). If however, the true economic weight for REI is used in the EBI with 20 observations for REI and 100 progeny per sire for all remaining traits (i.e., SO3), the predicted genetic responses for REI and NEI were -0.03 UFL/generation, and -0.25 UFL/generation, respectively. If further, the true economic weight for REI is used in the EBI and 100 progeny per sire for all remaining traits (i.e., SO4), the predicted genetic responses for REI and NEI were -0.04 UFL/generation, and -0.26 UFL/generation, respectively.

There is considerable evidence to suggest that feed efficiency should be included in a selection index or breeding goal (Van der Werf, 2004). Based on the results from the present study, it is possible to genetically breed for improved REI. The EBI currently includes cull cow weight and carcass weight (as well as other traits related to animal size). Van der Werf (2004) clearly showed that there is no additional benefit of including REI in a selection index or breeding goal that already includes NEI and the component traits. Including REI in the EBI instead of NEI would require a penalty to be placed on traits associated with body size in the EBI to account for mean differences in NEI since REI is phenotypically uncorrelated with body size.

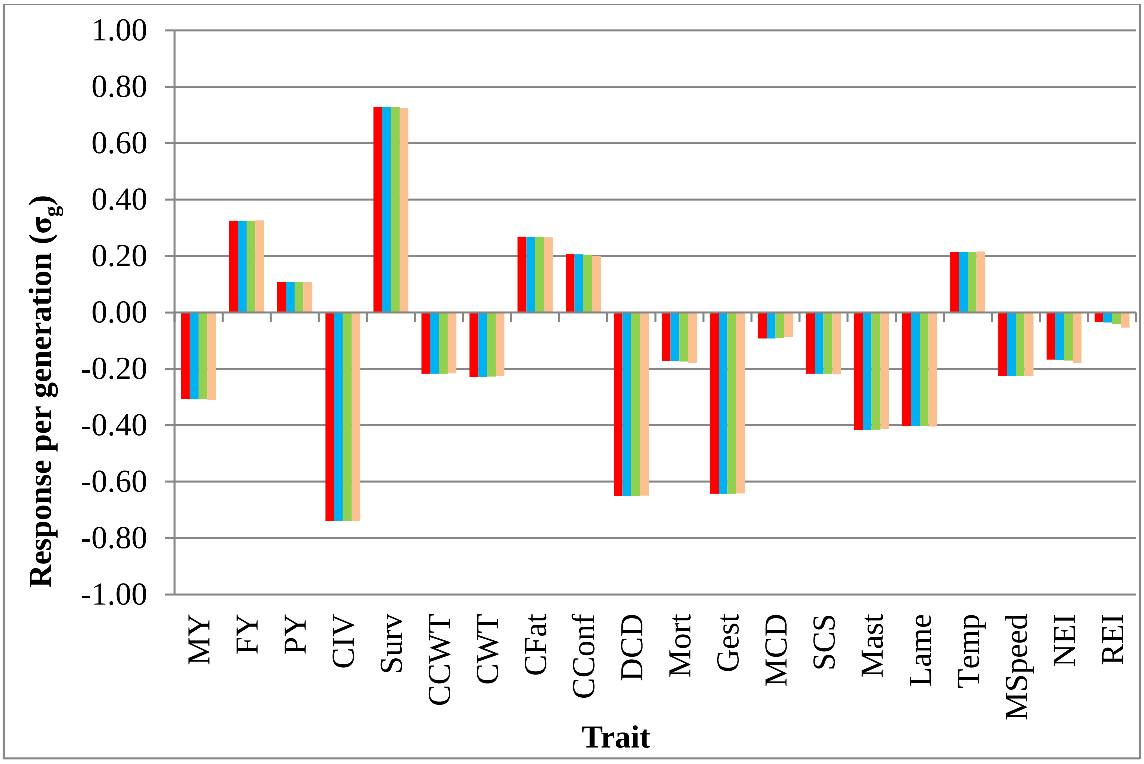

Figure 7.2. Predicted genetic responses per generation for SO1 (🟥), SO2 (🟦), SO3 (🟩), SO4 (🟧); all responses weighted by the genetic standard deviation per generation. MY = milk yield (kg); FY = fat yield (kg); PY = protein yield (kg); CIV = calving interval (%); Surv = survival (%); CCWT = cull cow weight (kg); CWT = carcass weight (kg); CFat = carcass fat (score); CConf = carcass confirmation (score); DCD = direct calving difficulty (%); Mort = mortality (%); Gest = gestation length (days); MCD = maternal calving difficulty (%); SCS = somatic cell score (cells/mL); Mast = mastitis (score); Lame = lameness (score); Temp = milking temperature (score); MSpeed = milking speed (score); NEI = net energy intake (UFL/d); REI = residual energy intake (UFL/d).

An alternative to including REI in a selection index or breeding goal would simply be to include NEI in a breeding goal with the appropriate weighting. This would be mathematically similar to including REI in the breeding goal if all other traits in the REI model were also in the breeding goal with the correct weights. The relative weighting on all other traits in the breeding goal would then be independent of their associated energy cost which may vary by time of the year (Wall et al., 2008) thus impacting the complexity of the calculations. Moreover, NEI in a breeding goal may be an easier concept to comprehend as REI is thought to be a difficult concept to understand (Wulfhorst et al., 2010).

Conclusion

Selection for feed efficiency in dairy cattle has historically relied on approximations of maintenance requirements; however, this is unlikely to capture all the variation in feed efficiency. Opportunities now exist to extend this to include feed efficiency measures such as REI. This study described the impact of the EBI on genetic change in REI; the rate of genetic gain in the EBI traits by including REI as a goal trait in the EBI, with either the true economic weight of the trait or sufficient emphasis to achieve restricted gains, were also investigated. Results showed that the EBI is currently selecting for higher REI cows but this could be reversed if REI was included in the EBI with the appropriate economic weight; however, the actual national monetary benefit of including feed efficiency (through REI) in the Irish total merit index is expected to be small.

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Appendix 7.1. Genetic correlations between breeding values for Holstein-Friesian bulls ranked on the EBI; also included are the genetic correlations between NEI and REI with all other traits in the EBI.

Trait[1]	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**
1. MY																			
2. FY	0.45																		
3. PY	0.78	0.73																	
4. CIV	0.53	0.05	0.24																
5. Surv	-0.28	0.12	-0.03[†]	-0.8															
6. CCWT	0.34	0.03[†]	0.20	0.24	-0.19														
7. CWT	0.35	0.07	0.21	0.27	-0.22	0.73													
8. CFat	-0.35	-0.10	-0.20	-0.35	0.19	-0.34	-0.13												
9. CConf	-0.49	-0.31	-0.43	-0.4	0.22	-0.31	-0.07	0.59											
10. DCD	0.17	-0.19	-0.08	0.52	-0.49	0.27	0.28	-0.22	-0.13										
11. Mort	0.04	-0.02[†]	0.01[†]	0.16	-0.13	0.08	0.04	-0.15	-0.16	0.24[†]									
12. Gest	0.01[†]	-0.31	-0.23	0.41	-0.41	-0.02[†]	0.11	-0.02	0.10	0.55	0.12								
13. MCD	-0.19	-0.20	-0.22	0.01[†]	-0.14	-0.29	-0.17	0.23	0.29	-0.14	-0.01[†]	0.14							
14. SCS	-0.06	-0.01[†]	0.01[†]	0.14	-0.29	-0.21	-0.06	0.13	0.16	0.12	-0.03[†]	0.12	0.13						
15. Mast	0.17	-0.04	0.10	0.40	-0.48	-0.19	0.04[†]	0.17	0.21	0.20	-0.02[†]	0.31	0.24	0.64					
16. Lame	0.07	-0.14	-0.08	0.30	-0.42	-0.08	0.04[†]	0.08	0.17	0.22	0.03[†]	0.31	0.24	0.28	0.71				
17. Temp	0.04[†]	0.10	0.10	-0.13	0.18	-0.08	-0.07	0.09	0.01[†]	-0.14	0.05[†]	-0.14	0.04[†]	0.05[†]	0.02[†]	-0.04[†]			
18.MSpeed	0.04[†]	-0.08	0.01[†]	0.17	-0.19	0.003[†]	0.10	-0.03[†]	0.001[†]	0.10	0.03[†]	0.16	0.11	0.09	0.21	0.21	0.03[†]		
19. NEI	0.45	0.31	0.29	0.52	-0.01	-0.10	-0.05	0.01[†]	0.02[†]	0.07	0.07	-0.02[†]	-0.12	0.07	0.16	0.15	-0.07	0.02[†]	
20. REI	0.50	0.18	0.36	0.10	-0.08	-0.35	-0.37	0.05	0.09	-0.12	0.13	-0.15	-0.08	0.13	0.14	0.07	0.04	0.02[†]	0.74

[1] MY = milk yield; FY = fat yield; PY = protein yield; CIV = calving interval; Surv = survival; CCWT = cull cow weight; CWT = carcass weight; CFat = carcass fat; CConf = carcass confirmation; DCD = direct calving difficulty; Mort = mortality; Gest = gestation length; MCD = maternal calving difficulty; SCS = somatic cell score; Mast = mastitis; Lame = lameness; Temp = milking temperature; MSpeed = milking speed; NEI = net energy intake; REI = residual energy intake.

[†] Correlations do not differ significantly at $P > 0.05$.

Chapter 8

General discussion

The overall objective of the thesis was to quantify the phenotypic and genetic (co)variances between the feed intake complex, performance, and fertility in grazing lactating Holstein-Friesian dairy cows. To meet this overall objective, five specific objectives were developed in this thesis:

1. To derive alternative definitions of feed efficiency in grazing lactating dairy cows and to quantify the inter-relationships among these alternative definitions.
2. To investigate the intra- and inter -relationships within and among the alternative feed efficiency metrics across different stages of lactation and across different parities.
3. To estimate genetic parameters across lactation for measures of energy balance, performance traits, and a range of alternative feed efficiency variables, as well as to quantify the genetic correlations between them.
4. To quantify the genetic correlations between reproductive performance and a range of alternative feed efficiency variables.
5. To quantify the impact of the Irish national dairy cow breeding objective, the Economic Breeding Index (EBI), on genetic change in residual energy intake (REI). The rate of genetic gain in the EBI traits by including REI as a goal trait in the EBI was also investigated.

Importance of dairy cow feed efficiency and gaps in knowledge

International interest in feed efficiency is intensifying due to a greater global demand for animal-derived protein and energy sources. Feed efficiency is a trait of economic importance, yet is overlooked in almost all national dairy cow breeding goals. This is due primarily to a lack of accurate data on individual commercial animals, but also a lack of clarity on the most appropriate definition of the feed intake and utilization complex. Shalloo et al. (2004) reported that feed accounts for approximately 80% of total variable costs in dairy production systems. Improving feed efficiency contributes to a greater percentage of total dry matter intake (DMI) being used for production (i.e., milk, meat). Ferrell and Jenkins (1985) reported that 65-75% of the total dietary energy cost in beef production systems is used for maintenance, while a 5% improvement in feed efficiency could lead to an economic impact four times greater than a 5% increase in average daily gain (Basarab et al., 2002). In dairy, it has been shown that over her lifetime, an elite dairy cow can partition three times more feed energy towards milk than towards maintenance (VandeHaar and St-Pierre, 2006). It is anticipated that genetic selection to improve feed efficiency in lactating dairy cows can result in significant gains in profit.

Although interest in the genetics of feed efficiency is increasing, there are still considerable gaps in knowledge within the scientific literature that need to be addressed. Moreover, genetic parameters are population specific, and therefore need to be estimated within the sample population of which they will be used. No estimates of genetic parameters are currently available for feed efficiency in Irish dairy cows. Irrespective of the definition, estimates of feed efficiency in dairy cows must account for different functions involved in energy usage and supply over the entire lactation, for example, lipid and protein body mass changes (Berry et al., 2006). All currently proposed measures of feed efficiency in lactating dairy cows are fundamentally flawed; for example, feed conversion efficiency and feed conversion ratio do not fully account for body tissue mobilization patterns to energy contribution. Moreover, the proposed measure of residual feed intake (RFI) in dairy cows does not equate to production efficiency as clearly demonstrated by Berry and Crowley (2013).

The existence of genetic variation in definitions of feed efficiency, as well as the extent of intra- and inter-trait genetic correlations, needs to be quantified prior to consideration in genetic evaluations and subsequent inclusion in breeding objectives. The possibility of altering the trajectories of the efficiency traits to suit a particular breeding objective should also be elucidated. Furthermore, precise estimates of the genetic correlations between feed efficiency with health and reproductive performance (and others) are non-existent in seasonal calving, grazing, lactating dairy cows. Also, the necessary information on which to guide a cost-benefit analysis of research in feed intake and efficiency is lacking.

Alternative definitions of feed efficiency

Feed efficiency can be defined using ratio or residual type traits; the latter are defined based on the residuals from regression-type statistical models, the most common of which is residual energy intake (REI) defined as the difference between actual and predicted intake. In lactating dairy cows, predicted intake is typically derived from least squares regression models. Predicted intake can also be estimated from table values such as those from the National Research Council (NRC, 2001); however, in beef cattle, this approach has produced RFI values that are phenotypically correlated with BW and average daily gain (Arthur et al., 2001). Nonetheless, animals with a negative REI have the ability to use less dietary energy relative to their contemporaries for body maintenance while also achieving an equivalent level of performance.

In Chapter 3, a range of alternative efficiency traits were developed with the aim of identifying the most optimal measure of efficiency for genetic selection in lactating dairy cows. Ratio traits were used as they are still the gold standard method of defining feed efficiency in the non-genetic world (and also still in many species for breeding purposes); however, there are various statistical complications to consider with ratio traits, particularly in assessing their correlations with traits that form important components of the numerator or denominator (Sutherland, 1965, Iwaisaki and Wilton, 1993). One of the main objectives of chapter 3 was to show their shortcomings, for example, good ECE in early lactation may be due to body tissue mobilisation which could translate to poor ECE in late lactation. Residual traits were used as they may be more applicable in a breeding program and are those that have gained most interest. Energy values of pasture and concentrate were based on the French Net Energy system where 1 unité fourragère du lait (UFL) is the net energy requirements for lactation equivalent of 1 kg standard air-dry barley (Jarrige et al., 1986). All energy values and energy sinks were also based on the French Net Energy system. The French Net Energy system was used as it is the energy system used in Ireland.

The definition of REI in the thesis was modified compared to that traditionally used (e.g., Coleman et al., 2010; Pryce et al., 2014b) to include an interaction between metabolic body weight ($BW^{0.75}$) and body condition score (BCS); this was to account for the greater lipid mass of a larger animal (Savietto et al., 2014). Net energy for lactation (NEL) was used in the definition of REI for comparative purposes across the different measures of efficiency (which was the goal of Chapter 3). This however does not guarantee independence from the component traits of NEL. This was reflected in the phenotypic correlations between REI and milk, fat, and protein yield, although, these correlations were close to zero. Consequently, milk, fat and protein yield should be included individually in the REI model to guarantee total independence of fat, and protein yield from REI. A strength of Chapter 3 is that the definition of REI is more comprehensive than most RFI models. To verify this, the REI definition was compared to a more simplistic RFI definition from Coleman et al. (2010) (i.e., RFI = DMI minus year, fat, protein and lactose yield, $BW^{0.75}$, ΔBW and BCS). The correlation between the traditional RFI definition of Coleman et al. (2010) and the alternative REI definition was less than unity (0.72). Consequently, the alternative definition of REI in the present study should be considered for future studies on RFI, as the definition better accounts for lipid mass (change). Nonetheless, the definition of REI, on average, penalise a smaller animal (i.e., reduced BW) compared to a larger animal. This is because the energy required to maintain the extra BW is used to derive the predicted NEI of the animal which, when subtracted from actual NEI, gives REI. Therefore, an alternative definition of REI, REI_{maint}, was defined where the energy demand of BW (i.e., $BW^{0.75}$ times the regression coefficient on $BW^{0.75}$) and lipid mass (i.e., $BW^{0.75}$ x BCS) was added back into REI. Table 8.1 illustrates the benefit of REI_{maint} using two cows from the database used in this thesis; both cows had identical REI (-3.07 UFL/d) and NEL (4.08 UFL/d) values, but had different BW (480 kg v 610 kg). The lighter cow consumed less (average of 9.01 UFL/d) and had a greater ECE value (0.45); in contrast, the heavier cow consumed more (average of 13.67 UFL/d) and had a lesser ECE value (0.29). Thus, the REI_{maint} trait considers the greater energy costs associated with a heavier cow although this is of little consequence for breeding programs if BW is also included in the breeding goal.

Table 8.1. The benefit of $\mathrm{REI}_{\mathrm{maint}}$ using two cows from the Moorepark feed intake database.

	Cow A	Cow B
Net energy intake (UFL/d)	9.01	13.67
Net energy for lactation (UFL/d)	4.08	4.08
Body-weight (kg)	480	610
Energy conversion efficiency (UFL/d)	0.45	0.29
Residual energy intake (UFL/d)	-3.07	-3.07
Residual energy intake taking account of maintenance (UFL/d)	15.85	20.86

In Chapter 3, moderate to strong phenotypic correlations existed between energy conversion efficiency (ECE) and the production traits (e.g., NEL, BCS) illustrating that ECE is strongly influenced by these traits and this agrees with reports elsewhere (Zamani, 2017).Therefore, ECE in Chapter 3 was modified where the contribution of body tissue mobilization to energetic efficiency was accounted for in energy conversion efficiency adjusted ($\mathrm{ECE}_{\mathrm{adj}}$) and energy conversion efficiency for maintenance ($\mathrm{ECE}_{\mathrm{maint}}$). Nonetheless, the $\mathrm{ECE}_{\mathrm{adj}}$ trait was not completely effective in achieving the desired outcome as greater $\mathrm{ECE}_{\mathrm{adj}}$ was still associated with loss in BW and body condition, although the correlations between $\mathrm{ECE}_{\mathrm{adj}}$ and BCS had weakened. The correlations with BCS and BW change were further weakened with the $\mathrm{ECE}_{\mathrm{maint}}$ trait, but the correlations remained negative, implying that both BCS and BW loss were still contributing to variability in $\mathrm{ECE}_{\mathrm{maint}}$.

Phenotypic correlations within and among traits across life stages

In Chapter 4, the phenotypic inter- and intra-relationships within and among alternative feed efficiency metrics across different stages of lactation and parities were investigated. The main objective of Chapter 4 related to understanding the dynamics of the phenotypic correlations among traits across time, as well as the factors phenotypically associated with these traits. Most studies investigating REI and other measures of efficiency in dairy cows assume that feed efficiency is phenotypically the same trait across lactation (Parke et al., 1999; Zamani et al., 2008; Manafiazar et al., 2015). However, results indicated that weak phenotypic correlations existed within almost all efficiency traits, both across parities and across lactation stages suggesting that the efficiency traits need to be recorded across an entire lactation in order to monitor feed efficiency at an individual cow level. The observed weak phenotypic correlations within each feed efficiency trait across time were in direct contrast to the generally strong within-trait phenotypic correlations for the production traits evaluated. These observed weaker phenotypic correlations for the composite efficiency traits could be due to the underlying physiological changes the cow is undergoing throughout lactation (e.g., underlying milk compositional changes), and its effect on the partitioning of NEI into the different components at these lactation stages. Phenotypic correlations among the different traits investigated across the productive life generally varied more by stage of lactation than by parity; this suggests the physiological mechanisms controlling feed efficiency across lactation stages are much greater than those across parities.

Variance components

One of the key questions in this thesis was if exploitable genetic variation exists for feed efficiency and results of this thesis clearly confirmed this is true in the sample population studied. In Chapter 4, sufficient genetic variability existed for the different efficiency traits as evidenced by the coefficient of genetic variation which was somewhat similar to the coefficient of genetic variation which existed for NEL (i.e., 6.74%). Therefore, genetic progress in efficiency is achievable given this genetic variability as is evident by the genetic gains achieved in milk production with a similar coefficient of genetic variation (Berry, 2008). In Chapter 5, the genetic variation for all feed efficiency metrics when estimated using random regression models were similar to reports elsewhere in lactating and growing cattle (Berry and Crowley, 2013; Tempelman et al., 2015). The genetic standard deviation for REI across lactation varied from 0.64 UFL/d (34 DIM) to 0.87 UFL/d (280 DIM). The genetic variance for REI was consistent with the findings of Tempelman et al. (2015) and Li et al. (2017). The increase in the genetic variance of the different efficiency traits evaluated on both peripheries of the lactation is likely due to the mathematical properties of a polynomial as relatively more weight is placed on observations at extremities of the parameter space (Meyer, 1998) and this is consistent with what is observed in other studies that used random regression models for a range of performance traits (Berry et al., 2003; Bohmanova et al., 2008).

Heritability estimates for the majority of the efficiency traits in Chapters 4 and 5 concur with estimates from most other international studies from cows offered TMR diets in confinement systems (Berry and Crowley, 2013; Tempelman et al., 2015). For example, the heritability of REI estimated in Chapter 6 varied from 0.04 (34 DIM) to 0.11 (280 DIM) and was generally the lowest of all the feed efficiency traits considered implying that more observations would be required to achieve a high accuracy of selection (Pryce et al., 2012; Lin et al., 2013). Estimated heritability of NEI in this thesis was greatest in mid lactation (0.28 at 151 DIM) agreeing with other studies based on lactating Holstein cows (Spurlock et al., 2012).

Heritability reflects how much of the phenotypic variation is due to genetics. However, heritability does not reflect the possible contribution of breeding to changes in performance. As an illustration, the heritability of reproductive performance in dairy cows is generally < 0.05 (Berry et al., 2014b); despite this Berry et al. (2014b) stated that breeding contributed 63% of the decline in reproductive performance in Irish Holstein-Friesian dairy cows. The contribution of genetics to the now observed improvements in phenotypic performance for reproductive performance in dairy cow populations globally is well recognized. For example, in the Irish total merit index, (Economic Breeding Index: EBI) the largest relative emphasis is placed on reproductive performance (i.e., 35%). Heritability is a poor statistic as it is a ratio; therefore, the ratio of two large numbers (e.g., 1000:10,000) can be the same as two small numbers (e.g., 1:10) and hence no inference can be made on the extent of the variation. Furthermore, there is no mention of heritability in the Rendel and Robertson (1950) genetic gain equation. Heritability does however contribute to the accuracy of selection but it becomes irrelevant when large progeny group sizes exist and the accuracy of selection is near 100%. Therefore, although some of the feed efficiency traits are lowly heritable, considerable genetic gain can still be achieved.

Genetic correlations within and among traits across lactation

In Chapter 5, the genetic inter-relationships were estimated among the alternative definitions of feed energy efficiency using random regression models. The genetic correlations among the various efficiency traits were almost all less than unity which agrees with the phenotypic analysis in Chapter 3. This suggests that the efficiency traits investigated are all measuring distinctly different components of efficiency. Additionally, the strength of the genetic correlations within each efficiency trait at different DIM sometimes deviated from unity suggesting the same efficiency traits could be governed by different genetic mechanisms throughout lactation. In general, the weakest genetic correlation among records for the same trait were rarely less than 0.80 for REI, KR, and FtW; therefore, these traits could be considered the same trait during the lactation with minimal repercussions (Robertson, 1959).

Strong phenotypic correlations existed between REI and energy balance (EB) in Chapter 3, and the strong positive genetic correlation between REI and EB in Chapter 5 indicates selection on lower REI (i.e., deemed efficient cows) would favour cows with a lower energy status; this correlation was strongest in mid-lactation when BW change was least. Although unfavourable genetic correlations have been reported between greater negative EB and both reproductive performance (Beam and Butler, 1998) and health (Collard et al., 2000), selection for REI within a balanced breeding goal could be used to overcome such antagonisms (Berry and Crowley, 2013). Nonetheless, genetic correlations with the feed intake and utilization complex with both reproduction and health traits need to be estimated prior to possible consideration in any breeding program.

Therefore, the objective of Chapter 6 was to quantify the genetic inter-relationships between alternative efficiency metrics and reproductive traits. Given the strong phenotypic and genetic correlations that existed between REI and EB in Chapters 3, 4, and 5, it was hypothesized that REI would be unfavourably genetically correlated with reproductive performance, especially when REI was measured in early lactation. The genetic correlations between REI and reproductive performance documented in Chapter 6, however, were either favourable or neutral, thus refuting the hypothesis. The somewhat unexpected associations between REI and reproductive performance are supported by Macdonald et al. (2016) and Coleman et al. (2010). Nonetheless, all estimated genetic correlations in Chapter 6 were associated with large standard errors. This was predominantly due to a combination of the low heritability of some of the efficiency and reproductive traits and the relatively small sample population size. These results need to be validated with another independent dataset, but measurements of DMI in grazing dairy cattle are not commonly available.

Selection for feed efficiency

Genetic gain in any given trait is estimated as (Rendel and Robertson, 1950):

$$\Delta G = \frac{i \cdot r \cdot \sigma_g}{L}$$

where ΔG is annual genetic progress, i is the intensity of selection, r is the accuracy of selection, σ_g is the genetic standard deviation, while L is the generation interval. The accuracy of selection increases with the heritability of the trait for an equal number of progeny; the accuracy of selection also increases with the number of progeny records available for the same heritability. Therefore, genetic gain for low heritability traits such as (some of) the efficiency traits is possible as long as there is genetic variation (Berry et al., 2011) and sufficient numbers of animals are measured. Figure 8.1 illustrates the relationship between the accuracy of selection as the number of progeny with phenotypic information increases. For the same number of progeny, a higher heritability will increase the accuracy of selection (Figure 8.1).

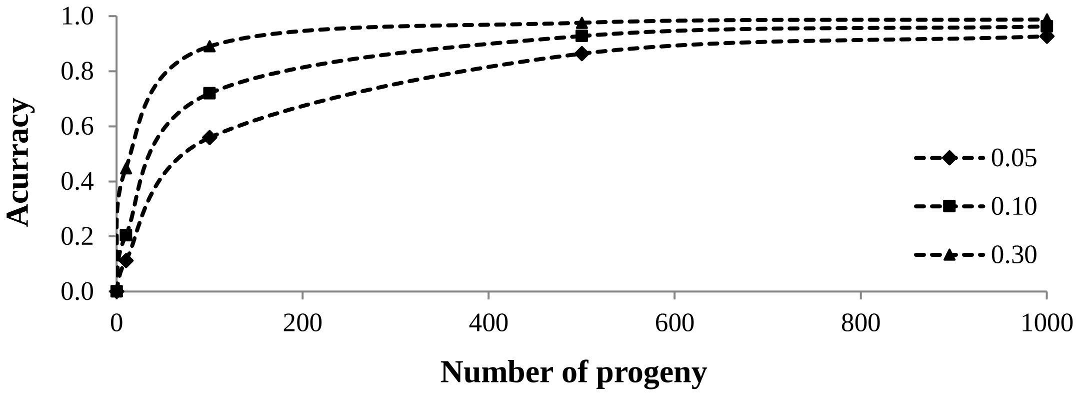

Figure 8.1. Simulated accuracy of selection for traits with varying heritability (typical of the efficiency traits in this thesis) across different number of progeny groups.

One way to accelerate genetic gain is by reducing the generation interval (i.e., the average age of the parents when their progeny is born). Berry et al. (2014a) using data collated from several populations in 9 countries reported a moderately strong genetic correlation (0.67 ± 0.24) between growing nulliparous heifers and lactating cows for DMI at 70 d post-calving. In support, Nieuwhof et al. (1992) reported a strong genetic correlation for DMI (0.74) between growing nulliparous heifers and first-lactation cows in early to mid-lactation. These moderate to strong genetic correlations suggest heifer DMI may be a useful predictor of genetic merit for DMI in lactating cows. Using feed intake from heifers as a predictor of feed intake of lactating cows could be a viable strategy for including feed intake in the breeding goal. Moreover, recording feed intake in heifers is likely to cause less disruption than in lactating dairy cows.

In Chapter 4, the impact on phenotypic performance of genetically selecting animals to be divergent for feed intake and efficiency based on parental average estimated breeding value was undertaken. The phenotypic performance of cows genetically predisposed to have lower REI (i.e., more efficient) consumed less NEI

(0.59 UFL/d) but were also in much greater negative EB, particularly in early lactation, relative to their genetically less efficient contemporaries. Cows ranked divergent on REI were also more efficient with higher ECE compared to their less efficient counterparts. These results illustrate that phenotypic differences in feed intake and efficiency can be achieved through genetic selection.

The objective of Chapter 7 aimed to quantify the impact of the EBI on genetic change in REI; the rate of genetic gain in the EBI traits by including REI as a goal trait in the EBI with either the true economic weight of the trait or sufficient emphasis to achieve restricted gains were also investigated. All responses to selection were estimated per generation. Selection based on the status quo for the EBI using the economic weights in March 2017 and 99% accuracy of genetic evaluations for all 19 traits (base scenario) is predicted to increase yields of protein and fat, but will also increase REI (+0.01 UFL/generation). However, when the true economic weight for REI is used, but no actual phenotypic data for REI is available, the predicted genetic response for REI improved (-0.05 UFL/generation). These results suggest that selection on the EBI which includes REI with an economic weight of €0.078/UFL will generate animals with lower REI.

When the true economic weight for REI is used in the EBI, but with no direct observations for REI yet 100 daughters per sire for all remaining traits, the predicted genetic responses for REI and NEI were -0.02 UFL/generation, and -0.24 UFL/generation, respectively. When the true economic weight for REI is used in the EBI and 100 daughters per sire for all remaining traits the predicted genetic responses for REI and NEI were -0.04 UFL/generation, and -0.26 UFL/generation, respectively. Therefore, the additional benefit of recording and extra 100 progeny records per sire was a reduction in NEI of -0.004 UFL/year. The cost of estimating herbage intake using n-alkanes (Mayes et al., 1986) is approximately €78/cow. In Chapter 5, one of the recommendations was that NEI should to be recorded across an entire lactation as some of the efficiency traits were genetically different throughout lactation; therefore, assuming 50 sires were progeny tested per year, each with 100 daughter records for NEI (tested three times per lactation) then the total cost to estimate NEI for these daughters is projected at almost €1.2 million.

Limitations of the thesis

Although this thesis attempted to quantify the phenotypic and genetic (co)variances between the feed intake complex, performance, and fertility traits, lacking from the analyses were the genetic association between the feed intake complex and other important traits, not measured routinely such as animal health and welfare, as well as, greenhouse gas emissions (e.g., CH_4). In lactating dairy cows, current research suggests that RFI is strongly genetically correlated with methane emissions (de Haas et al., 2011). This suggests that selection for lower RFI (i.e., more efficient) has the potential to reduce greenhouse gas emissions, as animals with lower RFI are expected to consume less DMI at the same level of production (Williams et al., 2011; Waghorn et al., 2012; Connor et al., 2013).

The size of the feed intake database used for the studies described in this thesis was small. However, no dataset exists globally to estimate genetic parameters accurately for feed intake where feed intake must be estimated using the data representing the population where it will be exploited. More feed intake observations would however result in more accurate estimates of the genetic parameters for feed intake; a larger dataset would also reduce the standard errors associated with genetic correlations, especially those associated with low heritability traits. The reported genetic correlations in this thesis are, nevertheless, the best estimates available as it is resource-intensive to generate sufficient sample population sizes for feed intake data to achieve precise genetic correlation estimates.

Future research work

While the genetic parameters estimated in this thesis for the efficiency traits were estimated from a larger dataset in comparison to many other published studies, the size of the dataset is still relatively small for the accurate estimation of genetic parameters. The main obstacle to the inclusion of the feed intake complex into the breeding objective is the lack of accurate feed intake phenotypes from a large population of daughters from individual bulls. To overcome the lack of feed intake phenotypes three strategies are possible:

1) pool international datasets
2) exploitation of genomic data
3) proxy measures of efficiency

When combining international datasets of phenotypes and genotypes, genotype-by-environment (e.g., age and diet) interactions need to be considered. In beef, Durunna et al. (2011) reported significant re-ranking of steers for feed efficiency across diets differing in composition. In dairy cattle, when international datasets of DMI phenotypes were collated, Berry et al. (2014a) reported weak to moderate genetic correlations between DMI recorded in different groups of countries. For example, a moderate genetic correlation (0.57) existed between grazing populations in Ireland and Australia with low-input feeding in the United Kingdom; however, a much weaker genetic correlation (0.14) existed between grazing populations in Ireland and Australia with confinement production systems in North America. These genetic correlations suggest genotype-by-environment interactions might exist for DMI in divergent production systems.

The standard errors of the estimated genetic correlations between the efficiency traits and reproductive performance in the present thesis were large. The accuracy of genetic parameters estimates could be improved by exploiting genomic information on individual animals. Forni et al. (2011) reported a slight reduction in the standard errors of heritability estimates by replacing the numerator relationship matrix with a genomic relationship matrix generated from genome wide markers. This approach could also reduce the standard errors of genetic correlations (Falconer and MacKay, 1996). The cost of genotyping is relatively small when compared to the cost of phenotyping for feed intake. Nonetheless, biological material is not available on the majority of the animals in the present study or indeed, internationally.

As novel traits (e.g., feed efficiency) are expensive to record, using nucleus research herds for phenotyping in combination with genomic information offers another source of targeted feed intake data. A sub-population of animals with phenotypes and genotypes can be used to establish a reference population from which a genomic prediction equation for feed efficiency could be generated (Berry et al., 2014b; Pryce et al., 2014a); this prediction equation can then be applied to the rest of the population. The cost of phenotyping for feed intake is approximately AU$1000/cow/year (Gonzalez-Recio et al., 2014) from which DNA profiles could be generated; this cost could be justified by the economic benefits offered to all producers if feed efficiency is used in selection decisions. The cost-benefit of phenotyping must however be appropriately quantified taking into account other alternative, lower-cost predictors. For example, milk mid-infrared spectroscopy could be a useful tool to accurately predict feed intake (McParland et al., 2011), and feed efficiency (McParland et al., 2014) at a much lower cost.

Although this thesis attempted to quantify the phenotypic and genetic (co)variances between the feed intake complex, performance, and fertility traits, lacking from the analysis was the genetic association between the feed intake complex and animal health. Not quantifying such associations prior to any recommendation could be damaging, and therefore such associations must be quantified. In Ireland, 3% of the EBI is directly targeted at improving health traits; these traits aim to reduce lameness, somatic cell count and mastitis.

The neutral or favourable genetic correlations between the efficiency traits and reproductive performance should be (in)validated from a larger independent dataset. Large datasets are necessary to obtain accurate estimates of genetic parameters, especially for lowly heritable traits (i.e., health and reproductive performance).

General conclusion

Prior to the inclusion of a trait (e.g., feed efficiency) in the breeding goal the trait must fulfil three criteria: 1) it must be important, either economically, socially, or environmentally, 2) must be measurable or genetically correlated with an easily measureable trait and, 3) it must exhibit genetic variation. Analysis from this thesis indicates that all efficiency traits, including REI possess all these criteria necessary to implement into the selection objectives in Ireland. However, the actual national monetary benefit of including feed efficiency (through REI) in the Irish total merit index was small.

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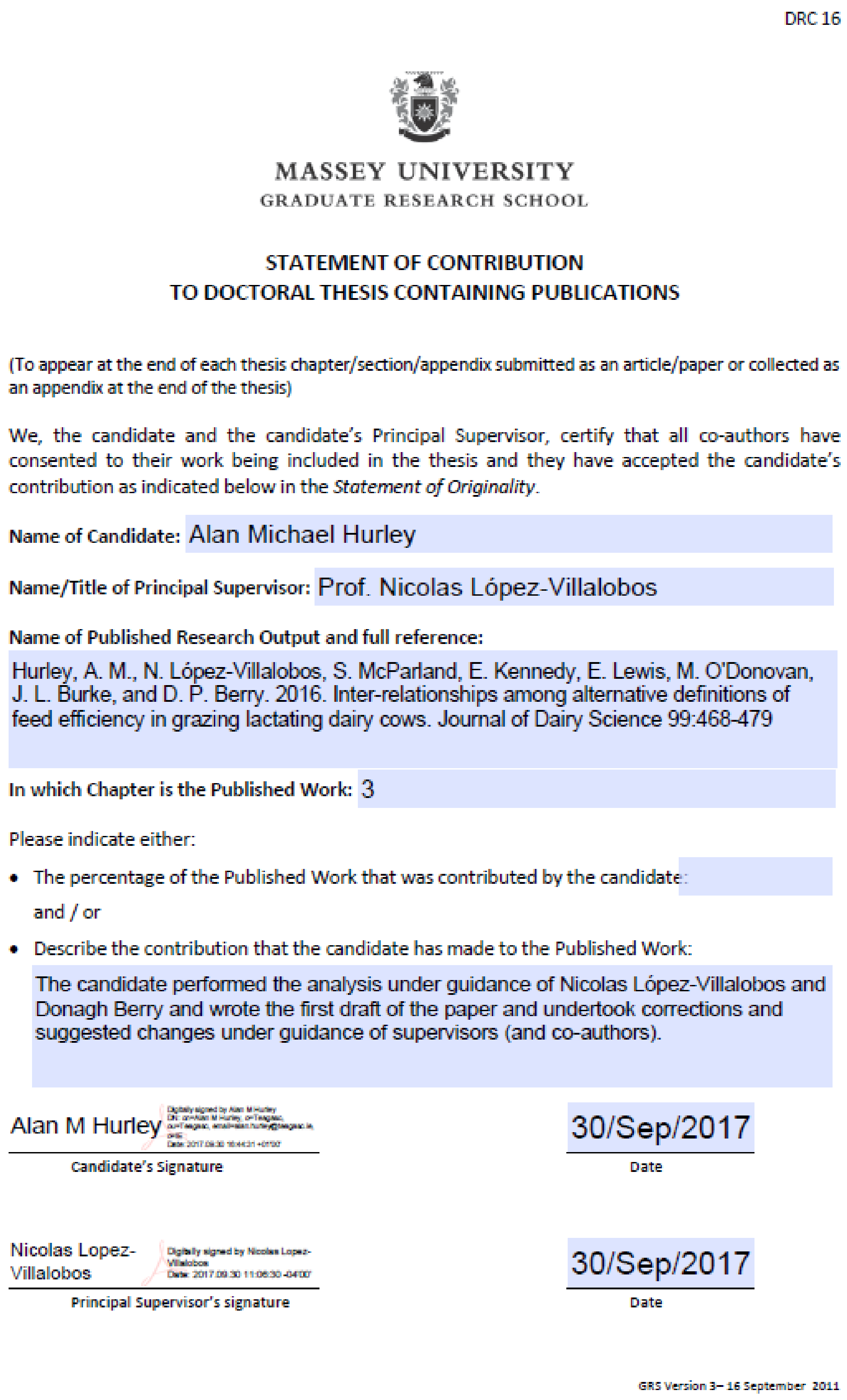
Appendix One

Statements of contribution to doctoral thesis containing publications for chapters 3-6.



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STATEMENT OF CONTRIBUTION
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(To appear at the end of each thesis chapter/section/appendix submitted as an article/paper or collected as an appendix at the end of the thesis)

We, the candidate and the candidate's Principal Supervisor, certify that all co-authors have consented to their work being included in the thesis and they have accepted the candidate's contribution as indicated below in the *Statement of Originality*.

Name of Candidate: Alan Michael Hurley

Name/Title of Principal Supervisor: Prof. Nicolas López-Villalobos

Name of Published Research Output and full reference:

Hurley, A. M., N. López-Villalobos, S. McParland, E. Kennedy, E. Lewis, M. O'Donovan, J. L. Burke, and D. P. Berry. 2016. Inter-relationships among alternative definitions of feed efficiency in grazing lactating dairy cows. Journal of Dairy Science 99:468-479

In which Chapter is the Published Work: 3

Please indicate either:

- The percentage of the Published Work that was contributed by the candidate:

  and / or

- Describe the contribution that the candidate has made to the Published Work:

  The candidate performed the analysis under guidance of Nicolas López-Villalobos and Donagh Berry and wrote the first draft of the paper and undertook corrections and suggested changes under guidance of supervisors (and co-authors).

Alan M Hurley
Digitally signed by Alan M Hurley
DN: cn=Alan M Hurley, o=Teagasc, ou=Teagasc, email=alan.hurley@teagasc.ie, c=IE
Date: 2017.09.30 16:44:31 +01'00'

Candidate's Signature

30/Sep/2017

Date

Nicolas Lopez-Villalobos
Digitally signed by Nicolas Lopez-Villalobos
Date: 2017.09.30 11:06:30 -04'00'

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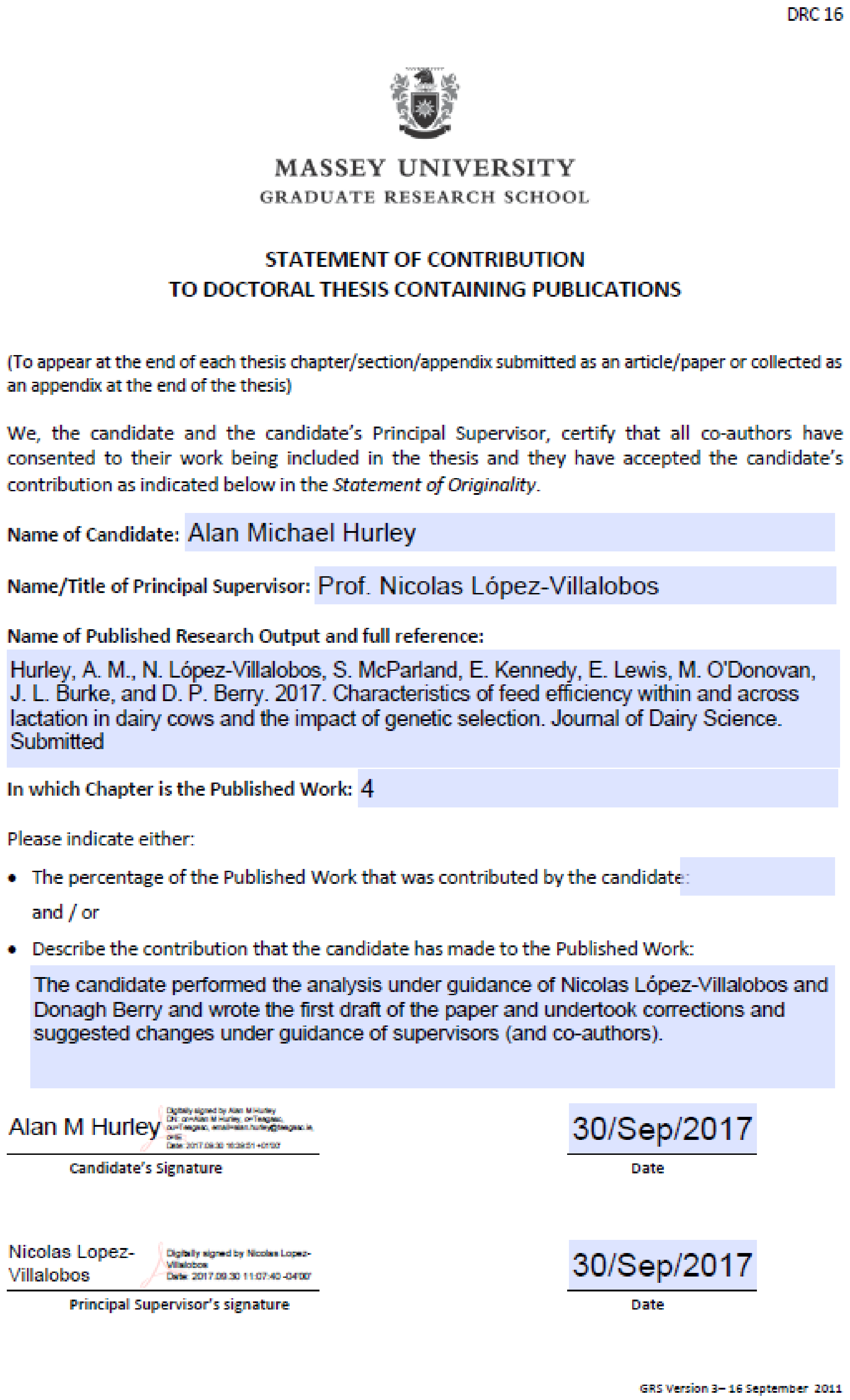

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Candidate's Signature

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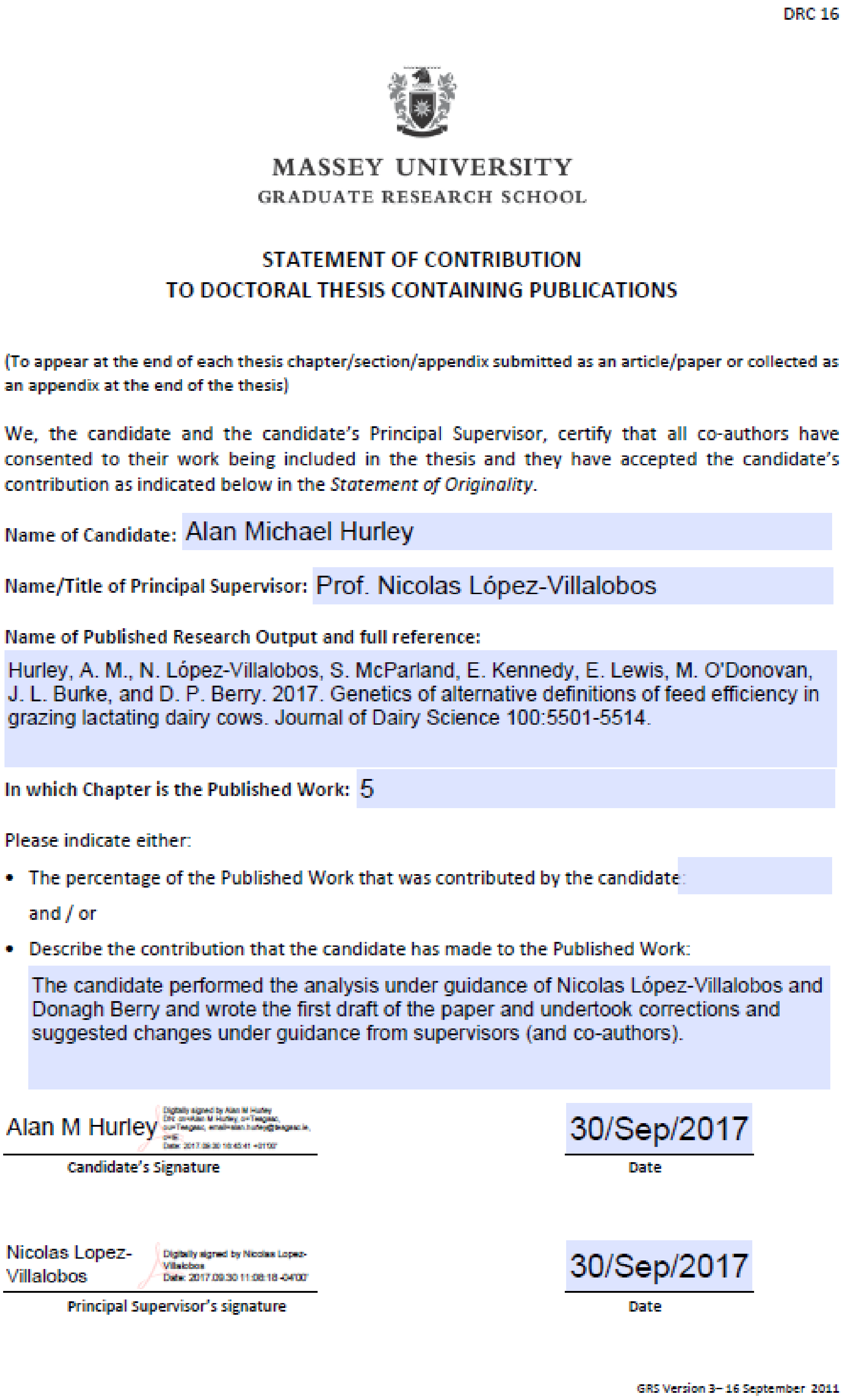

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Alan M Hurley Digitally signed by Alan M Hurley
DN: cn=Alan M Hurley, o=Teagasc, ou=Teagasc, email=alan.hurley@teagasc.ie, c=IE
Date: 2017.09.30 16:45:41 +01'00'
Candidate's Signature

30/Sep/2017
Date

Nicolas Lopez-Villalobos Digitally signed by Nicolas Lopez-Villalobos
Date: 2017.09.30 11:08:18 -04'00'
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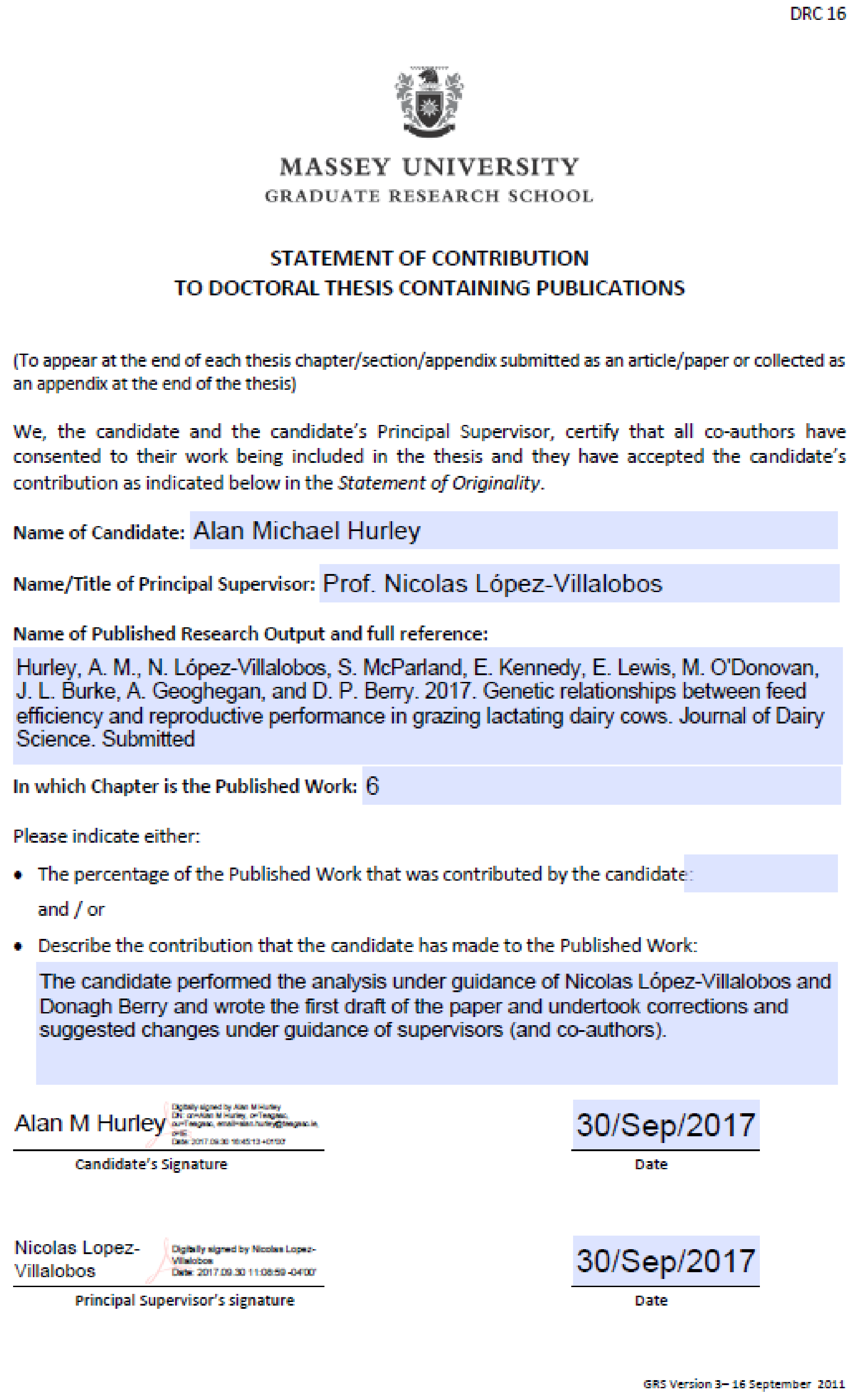

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In which Chapter is the Published Work: 6

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Principal Supervisor's signature

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