Genetic Prediction of Feed Efficiency in South African Holstein Cattle

By

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in Genetics

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Preface

The research work contained in this thesis was carried out by **Matome Andrias Madilindi**, while based at the Agricultural Research Council, Animal Production, Animal Breeding and Genetics, Irene and the Discipline of Genetics, School of Life Sciences, College of Agriculture, Engineering and Science, University of KwaZulu-Natal, Westville Campus, Durban, South Africa. This doctoral work received financial support from the University of KwaZulu-Natal, National Research Foundation, Agricultural Research Council of South Africa and International Atomic Energy Agency of the United Nations.

The contents of this research have not been submitted in any form to another university for any other degree. Except where the work of others is acknowledged in the text and references, the results reported are due to investigations by the candidate.

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Declaration 2: Publications, Presentations and Accolades

Candidate's role in each publication produced and presentation is bolded and/or explained.

Chapter 2

1. **Madilindi, M.A.**, Banga, C.B., Zishiri, O.T., 2019. Genetic selection for feed efficiency in dairy cattle using Fourier transform infrared spectroscopy of milk: A review. A poster presented during the 9th University of KwaZulu-Natal (UKZN) Postgraduate Research and Innovation Symposium, held on 17 October 2019, Durban, South Africa. Presented by Madilindi M.A.

2. **Madilindi, M.A.**, Zishiri, O.T., Dube, B., Banga, C.B., 2022. Technological advances in genetic improvement of feed efficiency in dairy cattle: A review. Livest. Sci. 258, 104871, 1-11. https://doi.org/10.1016/j.livsci.2022.104871

3. **Madilindi, M.A.**, Banga, C.B., Zishiri, O.T., 2023. Research makes headway towards genetic improvement of feed efficiency. The Dairy Mail, 30, 1, 77-78.

Chapter 3

4. **Madilindi, M.A.**, Banga, C.B., Zishiri, O.T., 2021. Prediction of dry matter intake and gross feed efficiency using milk production and live weight in first-parity Holstein cows. A poster presented during the 52nd South African Animal Science (SASAS) congress, held on the 10-12 August 2021 (Online), South Africa. Presented by Madilindi M.A. This poster was awarded first best prize in the Animal Breeding and Genetics category. The prize was sponsored by the Livestock Improvement Trust of South Africa, and included a floating trophy.

5. **Madilindi, M.A.**, Banga, C.B., Zishiri, O.T., 2022. Prediction of dry matter intake and gross feed efficiency using milk production and live weight in first-parity Holstein cows. Trop. Anim. Health Prod. 54, 278, 1-10. https://doi.org/10.1007/s11250-022-03275-8

Chapter 5

6. **Madilindi, M.A.**, Zishiri, O.T., Dube, B., Banga, C.B., 2021. Genetic parameters across lactation for predicted gross feed efficiency in primiparous South African Holstein cows. A flash presentation presented during the 11th UKZN Postgraduate Research and Innovation Symposium, held on 09-10 December 2021 (Online), South Africa. Presented by Madilindi M.A. This flash presentation was awarded second prize in the School of Life Sciences, sponsored by Apex Scientific.

7. **Madilindi, M.A.**, Zishiri, O.T, Dube, B., Banga, C.B., 2022. Genetic analysis of predicted gross feed efficiency in first-parity South African Holstein cows. Oral presentation by Madilindi M.A. at the 53rd South African Society of Animal Sciences Congress, held on 26-28 September 2022, Pietermaritzburg, South Africa.

8. **Madilindi, M.A.**, Zishiri, O.T, Dube, B., Banga, C.B., 2022. Genetic relationships among predicted feed efficiency traits across lactation in multiparous South African Holstein cows. Oral presentation made at the 12th UKZN Postgraduate Research and Innovation Symposium, held on 08-09 December 2022 (Online). Presented by Madilindi M.A.

9. **Madilindi, M.A.**, Zishiri, O.T, Dube, B., Banga, C.B., 2023. Genetic parameters for predicted gross feed efficiency and its association with energy-corrected milk in South African Holstein cattle. A full research article accepted in Trop. Anim. Health Prod. (Manuscript Number: TROP-D-23-00095R2).

10. **Madilindi, M.A.**, Zishiri, O.T, Dube, B., Banga, C.B., 2023. Genetic analysis for predicted gross feed efficiency and its correlation with energy-corrected milk in South African Holstein cattle. Accepted for an oral presentation at the 8th All Africa Conference on Animal Agriculture, to be held on 26-29 September 2023, Gaborone, Botswana. To be presented by Madilindi M.A.

Chapter 6

11. **Madilindi, M.A.**, Zishiri, O.T., Dube, B., Banga, C.B., 2022. Genetic analysis of predicted dry matter intake and gross feed efficiency in South African Holstein cows. Pages 300-303. In: R.F. Veerkamp and Y. de Haas (eds), Proceedings of the 12th World Congress on Genetics Applied to Livestock Production. Technical and species orientated innovations in animal breeding, and contribution of genetics to solving societal challenges. Wageningen Academic Publishers. https://doi.org/10.3920/978-90-8686-940-4_63

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Asante Sana!!

Dedication

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"Education is the most powerful weapon which you can use to change the world."

- Nelson Rolihlahla Mandela -

Pfunzo ndi ifa, li sa sini.

U guda, a hu gumi.

Mu funa pfunzo, ndi mu funa ndivho.

Ndaa!

Extended Abstract

Feed efficiency is a trait of outstanding importance in dairy cattle; however, it is difficult and expensive to measure and, therefore, not easy to improve through selection. The current study investigated the possibility of predicting the genetic merit for feed efficiency, in South African Holstein cattle, using routinely recorded easy-to-measure traits. The first two objectives were mainly to develop and validate models to predict dry matter intake (DMI) and gross feed efficiency (GFE) using milk production traits and live weight (LW). Data consisted of 30 daily measurements of DMI, milk yield (MY), energy-corrected milk (ECM), butterfat yield (BFY), protein yield (PROY), lactose yield (LACY), butterfat percent (BFP), protein percent (PROP), lactose percent (LACP), and 25 daily LW records of a group of 100 first-parity Holstein cows, fed a total mixed ration. Similar measurements were also collected from a group of 110 multiparous Holstein cows, in lactations 2 to 6. Gross feed efficiency was calculated as kg ECM divided by kg DMI. Forward stepwise regression analyses were performed to develop the models, using the PROC REG procedure of the Statistical Analysis System (SAS) software. Within-herd validation of the models for robustness and accuracy, was subsequently conducted by performing regression analyses between actual and predicted DMI and GFE records. The developed models reliably predicted daily DMI (kg/day) and GFE from milk, butterfat yield and/or live weight, with accuracies ranging from 66 to 98%. Validation of the best model to predict DMI, for first-parity cows, yielded a fairly moderate R^2 value (0.49) and a low root mean square error (RMSE) (1.46 kg/day), while the best prediction model for GFE yielded a fairly high R^2 value (0.64) and a low RMSE (0.13). The best prediction model for GFE, for multiparous cows, had a fairly moderate R^2 value (0.54) and a low RMSE (0.06), upon validation, suggesting reasonable robustness and accuracy. The developed models, therefore, present an opportunity to easily generate large quantities of phenotypic data on individual cow DMI and GFE, at a relatively low cost, which can be used to achieve accurate selection for feed efficiency.

The third objective was, essentially, to assess the extent of genetic variability for the predicted traits, in order to evaluate their utility as selection criteria for feed efficiency. First, repeatability animal models were used to estimate genetic parameters for predicted gross feed efficiency (pGFE) and its relationship with energy-corrected milk (ECM) in the first three parities, using the ASReml software. Data of 11,068 test-day milk production records on 1,575 Holstein cows that calved between 2009 and 2019, were used. Predicted gross feed efficiency was calculated

using the models developed in the first two objectives. Heritability estimates for pGFE ranged from 0.09 ± 0.04 in mid lactation to 0.18 ± 0.05 in late lactation. Estimates were moderate for primiparous (0.21 ± 0.05) and low for multiparous (0.10 ± 0.04) cows. Repeatability and heritability estimates across all lactations were 0.37 ± 0.03 and 0.14 ± 0.03, respectively. Genetic correlations between pGFE in different stages of lactation ranged from 0.87 ± 0.24 (early and mid) to 0.97 ± 0.28 (early and late), whereas a strong genetic correlation (0.90 ± 0.03) was obtained between pGFE and ECM, across all lactations. The average genetic merit for pGFE, across all lactations, increased at a marginal rate of 0.0058 per year, for cows born during the period 2007 to 2017. The low to moderate heritability estimates for pGFE suggest potential for genetic improvement of the trait through selection, albeit with a modest accuracy of selection. The high genetic correlation of pGFE with ECM may, however, assist to improve accuracy of selection for feed efficiency by including both traits in multi-trait analyses.

Due to the scarcity of information on the genetic variation exhibited by predicted dry matter intake (pDMI) from milk components, further genetic analyses were undertaken. Such analyses were important to determine whether pDMI could be a useful selection criterion for feed efficiency in dairy cattle. These analyses under the third objective involved estimation of heritabilities, repeatabilities and genetic correlations among predicted dry matter intake and gross feed efficiency, by repeatability animal models. Data consisted of 440,062 test-day records of 62,695 cows, in the first three parities, that calved between 2009 and 2019. Predicted dry matter intake was generated from milk yield data, using the developed prediction model, and pGFE was derived as kg ECM divided by kg pDMI. Heritability estimates ranged from 0.05 ± 0.02 for pGFE in mid lactation to 0.13 ± 0.03 for pDMI in late lactation. Estimates of heritability across parities were 0.08 ± 0.02 and 0.13 ± 0.02 for pGFE and pDMI, respectively. Corresponding estimates of repeatability across parities were 0.26 ± 0.01 and 0.41 ± 0.01 for pGFE and pDMI, respectively. Genetic correlations between pDMI and pGFE were moderate and negative in early (-0.42 ± 0.24) and mid lactation (-0.20 ± 0.24), and low and positive in late lactation (0.05 ± 0.17). The genetic correlation between pDMI and pGFE decreased with increase in parity, from 0.26 ± 0.16 to -0.09 ± 0.17. The low heritability estimates for pDMI and pGFE indicate low accuracy of selection for these traits in South African Holstein cattle. This can, however, be improved through multi-trait analyses including traits with which they are correlated.

Results of the current research pave the way for achieving genetic improvement in feed efficiency in the South African Holstein cattle population. This can go a long way towards the development of a more profitable and environmentally sustainable dairy industry. Higher rates of genetic change can be attained through genomic selection, by using the predicted phenotypes to identify genes or markers associated with feed efficiency.

Keywords: Genetic selection, predicted feed efficiency, predictor traits, prediction models, repeatability animal model, dairy cows

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List of Abbreviations

ARC	Agricultural Research Council
BFP	Butterfat Percent
BFY	Butterfat Yield
CV	Coefficient of Variation
DIM	Days in Milk
DMI	Dry Matter Intake
EB	Energy Balance
EBV	Estimated Breeding Value
ECM	Energy-Corrected Milk
FE	Feed Efficiency
GFE	Gross Feed Efficiency
GHG	Greenhouse Gas
GWAS	Genome-Wide Association Studies
h^2	Heritability
INTERGIS	Integrated Registration and Genetic Information System
LACP	Lactose Percent
LACY	Lactose Yield
LW	Live Weight
MIR	Mid-infrared
MY	Milk Yield
NMRIS	National Milk Recording and Improvement Scheme
pDMI	Predicted Dry Matter Intake
pGFE	Predicted Gross Feed Efficiency
PROC CORR	Procedure for Correlation
PROC REG	Procedure for Regression
PROP	Protein Percent
PROY	Protein Yield
QTLs	Quantitative Trait Loci
r	Pearson's Correlation
r	Repeatability
R^2	Coefficient of Determination
RAM	Repeatability Animal Model

RFI	Residual Feed Intake
r_g	Genetic Correlation
REML	Restricted Maximum Likelihood
RMSE	Root Mean Square Error
r_P	Phenotypic Correlation
RRM	Random Regression Model
SAS	Statistical Analysis System
SD	Standard Deviation
se	Standard Error
SNPs	Single Nucleotide Polymorphisms
TMR	Total Mixed Ration

Chapter 1

General Introduction

1.1 Background

Efficiency of feed utilisation by dairy cattle has become of paramount importance globally, due to the ever-rising cost of feed, coupled with heightened concerns about the contribution of livestock to greenhouse gas (GHG) emissions. Besides being more profitable, cows that are more feed efficient have been found to produce less GHG (Knapp et al., 2014; Connor, 2015; Løvendahl et al., 2018; Manzanilla-Pech et al., 2022). Feed typically constitutes over 60% of milk production costs (European Commission, 2013; Connor, 2015; USDA, 2016; Miglior et al., 2017); thus, it is a major determinant of herd profitability. In South Africa, it has recently been estimated to account for 60 to 70% of the total costs of dairy production (Lacto data, 2019; Madilindi et al., 2023). Greenhouse gas emissions from livestock have become an increasingly topical issue, with dairy cattle being reported to contribute about 50% of the global enteric methane (Gerber et al., 2013; Miglior et al., 2017; FAO and GDP, 2018) and 11% of the total methane emissions from livestock in South Africa (Milk SA, 2019; Madilindi et al., 2022a). The dairy industry is thus under immense pressure to improve the efficiency with which cows convert feed into milk (Miglior et al., 2017; Krattenmacher et al., 2019; Harder et al., 2020; Heida et al., 2021; Madilindi et al., 2022a; Manzanilla-Pech et al., 2022).

Genetic improvement of feed efficiency is appealing, as it is sustainable and cost effective; hence significant efforts have been made in recent years to breed cows that utilise feed more efficiently (Madilindi et al., 2022a). Feed efficiency in dairy cows has been documented in many studies to be under considerable genetic control, with heritability estimates ranging from 0.12 to 0.55 (Spurlock et al., 2012; Manzanilla-Pech et al., 2014, 2022; de Haas et al., 2015; Byskov et al., 2017; Hardie et al., 2017; Li et al., 2018; Lu et al., 2018; Köck et al., 2018; Krattenmacher et al., 2019). Furthermore, some research has revealed low to moderate estimates of accuracy of genomic predictions for feed efficiency (de Haas et al., 2012; Hardie, 2016; Manzanilla-Pech et al., 2017; Harder et al., 2020). Single nucleotide polymorphism (SNP) markers have also pointed to genomic regions on chromosomes BTA1, BTA4, BTA12, BTA16, BTA26 and BTA27, and putative genes ADAM12, ADIPOQ, ADRB3, IDO2, INPP4A and LEP, that may be associated with feed efficiency (Veerkamp et al., 2012; Tetens et al., 2014; Hardie et al., 2017; Lu et al., 2018; Krattenmacher et al., 2019). These findings suggest that selective breeding, or other genetic improvement approaches, can result in cows that are more efficient convertors of feed. Therefore, there has been growing interest globally to breed animals that utilise feed more efficiently, while producing large volumes of milk, with a low carbon footprint (e.g. Spurlock et al., 2012; Pryce et al., 2015; Köck et al., 2018; Krattenmacher et al., 2019; Manzanilla-Pech et al., 2022).

Despite its growing importance, feed efficiency is not included in most national dairy cattle breeding objectives. This is mainly due to a lack of dry matter intake (DMI) measurements, which are required to calculate feed efficiency phenotypes. In dairy cows, gross feed efficiency (GFE) measures the ability of lactating cows to convert feed into milk or milk components. Basically, GFE is a ratio trait and may be expressed as kilograms of energy-correct milk (ECM) produced per kilogram of DMI, which is widely understood by dairy producers (Spurlock et al., 2012; Connor, 2015; Chesnais et al., 2016; Heida et al., 2021). Higher values of GFE mean that cows are able to turn consumed feed into milk more efficiently. In general, it is costly and laborious to measure DMI in individual lactating cows, which presents a major challenge to obtaining sufficient records for a sound genetic evaluation programme. Unavailability of DMI records on daughters of progeny-tested bulls has thus been noted as a major hindrance to selection for feed efficiency (McParland and Berry, 2016; Miglior et al., 2017; Shetty et al., 2017).

To overcome the problem of measuring DMI, an alternative approach is to predict DMI from easy-to-measure traits such as milk components and live weight (LW). These traits can allow proper accounting for the quantities of feed required for production and maintenance (Liinamo et al., 2012; VandeHaar et al., 2016; Krattenmacher et al., 2019; Zhang et al., 2020). Reliable prediction of GFE or DMI could potentially limit the burden of measuring individual cow DMI, in order to calculate feed efficiency phenotypes for genetic evaluations. To that end, limited efforts have been made to explore the feasibility of developing models to predict GFE and DMI from milk components and LW (Lindgren et al., 2001; National Research Council, 2001; Beard, 2018; Guinguina et al., 2019). The models developed to predict DMI and GFE, so far, are somewhat inconsistent, with low to high prediction abilities ranging from coefficients of determination of 0.45 to 0.76 (Lindgren et al., 2001; National Research Council, 2001; Beard, 2018; Guinguina et al., 2019).

In order to be effective as selection criteria, predicted DMI and GFE should exhibit genetic variation in the population under selection. Only a few studies have estimated the heritability of predicted DMI and, according to our knowledge, there are no available estimates of heritability for predicted GFE. Zhang et al. (2020) reported a moderate heritability estimate (0.18) for DMI predicted from milk production, live weight and week of lactation in Belgian Holstein cows. This suggests that predicted DMI may be justifiable as a selection criterion for feed efficiency, although the accuracy of selection would be low. Improvements in accuracy of selection can, however, be achieved through multi-trait analyses with correlated traits. For example, Kelly et al. (2021) demonstrated that multi-trait analyses including metabolizable energy intake, metabolic live weight and feeding behaviour had a better predictive accuracy than univariate analysis for metabolizable energy intake.

South Africa has a state-of-the-art dairy genetic evaluation programme, which has contributed significantly to genetic change of many economically important traits (Banga, 2009). Exceptional genetic progress has been observed, especially for production and linear type traits, in South African Holstein cattle in the past three to four decades (Ramatsoma et al., 2014). Functional traits were, however, largely ignored in the past, which led to their retrogression (Banga et al., 2014). Nevertheless, efforts are being made to rectify this drawback and, currently, traits related with production, conformation, longevity, reproduction, and udder health are analysed for the Holstein cattle breed, under the South African genetic evaluation programme (Interbull, 2022). There are, however, no traits related to feed efficiency in this portfolio, and feed efficiency phenotypes are generally scarce. Inclusion of feed efficiency in the breeding objective requires the generation of reasonably large quantities of feed efficiency phenotypes, and their genetic parameter estimates, in order to compute accurate estimated breeding values.

1.2 Problem statement

Genetic improvement of feed efficiency through selection can contribute significantly towards increased economic and environmental sustainability of the dairy industry. However, dry matter intake records of lactating cows, which are required to calculate feed efficiency phenotypes, are not available in South Africa and this has generally hampered efforts to attain such improvement. It is too costly and laborious to collect large amounts of dry matter intake data, which is a prerequisite to achieving accurate selection for feed efficiency. There have been limited efforts to predict dry matter intake and gross feed efficiency from easy-to-measure predictor traits such as milk components and live weight, and the prediction models developed have been inconsistent. Little is also known about the genetic variability of the predicted traits; hence it is not clear if they will serve as suitable selection criteria for feed efficiency. There is also limited knowledge of the relationships of these predicted traits with other dairy traits, which may assist in improving accuracy of selection. Despite having a sound dairy genetic evaluation programme and achieving substantial genetic improvement for many objective traits, feed efficiency has not received much attention in South Africa.

1.3 Justification

Development of models that can accurately predict dry matter intake and gross feed efficiency of lactating cows, using routinely measured and easy-to-measure traits, presents a big opportunity to achieve genetic improvement in feed efficiency through selection. This could potentially enable generation of large quantities of data on individual cow dry matter intake and gross feed efficiency phenotypes, at a low cost. If the predicted traits have reasonable genetic variation, such data could be used to estimate accurate breeding values and, therefore, make it possible to include feed efficiency in the selection objective. The accuracy of selection could be improved through the application of multi-trait models including traits that are highly correlated with the selection criteria. The inclusion of feed efficiency in the breeding objective for South African Holstein cattle will make large contributions towards resolving the serious viability problems faced by the dairy industry, which are mainly caused by escalating feed costs. It will also assist in mitigating the effects of climate change, through the breeding of cows that have a lower carbon footprint.

1.4 Aim

The aim of the study was to investigate the possibility of predicting genetic merit for feed efficiency from milk components and live weight, in South African Holstein cattle.

1.4.1 Objectives

The objectives were to:

i. Develop and validate models to predict dry matter intake and gross feed efficiency, using milk components and live weight, in first-parity cows.

ii. Develop and validate models to predict gross feed efficiency from milk components and live weight in multiparous cows.

iii. Estimate genetic parameters for predicted dry matter intake and gross feed efficiency, and their relationships with energy-corrected milk.

1.5 Hypotheses

The hypotheses tested were:

i. Milk components and live weight cannot be used to reliably predict dry matter intake and gross feed efficiency in first-parity cows.

ii. Gross feed efficiency in multiparous cows cannot be predicted reliably from milk components and live weight.

iii. Predicted dry matter intake and gross feed efficiency do not exhibit significant genetic variation, and they have no relationships with energy-corrected milk.

1.6 Outline of the chapters

This thesis has been prepared with the promotion of Prof. Cuthbert Banga from the Department of Animal Science, Faculty of Animal and Veterinary Sciences, Botswana University of Agriculture and Natural Resources, and Prof. Oliver Zishiri of the Discipline of Genetics, College of Agriculture, Engineering and Science, University of KwaZulu-Natal. It comprises of seven chapters, including a general introduction, literature review written as a manuscript, four research manuscripts and an epilogue with a general discussion, conclusions and recommendations. The literature review (Chapter 2) is published in the peer-reviewed journal **Livestock Science** as an article entitled "*Technological advances in genetic improvement of feed efficiency in dairy cattle: A review*". Chapter 3 is published as an article entitled "*Prediction of dry matter intake and gross feed efficiency using milk production and live weight in first-parity Holstein cows*" in the journal **Tropical Animal Health and Production**. Chapter 4 is a manuscript entitled "*Predicting gross feed efficiency from milk production and live weight in multiparous Holstein cows*". Chapter 5 has been accepted for publication in **Tropical Animal Health and Production** as a manuscript entitled "*Genetic parameters for predicted* *gross feed efficiency and its association with energy-corrected milk in South African Holstein cattle*". Chapter 6 is a manuscript entitled "*Genetic analysis of predicted dry matter intake and gross feed efficiency in South African Holstein cows*" and it was published In: **Proceedings of the 12th World Congress on Genetics Applied to Livestock Production, by Wageningen Academic Publishers in 2023**. An overview of each chapter is presented as follows:

Chapter 1: General Introduction

Provides context to the study by discussing the background, problem statement and justification for the research. The primary aim, objectives and hypotheses of the study are also articulated.

Chapter 2: Technological advances in genetic improvement of feed efficiency in dairy cattle: A review

Presents a review of the importance of improving feed efficiency, and the related challenges, in dairy cattle. This is followed by an in-depth discussion of technological advances that have been made towards predicting feed efficiency traits from easy-to-measure traits such as milk components, live weight and mid-infrared spectra of milk. Opportunities to improve feed efficiency in dairy cattle through genetic and genomic approaches are then explored.

Chapter 3: Prediction of dry matter intake and gross feed efficiency using milk production and live weight in first-parity Holstein cows

Results of the first part of the study, which explored the feasibility of predicting dry matter intake and gross feed efficiency in first-parity Holstein cows from milk components and live weight, are published in this chapter. This was an empirical study, which used actual feed intake, milk production and live weight data on first-parity Holstein cows. The first step of the study was to estimate correlations of milk components and live weight with dry matter intake and gross feed efficiency, in order to identify the most prospective predictors of the latter traits. Prediction models for daily dry matter intake and gross feed efficiency were subsequently developed using these traits, and their accuracy evaluated. The limitations of the developed models, and recommended future work to improve their utility, are also discussed.

Chapter 4: Predicting gross feed efficiency from milk components and live weight in multiparous Holstein cows

Development and validation of prediction models for gross feed efficiency from milk components and live weight were extended to multiparous cows, in this chapter. This study was carried out to further explore viability of predicting gross feed efficiency for Holstein cows in multi-lactations from milk components and live weight. Basically, the same procedures used for primiparous cows (Chapter 3) were followed. The model developed was slightly different from those for primiparous cows.

Chapter 5: Genetic parameter estimates for predicted gross feed efficiency and its association with energy-corrected milk in South African Holstein cattle

Estimates of heritability, repeatability and genetic correlations among predicted gross feed efficiency and energy-corrected milk, in the first three parities of South African Holstein cattle, are presented in this chapter. Gross feed efficiency data were generated using the prediction models developed in Chapters 3 and 4. The results of this chapter are important in developing strategies for the genetic improvement of feed efficiency through selection, using predicted gross feed efficiency as the selection criterion.

Chapter 6: Genetic analysis of predicted dry matter intake and gross feed efficiency in South African Holstein cows

There is limited information pertaining to the genetic variation exhibited by predicted dry matter intake from milk production traits, to determine if it could be a suitable selection criterion for feed efficiency in dairy cattle. In this chapter, dry matter intake was predicted from milk yield, in South African Holstein cattle on pasture-based and intensively-fed production systems, using a prediction model developed by Lindgren et al. (2001). The dry matter intake so predicted was then used to calculate gross feed efficiency expressed as kg energy-corrected milk divided by kg dry matter intake. This was followed by estimation of genetic (co)variances among predicted dry matter intake and gross feed efficiency. Results of heritability, repeatability estimates and genetic correlations among predicted dry matter and gross feed efficiency, are presented in this chapter.

Chapter 7: General discussion, conclusions and recommendations

The overall findings and conclusions drawn from the different component studies are put together in this chapter, while highlighting the limitations of the study. Recommendations on practical application of the results, and suggested future research work and development, are also discussed.

1.7 Animal ethics declaration

The experiment involving the recording of dry matter intake, milk yield measurement, and collection of milk samples and weighing of animals, for studies in Chapters 3 and 4, complied with the guidelines of the respective national legislations on animal experimentation and care of animals. The studies in Chapters 5 and 6 used secondary data from the Integrated Registration and Genetic Information System (INTERGIS) of South Africa. Animal ethics approval was granted by the Animal Ethics Committee of Agricultural Research Council (APAEC[2020/08]) and Animal Ethics of the University of KwaZulu-Natal (AREC/033/020D).

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Chapter 2

Technological advances in genetic improvement of feed efficiency in dairy cattle: A review

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Abstract

Improving feed utilization in dairy cattle has become increasingly important, for economic and environmental reasons. Evidence from the literature suggests that feed efficiency traits are under considerable genetic control, and thus can be genetically improved through selection. Lack of feed intake measurements, however, remains a major constraint to genetic evaluation of feed efficiency traits in commercial dairy herds, particularly in developing countries. Easy-to-measure traits such as milk production components, live weight (LW) and mid-infrared (MIR) spectra (from milk samples) may serve as predictor traits for estimating feed intake or efficiency on large numbers of animals, non-invasively and at a low cost, thus facilitating genetic improvement. The use of single nucleotide polymorphism markers in genome-wide studies has the potential to identify genomic regions, and subsequently genes, associated with feed efficiency. These markers also provide a means to understand the genetic mechanisms underlying feed utilization, for possible marker-assisted selection. This review discusses the importance of improving feed efficiency, and the associated challenges, in dairy cattle. It further explores the opportunities of predicting feed efficiency traits from easy to measure traits such as milk production components, LW and MIR spectra. Possible genetic and genomic approaches to improving feed utilization in dairy cattle are also discussed.

Keywords: Breeding objective, feed efficiency, genetic selection, genome-wide association studies

2.1 Introduction

Feed is a major input in dairy production, and is required to produce milk as well as provide nutrients for metabolic processes and other body functions of the cow. It accounts for over 60% of dairy farm production costs (European Commission, 2013; Connor, 2015; USDA, 2016; Miglior et al., 2017; Lacto data, 2019). Hence, it is necessary to improve the efficiency of feed utilisation by either reducing feed for the same level of milk production or maintaining the current level of feed input and increasing production.

Improvement of feed efficiency will result in a decrease in feed costs without decreasing milk production and, therefore, contribute towards improved herd profitability (Hemme et al., 2014; Pryce et al., 2015). In addition, an increase in feed efficiency has been linked to a reduction in major greenhouse gas emissions, including methane (CH_4) (Knapp et al., 2014; Connor, 2015; Puillet et al., 2016; Løvendahl et al., 2018). Results from several studies indicate that there is genetic variation in feed intake, with heritabilities ranging from 0.21 to 0.55, using random regression models (Manzanilla-Pech et al., 2014; Byskov et al., 2017; Hardie et al., 2017; Li et al., 2018; Krattenmacher et al., 2019); thus indicating scope for genetic improvement through selection. Most of these estimates are, however, based on small numbers of records from research herds and therefore, have large sampling errors, since feed intake is not recorded in most commercial herds (Vallimont et al., 2010; Veerkamp et al., 2012; Berry and Crowley et al., 2013; Manzanilla-Pech et al., 2014; de Haas et al., 2015; Li et al., 2018).

Accuracy of genetic selection is highly dependent on the availability and quality of phenotypic records (FAO, 2007; ICAR, 2012). Feed intake is the major parameter that is used to calculate feed efficiency traits [e.g., dry matter intake (DMI), gross feed efficiency (GFE), energy balance (EB) and residual feed intake (RFI)]. The difficulty of recording feed intake hampers direct selection for DMI, GFE, RFI and EB, as records are scarcely available on daughters of progeny-tested bulls. This challenge might be overcome through various alternative approaches. Milk components and live weight (LW), which are easier and cheaper to record, may be used as predictors of feed efficiency traits (Liinamo et al., 2012; Pszczola et al., 2013; Manzanilla-Pech et al., 2014; Krattenmacher et al., 2019). Another option is mid-infrared (MIR) spectroscopy, which is a rapid and cost-effective tool for recording phenotypes at the population level (Shetty et al., 2017a). This technology is based on the study of the interaction between matter and electromagnetic waves from either gas, liquid or solid, e.g. milk sample (McParland et al., 2014). It involves the absorption of electromagnetic radiation by a sample at frequencies (900 - 5,000 cm−1) that are characteristic of specific chemical bonds of a molecule (Van de Voort, 1992; McParland et al., 2014). Mid-infrared spectroscopy is commonly used to determine traditional milk quality traits such as protein, fat, casein, lactose and urea content in official milk laboratories (ICAR, 2017). Recently, several studies have also shown the potential use of milk MIR spectral data as a valuable tool for predicting feed efficiency traits such as DMI, RFI, GFE and EB, with accuracy of prediction varying from 0.29 to 0.80, using partial least squares regression analyses (McParland et al., 2014, 2015; Shetty et al., 2017a, 2017b; Bittante and Cipolat-Gotet, 2018; Dórea et al., 2018).

Challenges in identifying genetically superior animals for feed efficiency is a major weakness to traditional selection based on DMI, RFI, GFE and EB phenotypes only (Hardie et al., 2017; Li et al., 2018; Pszczola et al., 2018; Krattenmacher et al., 2019). Thus, genomic approaches are an alternative approach towards making selection decisions for genetic improvement of feed efficiency in dairy cattle. Genomic selection may be a better approach to improving these traits as it permits the use of genetic markers across the whole genome, thus capturing genetic variation due to many loci (Meuwissen et al., 2001; Pszczola et al., 2018; Krattenmacher et al., 2019). This method requires the development of prediction equations based on a reference population of preferably more than 10,000 animals with phenotypes and genotypes, to obtain accurate genomic breeding values (Calus et al., 2013). An average accuracy of genomic prediction of around 0.44 has been reported for RFI in dairy cattle (Pryce et al., 2014, 2015; de Haas et al., 2015). The use of single nucleotide polymorphism (SNP) markers in genome-wide association studies (GWAS) has the potential to identify genomic regions and subsequently genes (e.g., *ADAM12*, *ADRB3* and *LEP*) associated with DMI, RFI and EB, as well as understanding the mechanisms underlying feed utilization, for possible marker-assisted selection in dairy cattle (Hardie et al., 2017; Li et al., 2018; Pszczola et al., 2018; Krattenmacher et al., 2019). It is, however, not clear whether the markers and genes associated with feed efficiency can be detected reliably from predicted feed efficiency traits.

This paper presents a review of the importance and genetic variability of feed efficiency traits, as well as challenges and opportunities of improving them genetically in dairy cattle. The discussion on opportunities focusses mainly on the technological advance that have been made to use easy-to-measure predictor traits such as milk production, LW and MIR spectra, as well as the application of genomic approaches.

2.2 Benefits of genetic improvement of feed efficiency in dairy cattle

2.2.1 Economic benefits

Ever-rising feed costs necessitate genetic selection for more efficient production of milk (Connor et al., 2013; Miglior et al., 2017). If feed utilization is improved, less land will be required for arable crops and forages; therefore, dairy producers may need to purchase less feed (von Keyserlingk et al., 2013; Connor, 2015). It will also result in escalated herd profitability, as more milk will be produced per unit of dry matter fed (de Haas et al., 2012; Veerkamp et al., 2012; USDA, 2016; Miglior et al., 2017). Thus, selection for improved feed efficiency in dairy cattle may result in large economic benefits through reduced feed costs, as feed represents more than 60% of the total cost of milk production (USDA, 2016; Miglior et al., 2017; Lacto data, 2019). For example, in the United States, genetic improvement of feed efficiency has been reported to save a producer \$540 million annually (Farm and Dairy, 2019). In Europe, estimates suggest that improving the feed efficiency of dairy cattle could lead to savings of about two eurocents per kilogram of milk in feed costs, which equates to about 10% of the feed costs (CRV, 2020). There are, however, no available estimates on the economic benefits of improving feed efficiency in dairy cattle in Africa. Nevertheless, efforts towards breeding for feed efficient animals should be prioritized in order to achieve sustainable economic benefits in the African dairy sector.

2.2.2 Environmental benefits

The growing concerns about greenhouse gas (GHG) emissions and loss of nutrients to the environment through manure, from animal production, justify selection for more efficient dairy cattle (Connor et al., 2013; Pszczola et al., 2018). Globally, GHG emissions from cattle represent about 65% of the livestock sector emissions (4.6 gigatonnes CO_2-eq), making cattle the largest contributor to total sector emissions (Gerber et al., 2013). Dairy cattle contribute approximately 20% of the total cattle sector emissions (Gerber et al., 2013). Methane (CH_4) production from gastro enteric fermentation in dairy cows is not only an energy loss for the animal, but also a contributor to GHG emissions (Puillet et al., 2016). Enteric CH_4 is responsible for around 50% of all GHG emissions along the production chain of milk in Western countries, and an even higher percentage in developing countries with low-yielding cows (FAO and GDP, 2018). In South Africa, the agriculture sector's contribution to GHG is 8 to 9%, with livestock contributing between 5.5% and 6% (Botha, 2019). Dairy cattle contribute about 11% to the total methane emissions from livestock in South Africa (Milk SA, 2019).

Improving feed utilization has been demonstrated to result in a reduction in GHG emissions (Knapp et al., 2014; Puillet et al., 2016). Feed-efficient cows consume less energy and emit less methane (Connor et al., 2012). It has been reported that a reduction of 9 to 19% in enteric CH_4 per unit of energy corrected-milk (ECM) (g of CH_4/kg of ECM) can be achieved through improved feed efficiency (Gerber et al., 2013; Pszczola et al., 2018). If animals convert feed more efficiently into an exportable product (i.e. milk), then less manure would be produced. Thus, selection for improved feed efficiency in dairy cattle may result in more environmental-friendly animals, with a potential to mitigate GHG emissions and ensure more sustainable dairy production.

2.3 Measures of feed efficiency in dairy cows

Feed efficiency (FE) forms an essential component of dairy cattle breeding objectives (Vallimont et al., 2011; Pryce et al., 2015; Tempelman et al., 2015). However, it is a broad concept with multiple definitions (Connor, 2015). Moreover, it is a genetically complex trait (outcome) that is influenced by multiple underlying traits, including dry matter intake (DMI), milk production, and maintenance energy requirements (Chesnais et al., 2016). It is basically described as units of product output (e.g. kg milk) per unit of feed input. Generally, feed efficiency traits are classified into two categories, which are ratio traits (e.g., gross feed efficiency, GFE) and residual or regression traits (e.g., residual feed intake, RFI) (Berry and Crowley, 2013). This study mainly focusses on four FE measures that are commonly used to determine feed efficiency in lactating dairy cows, which are DMI, GFE, RFI and energy balance (EB).

2.3.1 Dry matter intake

Dry matter intake describes the amount of feed consumed by an animal (Connor, 2015). It is an important variable in the calculation of FE, and is measured as the difference between the feed offered and that which remains uneaten. All available FE traits involve measurement of DMI. Reducing DMI for the same level of milk production or maintaining the current level of DMI and increasing milk production implies more efficient utilisation of feed.

2.3.2 Gross feed efficiency

In dairy cows, gross feed efficiency (GFE) is used as a measure to determine the capacity of lactating cows to convert feed nutrients into milk or milk components. In simplest terms, GFE is a ratio trait and may be expressed as kilograms of milk produced per kilogram of dry matter consumed, as presented in equation 2.1 (Chesnais et al., 2016). Cows with higher gross feed efficiency values are able to convert feed nutrients into milk production more efficiently.

$$GFE = \frac{Milk\ \ (kg)}{Dry\ matter\ intake\ (kg)} \qquad [2.1]$$

2.3.3 Residual feed intake

Basically, RFI is calculated as the difference between actual DMI and predicted DMI based on energy requirements for production and maintenance (Connor, 2015). A low or negative value of RFI is preferred, since it indicates that an animal is consuming much less feed than predicted (Connor, 2015). For a lactating cow, RFI can be calculated as the residual of the regression of DMI on milk energy, metabolic body weight and change in body weight (Hardie et al., 2017). It is a better alternative to the ratio-based (i.e., output: input) measure, because feed efficiency in lactating cows must consider the contribution of mobilization of body reserves to the cow's energy supply (Berry and Crowley, 2013). Equation 2.2 shows how to calculate RFI for a lactating cow.

$$RFI = DMI - \beta 1 \text{ x ECM } + \beta 2 \text{ x MBW } + \beta 3 \text{ x } \boldsymbol{\Delta}\text{BW} \qquad [2.2]$$

Where, *RFI* is the residual feed intake, *DMI* is the dry matter intake, *ECM* is the energy corrected milk, *MBW* is the metabolic body weight, *ΔBW* is the change in body weight, *β1, β2 and β3* are partial regression coefficients.

2.3.4 Energy balance

Energy balance is basically the difference between energy intake and energy output. For a dairy cow, EB computation is illustrated in equation 2.3 (MacParland and Berry, 2016). It represents the difference between the energy expended for lactation, maintenance, growth, and reproduction and that gained from the intake of nutrients (Forbes, 1983). When the daily dry matter intake does not meet increased energy requirements of the cow, a status of negative energy balance develops (Nigussie, 2018). Energy balance essentially measures an intake-derived energy efficiency in dairy cows (Liinamo et al., 2012).

$$\text{Energy balance} = \text{Energy intake} - (\text{Energy expendixure for milk} + \text{maintenance} + \text{growth} + \text{pregnancy}) \quad [2.3]$$

2.4 Challenges to selection for feed efficiency

2.4.1 Measurement of feed intake

Selection for feed efficiency is a challenging task, since it requires many animals with individual feed intake records to accurately predict genetic merit, prior to inclusion in the breeding objective (McParland et al., 2014; Hardie et al., 2017). In practice, measuring individual feed intake for the calculation of feed efficiency traits is difficult and expensive, especially on a daily basis and for a large population (Miglior et al., 2017). This has been a major factor hindering the inclusion of feed efficiency traits in dairy cattle breeding objectives in many countries (Berry and Crowley, 2013; McParland and Berry, 2016; Shetty et al., 2017a). The problem of measuring the amount of feed a cow has consumed is even more daunting in the pasture-based production system (Williams et al., 2016). Dairy farmers using the total mixed ration (TMR) feeding system may measure intake for groups of animals only. Measuring individual feed intake requires highly automated feed bunks that can measure individual intake and feeding behaviour, which are very expensive. These feed bunks may be used in research herds; however, incorporating this technology into a commercial farm would be a huge investment.

2.4.2 Undesirable correlated response to selection

Another challenge in incorporating feed efficiency into the breeding objective is the identification of an appropriate selection criterion. Such a trait should improve feed efficiency without negatively affecting other functional traits, such as fertility and health (Connor, 2015). A common concern when selecting for improved feed efficiency is reduced health due to the animal not eating enough to meet her energy demands for adequate immune function (Puillet et al., 2016). The concern is that selection is done for animals to feed less, yet maintain production, and their intake is reduced such that they will not have enough energy to fight off pathogens upon infection. Simultaneous selection for low feed intake and high milk yield might improve feed efficiency; however, it poses the risk of promoting negative energy balance which is associated with health and reproductive problems in dairy cattle (Tetens et al., 2014; Connor, 2015; Puillet et al., 2016). Selection for high production has led to undesired responses by causing a correlated increase in negative energy balance, i.e. greater body reserve mobilization during early lactation that leads to more reproductive or health problems (Puillet et al., 2016). As a result, the gains in production may be offset by a decline in productive lifespan, because of poor health and/or fertility. Thus, when selecting to improve feed efficiency, one needs to proceed with caution and consider correlated responses, especially in regard to cow health and fertility.

2.5 Genetic parameters for feed efficiency traits

Estimates of genetic parameters such as heritability and genetic correlations are a prerequisite for incorporating a trait in the breeding objective. Genetic variation for feed efficiency traits has been studied in dairy cattle using different analytical models (e.g., Spurlock et al., 2012; Manzanilla-Pech et al., 2014; Byskov et al., 2017; Hardie et al., 2017; Krattenmacher et al., 2019). Most of the studies used random regression model, while some studies used other models such as the animal repeatability model. Generally, these studies demonstrated low to moderate heritabilities, and low to high estimates of genetic correlations, for feed efficiency traits. These genetic parameter estimates were observed to vary among stages of lactation as well as parities. Table 1 presents heritability estimates for feed efficiency traits in dairy cattle available in the literature.

2.5.1 Heritability estimates

2.5.1.1 Dry matter intake

Several studies have reported moderate heritability estimates, ranging from 0.21 to 0.49, for DMI in Holstein and Jersey cattle (Li et al., 2016, 2018; Manzanilla-Pech et al., 2016; Byskov et al., 2017; Hardie et al., 2017; Krattenmacher et al., 2019), indicating potential for genetic improvement through selection. Heritability was generally found to vary with stage of lactation, and this should be considered in breeding programs (Tetens et al., 2014; Li et al., 2016; Manzanilla-Pech et al., 2016; Krattenmacher et al., 2019). Limited studies have estimated genetic parameters for DMI in other dairy cattle breeds such as Jersey, based on small datasets (e.g., Li et al., 2016). Li et al. (2016) reported moderate heritability estimates for DMI in Jersey cows, ranging from 0.17 to 0.42; however, their small dataset resulted in large standard errors of the estimates. Heritability estimates also changed during the course of lactation (Li et al., 2016). Selection for DMI should, therefore, be implemented based on stage of lactation.

2.5.1.2 Gross feed efficiency

Limited studies have estimated the heritability of GFE in dairy cattle. A study by Spurlock et al. (2012) described GFE as being moderately heritable trait in American Holstein cattle, during the first half of lactation (2 to 150 DIM). These estimates were higher in primiparous (0.47) compared to multiparous (0.43) cows and across all parities (0.32). Heritability estimates for GFE in early lactation (0.32) were also higher than in mid lactation (0.20). These results indicate that the rate of genetic improvement of GFE may differ depending on the parity or lactation stage in which selection is applied, and this should be considered in the breeding programs. However, more studies using test day records across entire lactations may be necessary to substantiate these findings.

2.5.1.3 Residual feed intake

Studies have consistently described RFI as lowly to moderately heritable trait. Heritability estimates varying from 0.13 to 0.40 have been obtained for RFI in lactating Holstein cows (e.g., Pryce et al., 2012; Connor et al., 2013; Tempelman et al., 2015; Byskov et al., 2017; Hardie et al., 2017). Low heritability estimates, ranging from 0.13 in multiparous to 0.14 in primiparous cows, were reported for RFI in mid-lactating American, Dutch, Canadian and Scottish Holstein cattle (Hardie et al., 2017). This indicates that the underlying genetic variation of RFI differs between primiparous and multiparous cows. Moderate heritability estimates for RFI were found in primiparous Danish Holstein cows, varying from 0.23 in mid lactation to 0.36 in early lactation (Byskov et al., 2017). These results indicate that RFI is under considerable genetic control, and that lactation stage-specific selection may be necessary. Most of the studies were generally conducted on primiparous cows, with moderate heritability estimates for RFI, averaging 0.23 in Danish Holsteins, 0.27 in Australian Holsteins and 0.4 in Dutch Holsteins across the entire lactation (de Haas et al., 2011; William et al., 2011; Byskov et al., 2017). The variation in estimates of heritability for RFI could be attributable to discrepancies in the data sets used, such as test length, feed intake collection methods, body weight and body condition score data collection intervals and other management procedures (de Haas et al., 2011; William et al., 2011; Connor et al., 2013; Byskov et al., 2017; Hardie et al., 2017). Expansion of these studies to multiparous dairy populations may be also necessary, for appropriate selection for RFI genetic improvements across parities.

2.5.1.4 Energy balance

Results across studies consistently describe EB as a lowly to moderately heritable trait. In Finnish Red dairy cattle, and American and German Holstein cattle, heritability estimates for EB were reported to range from 0.07 to 0.49 (Liinamo et al., 2012; Spurlock et al., 2012; Krattenmacher et al., 2019). Spurlock et al. (2012) found that the heritability for EB peaked at approximately 30 days in milk (DIM), whereas maximal estimates were previously observed at the onset of lactation (Buttchereit et al., 2011). In an experiment using research herds, the peak heritability estimates of EB occurred earlier in multiparous (month 3) compared to primiparous (month 4) cows (Spurlock et al., 2012). Differences in heritability estimates between primiparous and multiparous cows may reflect differences in metabolism, such as the need for primiparous cows to partition energy resources toward growth (Wathes et al., 2007). The number of cows in the study was, however, small comprising of 227 multiparous and 175 primiparous cows. In addition, the data set for multiparous cows may have represented a biased population, because only cows that successfully completed two or more lactations were included. Therefore, differences in heritability estimates between primiparous and multiparous cows should be interpreted with caution and warrant further investigation. A study on primiparous Finnish Red dairy cattle found a higher heritability estimate of EB in early lactation (0.37) compared to late lactation (Liinamo et al., 2012). In agreement, a study on primiparous German Holstein cattle also found higher heritability estimate of EB in early lactation (0.49) than in mid lactation (0.29) (Krattenmacher et al., 2019). These findings indicate that heritability estimates of EB change across lactation, thus lactation stage-specific selection may be required.

Table 2.1 Heritability estimates for feed efficiency traits from the literature

Trait	Heritability	Models	Breed	Country	References
DMI	0.21 - 0.40	RRM	Holstein-Friesian	Netherlands	Manzanilla-Pech et al. (2014)
DMI	0.26 - 0.37	RRM	Holstein-Friesian	Germany	Tetens et al. (2014)
DMI	0.20 - 0.40	RAM	Holstein	Denmark and Sweden	Li et al. (2016)
DMI	0.17 - 0.42	RAM	Jersey	Denmark	Li et al. (2016)
DMI	0.32 - 0.49	AM	Holstein	Denmark	Byskov et al. (2017)
DMI	0.23 - 0.32	RRM	Holstein	USA, UK, Canada, Netherlands	Hardie et al. (2017)
DMI	0.28	AM	Holstein	Canada	Manafiazar et al. (2016)
DMI	0.30 - 0.55	RRM	Holstein	Denmark, Finland and Sweden	Li et al. (2018)
DMI	0.26 - 0.37	RRM	Holstein	Germany	Krattenmacher et al. (2019)
GFE	0.43 - 0.47	RRM	Holstein	United State of America	Spurlock et al. (2012)
RFI	0.40	RRM	Holstein-Friesian	Netherlands	de Haas et al. (2011)
RFI	0.27	SM	Holstein-Friesian	southern Australia	William et al. (2011)
RFI	0.22 - 0.38	AM	Holstein	Australia and New Zealand	Pryce et al. (2012)
RFI	0.36	RRM	Holstein	United State of America	Connor et al. (2013)
RFI	0.20	AM	Holstein	Canada	Manafiazar et al., (2016)
RFI	0.23 - 0.36	AM	Holstein	Denmark	Byskov et al. (2017)
RFI	0.13 - 0.14	RRM	Holstein	USA, UK, Canada, Netherlands	Hardie et al. (2017)
EB	0.10	RRM	Nordic Red	Finland	Liinamo et al. (2012)
EB	0.07 - 0.22	RRM	Holstein	United State of America	Spurlock et al. (2012)
EB	0.29 - 0.49	RRM	Holstein	Germany	Krattenmacher et al. (2019)

DMI=dry matter intake; EB=energy balance; GFE=gross feed efficiency; RFI=residual feed intake; AM=animal model; RRM=random regression model; RAM=repeatability animal model; SM=sire model.

2.5.2 Genetic correlations

Genetic correlations may help to determine how selection on one feed efficiency trait can affect the other. It is equally important to know how selection for a given trait in one lactation stage or first lactation might affect expression of the trait in another stage or successive lactations.

2.5.2.1 Genetic correlations among DMI, RFI and EB

Studies on the genetic correlations among feed efficiency traits are generally scarce. Manzanilla-Pech et al. (2016) reported high genetic correlations of 0.70 and 0.89 between DMI and RFI in Dutch and American Holstein populations, respectively, using test-day records. In a study on 301 Canadian Holstein lactation records, Manafiazar et al. (2016) found a moderate genetic relationship of 0.51 between DMI and RFI. The variation in these results could be attributable to the nature of the data analysed, which were test-day records for the Dutch and American Holstein populations and lactation records for the Canadian Holstein population. High positive genetic relationships (0.71 - 0.81) were obtained between DMI and EB in a study on primiparous German Holstein cattle (Krattenmacher et al., 2019). These results suggest that selection for increased DMI will result in a favourable correlated response in RFI and EB.

2.5.2.2 Genetic correlations among stages of lactation

2.5.2.2 (a) Dry matter intake

Research suggests that genetic correlations among DMI in different stages of lactation ranges from low to high. Tetens et al. (2014) reported positive genetic correlations between daily DMI observations at days in milk (DIM) 11, 30, 80, 130, and 180, ranging from 0.29 (between DIM 11 and 180) to 0.97 (DIM 11 and 30). The strength of the genetic correlation was inversely related to the time interval between DIM. Observations for DMI in mid lactation had a low predictive value in relation to early lactation DMI, and vice versa. Uncertainty remains about the genetic association between DMI in early and late lactation as well as mid and late lactation, as the study was limited to the first 180 DIM. Nonetheless, these results showed that DMI at different stages of lactation should be treated as separate traits. In a breeding program aiming to optimize overall feed efficiency of dairy cows over the entire lactation, repeated measurements of DMI in different stages of lactation would be necessary (Liinamo et al., 2012). In an experiment with 650 Danish Holstein cows, DMI was found to be most strongly genetically correlated between mid (7-28 DIM) and late lactation (126-147 DIM) (0.95), followed by between early (7-28 DIM) and late (210-231 DIM) (0.71), as well as between early (7-28 DIM) and mid lactation (126-147) (0.70) (Byskov et al., 2017). These results were comparable to recent findings by Harder et al. (2020), which showed strong genetic correlations between mid (130 DIM) and late (340 DIM) (0.84) as well as between early (40 DIM) and mid-lactation (0.70) (130 DIM) in German Holstein-Friesian cows. Harder et al. (2020) further observed weak genetic correlations (0.05) between early (DIM 10) and late lactation (DIM 340), which concurred with previous studies (Liinamo et al., 2012; Li et al., 2018). These findings were, however, inconsistent with strong genetic correlations between early and late lactation reported by Byskov et al. (2017). The inconsistency between these studies for early vs late lactation may be attributable to the fact that Byskov et al. (2017) used an animal model, whereas several studies (Liinamo et al., 2012; Li et al., 2018; Harder et al., 2020) used random regression models (which account for the shape of the lactation curve); thus more studies may be necessary to explicate these inconsistences. The results where genetic correlations are high suggest that selection for increased DMI in early lactation will result in a favourable correlated response in mid and late lactations but uncorrelated responses between those lactation stages may result where correlations are poor.

2.5.2.2 (b) Gross feed efficiency

There is limited literature on genetic associations for GFE across stages of lactation. Nonetheless, a study by Spurlock et al. (2012) found a strong genetic correlation (0.96) between early (DIM 2) and mid lactation (DIM 75) for GFE, in the American Holstein population. This suggests that selection for GFE in early lactation will also improve GFE in mid lactation. More studies are however required to validate these results.

2.5.2.2 (c) Energy balance

Studies on the genetic correlations for EB in different stages of lactation are also scarce. A recent study by Harder et al. (2020) reported a weak negative genetic correlation (-0.05) between EB in early (DIM 10) and late lactation (DIM 340), with values between early (10 DIM) and mid lactation (180 DIM) tending to be lower at 0.03, in German Holstein-Friesian cows. This was in agreement with some earlier studies (Liinamo et al., 2012; Li et al., 2018). In another earlier experiment based on the first 180 DIM, a much higher genetic correlation of 0.37 was observed between EB in early (DIM 11) and mid-lactation (DIM 180), in German Holstein cows (Krattenmacher et al., 2019). The pattern of genetic correlations across lactation suggests that selection for EB in early lactation may improve EB in mid-lactation, whereas weak genetic correlations may suggest uncorrelated response of EB at given stage of lactation. There is, however, a need for more studies to validate these results.

2.5.2.3 Genetic correlations between primiparous and multiparous

Literature on the genetic correlations for feed efficiency traits between primiparous and multiparous cows is scanty. Hardie et al. (2017) analysed data on the first 200 DIM of American, Scottish, Canadian and Dutch Holstein cows, to determine whether there were any differences in DMI and RFI between primiparous and multiparous cows. Such differences may arise due to the fact that primiparous cows typically continue to grow in frame throughout their first lactation, which may affect their utilization of energy (Perotto et al., 1992). A genetic correlation of 0.78 was found for DMI between primiparous and multiparous cows (Hardie et al., 2017). On the other hand, the genetic correlation between RFI in primiparous and multiparous cows was 0.76 (Hardie et al., 2017). These findings suggest that selecting for DMI and RFI in primiparous cows might be adequate for improvement of the trait in successive parities; however, more studies may be necessary to validate these results. Analysis throughout the entire lactation periods may be necessary as well.

2.6 Predicting feed efficiency traits

2.6.1 Prediction of DMI

Improvement of the efficiency of feed utilisation in dairy cows may be achieved by selecting for either reduced DMI for the same level of milk production or maintaining the current level of DMI and increasing production. Dry matter intake (DMI) is an important component for computing any feed efficiency trait. However, measurement of DMI is labour-intensive and, therefore, expensive. Thus, DMI is hardly recorded on commercial herds and, as a result, there is limited data available, mostly from research herds. Difficulty in recording DMI hinders direct selection for it, due to insufficient records being available on daughters of progeny-tested bulls (Manzanilla-Pech et al., 2017). This problem might be overcome by predicting DMI from other traits (Berry and Crowley, 2013; Manzanilla-Pech et al., 2016). Use of such predictor traits may result in improvement of the trait of interest at a low cost (Pszczola et al., 2013). Prediction of DMI, using certain traits and through prediction equations, has been suggested (e.g., Lindgren et al., 2001; NRC, 2001; Madilindi et al., 2021). In dairy cattle, such traits include production traits such as energy corrected-milk (ECM), fat and protein corrected milk (FPCM) and/or traits reflecting maintenance costs, such as live weight (LW) (Manzanilla-Pech et al., 2017; Zhang et al., 2020). These traits are easy and cheap to measure and, therefore, widely recorded on commercial herds (Manzanilla-Pech et al., 2017; Zhang et al., 2020).

Energy corrected-milk, FPCM and LW are widely known to have strong phenotypic correlations with DMI (Vallimont et al., 2010; Manafiazar et al., 2016; Manzanilla-Pech et al., 2014, 2017; Madilindi et al., 2021). Several studies have estimated moderate to high (0.33 to 0.76) phenotypic correlations between DMI and ECM, FPCM and LW (Vallimont et al., 2010; Manafiazar et al., 2016; Manzanilla-Pech et al., 2014; 2017; Madilindi et al., 2021). These results suggest that DMI can be reliably predicted from these easy-to-measure traits.

2.6.2 Use of mid-infrared spectroscopic technology to measure milk components

Mid-infrared (MIR) technology is based on the study of the interaction between matter and electromagnetic waves from either gas, liquid or solid, e.g. milk sample (McParland et al., 2014). It involves the absorption of electromagnetic radiation by a sample at frequencies (900 to 5,000 cm^{-1}) that are characteristic of specific chemical bonds of a molecule (Van de Voort, 1992; McParland et al., 2014). The technology has gained considerable interest in the dairy industry worldwide in recent years, since it provides analyses with high throughput, with ease of measurement, at low cost, non-invasively and on a large scale (Shetty et al., 2017a). Thus, it is used in official milk recording schemes to measure major milk components such as protein, fat, casein, lactose and urea for milk quality control, milk payment, management of herds, or genetic studies (De Marchi et al., 2014; Gengler et al., 2016; ICAR, 2017). Since individual animal milk samples are routinely taken as part of day-to-day dairy herd management, using these samples to also predict feed efficiency traits (e.g. feed intake) would be a cost-effective strategy for generating data for management purposes as well as genetic evaluation.

2.6.3 Prediction of feed efficiency traits from MIR spectra

Recent studies on MIR spectra from milk samples have shown the potential to predict traits that are difficult or expensive to record in dairy cattle, such as DMI and energy intake (McParland et al., 2014; Dórea et al., 2018; Wallen et al., 2018), RFI (McParland et al., 2014; Shetty et al., 2017b) and intake conversion ratio (ICR), expressed as daily DMI corrected for daily fat production (Beard, 2018).

There are still limited studies on the effectiveness of MIR spectra to predict feed efficiency traits, since the technique is relatively novel. In a study on Irish Holstein cows, coefficients of correlation ranging from 0.48 to 0.60 were obtained between RFI predicted from MIR data across lactation and an external validation data set, with the strongest predictive ability being found in the first 60 days of lactation (McParland et al., 2014). This study also reported that the inclusion of milk yield together with MIR, as a predictor variable, improved the accuracy of predicting energy intake across lactation (REX = 0.70) (McParland et al., 2014). In another study on Danish Holstein and Jersey populations, the most effective prediction model for DMI included milk yield, live weight, and MIR spectral data as explanatory variables, with a strong predictive ability (R^2 = 0.81) (Shetty et al., 2017b). However, when only milk MIR spectra was used, a low prediction ability (R^2 = 0.30) was obtained (Shetty et al., 2017b). The accuracy of prediction of RFI was also highest in early lactation (1 to 9 weeks), ranging from 0.29 to 0.46, compared to across lactation or mid- and late-lactation stages (Shetty et al., 2017b). It therefore appears that prediction of DMI and RFI using MIR spectra may be more reliable from early lactation data.

Dorea et al. (2018) observed a fairly high prediction accuracy (R^2 = 0.70) for DMI, in models including milk production traits, live weight and MIR spectra data, in a lactating American Holstein cattle population. On the other hand, prediction equations for ICR that included only milk yield and milk components, were found to have low to moderate prediction accuracy, with a coefficient of determination of cross validation (R^2CV) ranging from 0.25 to 0.61 (Beard, 2018). This prediction accuracy was however low, with R^2CV ranging from 0.20 to 0.30, when MIR spectral data was included with milk yield and milk components (Beard, 2018). Beard (2018) further noted that ICR could be best predicted within 101 to 150 days of lactation (R^2CV=0.48).

Results from the literature have shown the effectiveness of predicting feed efficiency traits from milk MIR spectral data. However, the prediction equations with only MIR spectra appear to have lower prediction accuracy compared to those with other explanatory variables such as live weight, milk yield, and milk components only and/or together with MIR spectra. Further studies are required to validate these prediction accuracies with data from commercial dairy herds, where possible. In addition, the potential of including other variables such as energy corrected-milk together with milk MIR spectra in the prediction of feed efficiency traits is unknown, and such studies may be useful.

2.7 Genetic parameter estimates for MIR predicted feed efficiency traits

Knowledge of genetic variation is important for deciding on the selection criteria to be used. Genetic correlations between MIR predicted and directly measured feed efficiency traits such as RFI, energy intake (EEI) and EB, as well as their heritabilities, are available from a few studies (McParland et al., 2014, 2015, 2016).

2.7.1 Genetic correlations between MIR predicted traits

There is paucity of information on genetic correlations between milk MIR predicted feed efficiency traits. However, McParland et al. (2014) predicted EB and RFI from milk MIR spectral data of 378 Irish Holstein cows, using a partial least squares regression analysis, and found a fairly strong genetic correlation (0.65) between the two predicted traits. This relationship could be explained by the fact that EB and RFI are, in principle, similar traits (Savietto et al., 2014). This implies that RFI may be improved through selection on predicted EB, and vice versa, in dairy cattle. This dispenses with the need to include both traits in the breeding objective.

2.7.2 Genetic correlations between directly measured and MIR predicted traits

A stronger genetic correlation was estimated between directly measured and MIR predicted EEI (0.84) than between measured and MIR predicted EB (0.54), in a study on 2,441 Irish Holstein-Friesian cows (McParland et al., 2015). This implies that MIR predicted EEI or EB may be used as reliable selection criteria for the measured traits.

2.7.3 Heritability of MIR predicted feed efficiency traits

Estimates of heritability for milk MIR predicted DMI and RFI are scarce in the literature. However, heritability estimates ranging from 0.1 to 0.20 have been reported for MIR predicted energy balance, energy intake and residual energy intake (Figure 1) in Irish Holstein cows (McParland et al., 2015, 2016), indicating fairly considerable genetic influence.

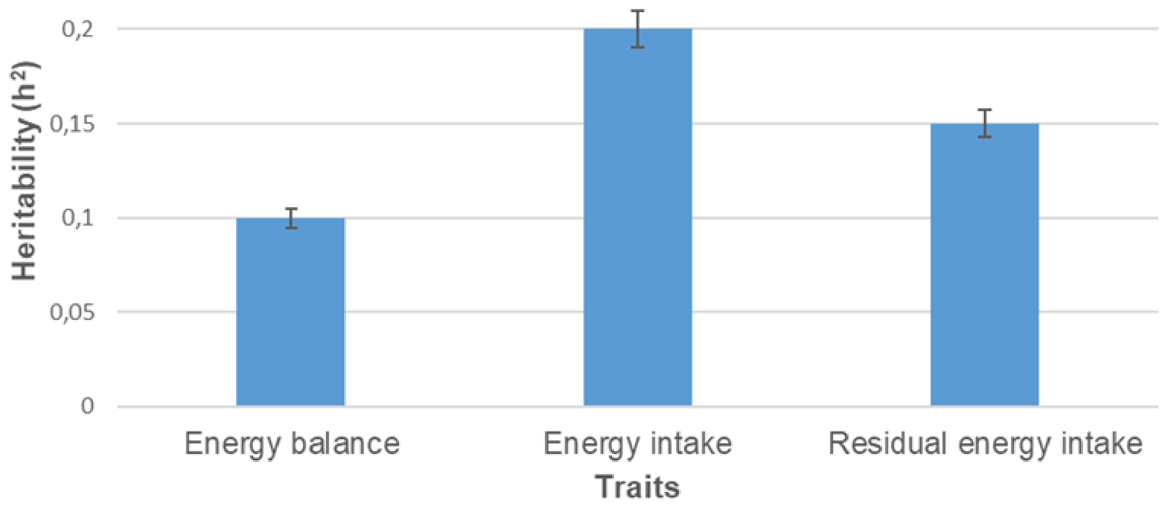

Figure 2.1 Heritability estimates for MIR predicted energy balance, energy intake and residual energy intake in Irish Holstein cattle (Source: McParland et al., 2015, 2016).

2.8 Heritability of predicted feed efficiency traits estimated from milk production traits and live weight

There is still limited work on genetic parameters for feed efficiency traits predicted from milk production traits and LW. A recent study by Zhang et al. (2020) examined the genetic variability of predicted feed efficiency traits such as predicted dry matter intake (pDMI) and consumption index (pIC), in first and second parity Belgian Holstein populations. Dry matter intake records at specific test days were predicted (pDMI in kg/day) using pBW, fat-corrected milk (FCM), and the week of lactation using the National Research Council (NRC) equation (NRC, 2001). A consumption index (pIC) was predicted as the ratio of pDMI to FCM. The heritability estimates for pDMI in first and second lactation were 0.14 and 0.11, respectively (Zhang et al., 2020). A previous study (Song, 2010) also found higher heritability for predicted 305-d DMI for first parity cows (0.12) than for those in the third parity (0.08) in Canadian Holstein cattle. Heritability was also higher for pIC in first parity (0.14) than second lactation cows (0.09) (Zhang et al., 2020), and they were comparable to the average heritability estimate (0.14) for feed efficiency defined as 305-d FCM divided by net-energy intake reported for American Holstein cattle (Vallimont et al., 2011). These heritabilities indicate that predicted DMI and consumption index are lowly to moderately heritable traits. Thus, it may be possible to improve efficiency of feed utilization from these predicted traits in dairy cattle.

2.9 Relationship between cow size and feed efficiency

Genetic knowledge about cow size in relation to feed efficiency is important for determining how selecting for one trait would affect the other. Few studies have been carried out to determine the genetic correlations between cow size and feed efficiency traits in dairy cows. Vallimont et al. (2011) reported negative genetic correlations for live weight with feed efficiency defined as 305-d FCM divided by net-energy intake (-0.66) and net energy for lactation efficiency (-0.64) in American Holstein cattle. In another study on 5700 American Holstein cows, a moderate genetic correlation of -0.3 was found between body weight and gross feed efficiency (Lu et al., 2015, unpublished), and the correlation was consistent with the estimate (-0.58) reported on 539 Nordic Red cows (Lidauer et al., 2018). These correlations were also consistent with those from a previous study, which obtained a fairly strong unfavourable genetic correlation (-0.7) between stature and gross feed efficiency on 1900 American Holstein cows (Manzanilla-Pech et al., 2015, unpublished). Body weight and gross feed efficiency were, however, poorly genetically correlated (0.07 to 0.18) in a study on 260 Canadian Holstein cows (Manafiazar et al., 2016), and the inconsistency of these results with others may warrant further studies. Typically, larger and fatter cows have higher maintenance requirements than smaller and thinner cows and, therefore, less feed efficient. Unfortunately, in the past, the dairy industry was focussed on selecting for both tall and heavy cows on the basis that they would produce more milk (VandeHaar et al., 2016). It may be deduced that, selecting for large and tall cows will thus decrease feed efficiency due to higher maintenance requirements.

2.10 Molecular genetics approaches to improve feed efficiency in dairy cattle

Challenges in identifying animals with high efficiency of feed utilization is a major weakness to traditional selection based on phenotypes only. Hence, genomic approaches are an alternative towards making selection decisions for genetic improvement of feed efficiency in dairy cattle.

2.10.1 Accuracy of genomic predictions

Genomic selection holds a promise to improved accuracy of selection for feed efficiency (Miglior et al., 2017). Accuracies of genomic prediction for feed efficiency in dairy cattle, obtained from some studies, are presented in Table 2. There are, however, no corresponding estimates for GFE available in the literature. Accuracy of genomic prediction for DMI has been estimated to vary from 0.21 to 0.61 in Holstein cattle (de Haas et al., 2012; Pszczola et al., 2013; de Haas et al., 2015; Manzanilla-Pech et al., 2017; Harder et al., 2020). Pryce et al. (2012, 2014) reported accuracies ranging from 0.27 to 0.40 for RFI in Australian Holsteins. Comparable estimates, ranging from 0.10 to 0.39, were obtained for RFI in mid-lactation in American, Canadian, Dutch and Scottish Holstein cattle (Hardie, 2016). Verbyla et al. (2010) found a slightly lower accuracy of 0.29 for EB, in a study on Dutch Holstein-Friesian population. On the other hand, Harder et al. (2020) recently reported a higher accuracy of 0.47 for EB in German Holstein-Friesian cattle. The variation in accuracy of genomic predictions from different studies could be explained by the size of the reference population used in each study as well as the estimates of heritability and genetic relationships of the traits (Goddard and Hayes, 2009; Egger-Danner et al., 2014; de Haas et al., 2015).

Although the accuracy of genomic selection for DMI, RFI and EB is lower than that for production traits, this can be considered as considerable progress because researchers were incapable of including these traits in breeding objectives until the genomics era (Veerkamp et al., 2012; Pryce et al., 2014; de Haas et al., 2015; Krattenmacher et al., 2019). The low to moderate estimates of accuracy of genomic predictions reported thus far indicate that significant genetic gains in feed efficiency could be achieved through genomic selection.

However, most of the results are from on-station experiments and research herds, and not from commercial herds. It would be vital to perform such investigations in commercial herds across different stages of lactation, using feed efficiency traits predicted from easy-to-measure traits.

There is a potential to generate large datasets from commercial dairy herds, using this approach, which may improve the accuracy of genomic predictions.

Table 2.2 Accuracy of genomic predictions of feed efficiency traits in dairy cattle reported in the literature

Traits	Accuracy	Breed	No. of Animals X No. of SNPs	Country	References
DMI	0.35	Holsteins	1801 X 30947	UK, Netherlands & Australia	de Haas et al. (2012)
DMI	0.37	Holstein-Friesian	6953 X 583375	Europe, North America & Australia	de Haas et al. (2012)
DMI	0.33	-	824 X 36346	Ireland, UK & Netherlands	Pszczola et al. (2013)
DMI	0.21 - 0.38	Dutch dairy cows	1496 X 76439	Netherlands	Manzanilla-Pech et al. (2017)
DMI	0.33 - 0.61	Holstein-Friesian	1828 X 45373	Germany	Harder et al. (2020)
RFI	0.40	Holsteins	1582 X 624930	Australia & New Zealand	Pryce et al. (2012)
RFI	0.27	Holsteins	78 X 609321	Australia	Pryce et al. (2014)
RFI	0.25 - 0.39	Holsteins	4916 X 60671	USA, Canada, Netherlands & UK	Hardie (2016)
EB	0.29	Holstein-Friesian	527 X 43011	Netherlands	Verbyla et al. (2010)
EB	0.27 - 0.47	Holstein-Friesian	1828 X 45373	Germany	Harder et al. (2020)

DMI=dry matter intake; EB=energy balance; RFI=residual feed intake.

2.10.2 Genome-wide association studies on feed efficiency traits

The use of genetic markers such as SNPs in genome-wide association studies (GWAS) offers the potential to identify loci or genomic regions associated with feed efficiency traits, as well as understand the biological mechanisms underlying feed utilization. Knowledge of the location of loci linked to genes causing variation in feed efficiency traits can be exploited to increase effectiveness of selection. A limited number of studies have been performed to identify quantitative trait loci (QTLs), and subsequently candidate genes, related to feed efficiency traits in dairy cattle (e.g., Veerkamp et al., 2012; Hardie et al., 2017; Lu et al., 2018). Most of these studies have generally used relatively small populations from research dairy herds and/or only primiparous cows (e.g., Verbyla et al., 2010; Yao et al., 2013; Veerkamp et al., 2012; Tetens et al., 2014; Hardie et al., 2017; Lu et al., 2018). However, some QTLs and candidate genes associated with feed efficiency traits have been detected in these studies, which paves the way for marker-assisted selection for feed efficiency in dairy cattle.

2.10.2.1 Quantitative trait loci

A few studies have identified quantitative trait loci (QTLs) associated with feed efficiency traits in dairy cattle (e.g., Veerkamp et al., 2012; Hardie et al., 2017; Lu et al., 2018; Krattenmacher et al., 2019). These QTLs are available on the Animal Quantitative Trait Loci database (QTLdb) (www.animalgenome.org/ QTLdb/; Hu et al., 2016). A recent study by Lu et al. (2018) reported two significant genomic regions on chromosomes BTA12 and BTA26 associated with DMI and RFI in American, Canadian, Dutch and Scottish Holstein cows. In a previous study on American, Canadian, Dutch and Scottish Holsteins, positive associations with DMI and RFI were found on chromosome BTA4 in primiparous and BTA27 in multiparous cows (Hardie et al., 2017). The significant QTL on BTA27 was previously also associated with variation in DMI on primaparous Irish, Scottish, Dutch, Swedish and German Holstein–Friesian cows (Veerkamp et al., 2012; Tetens et al., 2014). It should be noted, however, that biological mechanisms underlying variation in feed efficiency in growing animals may not be the same as that for mature lactating animals (Spurlock and VandeHaar, 2013).

Significant associations with EB and DMI were detected on chromosomes BTA1 and BTA16, in a study on 876 primiparous German Holstein cows (Krattenmacher et al., 2019). Trait associations in this study (Krattenmacher et al., 2019) were lactation stage specific, with a peak at particular days in milk (DIM). The QTL region was located on BTA1 and reliably showed association around 65 DIM on EB and DMI (Krattenmacher et al., 2019). These findings were consistent with the genetic correlations among lactation stages (Krattenmacher et al., 2019), and these underline the changing genomic architecture of energy metabolism across the lactation (Puillet et al., 2016), which has to be considered when incorporating this complex trait into a breeding objective.

There is scarce information on QTLs for GFE in the literature. The use of predicted feed efficiency traits might help to address these gaps in knowledge.

2.10.2.2 Candidate genes

Genome-wide association studies are an insightful tool in identifying candidate genes associated with complex traits such as feed efficiency. A recent study by Lu et al. (2018) reported an association of the gene *ADAM12* with DMI and RFI in Scottish, Dutch, Canadian, and American Holstein cows. This gene is responsible for regulating muscle development and fatty acid utilization in primiparous cows (Lu et al., 2018). Hardie et al. (2017) identified a positional candidate gene *ADRB3*, in primiparous American, Canadian, Dutch and Scottish Holstein cows, and this gene was associated with physiological complexity underlying the genetic regulation of RFI in lactating dairy cows. The gene encoding leptin (*LEP)* was also found to be associated with RFI and DMI in multiparous cows (Hardie et al., 2017). This gene was associated with the maintenance of glucose homeostasis and regulation of appetite and energy metabolism in dairy cattle (Priyadarshini et al., 2015). Furthermore, leptin gestures through the central nervous system to elicit changes in feeding behaviour, metabolism, and endocrine physiology (Fruhbeck et al., 1998).

Veerkamp et al. (2012) identified *IDO2* as an ideal candidate gene associated with DMI in Irish, Scottish, Dutch and Swedish Holstein cattle. This gene plays an important role in tryptophan metabolism. Tryptophan is an essential amino acid that cannot be produced in the body and is therefore linked to feed intake in cattle (Choung and Chamberlain, 1992). It serves as the immediate precursor to serotonergic activity in the brain, and has been implicated in the directive of feed intake (Koopmans et al., 2006). Tetens et al. (2014) identified a cluster of at least 23 olfactory receptor genes found in the vicinity of the associated SNP UA-IFASA-4358, in primiparous German Holstein-Friesian cows. These olfactory receptors serve to influence palatability of feed and thus is associated with DMI (Tetens et al., 2014; Veerkamp et al., 2012). Recently, Krattenmacher et al. (2019) identified the genes encoding fumarate hydratase and adiponectin (*ADIPOQ*) as highly promising candidate genes associated with EB in primiparous German Holstein cows. Fumarate hydratase, also termed fumarase, is an enzyme that belongs to the Krebs cycle, which could be viewed as the "turntable" of energy metabolism (Krattenmacher et al., 2019). A gene *ADIPOQ*, which is secreted by adipocytes, exerts insulin-sensitizing effects and, in obesity-linked insulin resistance, it has been shown to be downregulated along with its receptors (Caselli, 2014). In dairy cows, positive associations between serum adiponectin levels and insulin responsiveness of the glucose and fatty acid metabolism have been established, whereas a negative association has been reported with body condition scores during the dry period (De Koster et al., 2017).

To our knowledge, no genes associated with gross feed efficiency in dairy cattle have been reported in the literature.

2.11 Conclusions

Selection for feed efficient cattle, through the incorporation of feed efficiency traits in breeding objectives, could minimize feed costs and greenhouse gas emissions in the dairy industry. Lack of phenotypic data on feed intake poses a major challenge to the genetic improvement of feed efficiency, particularly in pasture-based commercial dairy herds. Predictor traits, including milk production, live weight and MIR spectra, however, may be reliably used to predict feed efficiency in cases where there is insufficient recording of feed intake. Research points to significant genetic variation in feed efficiency traits in dairy cattle. Generally low to moderate heritability estimates for traits such as DMI, GFE, RFI and EB, suggest that there is scope for the improvement of feed efficiency through genetic selection. Genomic selection presents a promise to improving feed efficiency traits. Genomic regions and genes associated with actual feed efficiency traits have been identified through genome-wide association studies, and these may help to improve rates of genetic gain. It is, however, still unknown if predicted feed efficiency traits could be used reliably to detect genomic regions and subsequently genes associated with feed efficiency in dairy cattle. Such knowledge may assist towards accelerated genetic improvement of feed utilization through marker-assisted selection in dairy herds.

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Chapter 3

Prediction of dry matter intake and gross feed efficiency using milk production and live weight in first-parity Holstein cows

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Abstract

Direct measurement of dry matter intake (DMI) presents a major challenge in estimating gross feed efficiency (GFE) in dairy cattle. This challenge can, however, be resolved through the prediction of DMI and GFE from easy-to-measure traits such as milk production (i.e. milk yield, energy-corrected milk (ECM), butterfat, protein, lactose) and live weight (LW). The main objective of this study was, therefore, to investigate the feasibility of predicting dry matter intake and gross feed efficiency for first-parity Holstein cows using milk production traits and LW. Data comprised of 30 daily measurements of DMI and milk production traits, and 25 daily LW records of a group of 100 first-parity Holstein cows, fed a total mixed ration. Gross feed efficiency was calculated as kg ECM divided by kg DMI. The initial step was to estimate correlations of milk production traits and LW with DMI and GFE, to identify the best potential predictors of DMI and GFE. Subsequently, a forward stepwise regression analysis was used to develop models to predict DMI and GFE from LW and milk production traits, followed by within-herd validations. Means for DMI, butterfat yield (BFY) and LW were 21.91 ± 2.77 kg/day, 0.95 ± 0.14 kg/day and 572 ± 15.58 kg/day, respectively. Mean GFE was 1.32 ± 0.22. Dry matter intake had positive correlations with milk yield (MY) (r = 0.32, $p < 0.001$) and LW (r = 0.76, $p < 0.0001$) and an antagonistic association with butterfat percent (BFP) (r = − 0.55, $p < 0.001$). On the other hand, GFE was positively associated with MY (r = 0.36, $p < 0.001$), BFP (r = 0.53, $p < 0.001$) and BFY (r = 0.83, $p < 0.0001$), and negatively correlated with LW (r = − 0.23, $p > 0.05$). Dry matter intake was predicted reliably by a model comprising of only LW and MY (R^2 = 0.79; root mean squared error (RMSE) = 1.05 kg/day). A model that included BFY, MY and LW had the highest ability to predict GFE (R^2 = 0.98; RMSE = 0.05). Live weight and BFY were the main predictor traits for DMI and GFE, respectively. The best models for predicting DMI and GFE were as follows: DMI (kg/day) = − 54.21 − 0.192 × MY (kg/day) + 0.146 × LW (kg/day) and GFE = 4.120 + 0.024 × MY (kg/day) + 1.000 × BFY (kg/day) − 0.008 × LW (kg/day). Thus, daily DMI (kg/day) and GFE can be reliably predicted

from LW and milk production traits using these developed models in first-parity Holstein cows. This presents a big promise to generate large quantities of data of individual cow DMI and GFE, which can be used to implement genetic improvement of feed efficiency.

Keywords: Correlation, easy-to-measure traits, feed intake, feed efficiency, stepwise regression

3.1 Introduction

Feed efficiency (FE) has large implications on animal production profitability and environmental sustainability; hence, it has become a common standard for monitoring the economic viability of milk production and environmental footprint (Vallimont et al., 2011; Pryce et al., 2015; Tempelman et al., 2015). Thus, extensive efforts are being made worldwide to include FE in dairy cattle breeding objectives. Such efforts include genome-wide association analyses for FE using international dairy FE research consortium data, aiming to implement marker-assisted selection (e.g. de Haas et al., 2015; Lu et al., 2018).

All FE traits such as gross feed efficiency and residual feed intake require the measurement of dry matter intake (DMI). Dry matter intake is a key variable in the calculation of an individual cow's feed efficiency. However, direct measurement of individual animal DMI remains a major challenge in assessing dairy feed efficiency. Measurement of individual DMI is generally difficult and expensive, especially for animals on a pasture-based feeding system. This has been a major factor hindering the inclusion of FE traits into selection objectives (Shetty et al., 2017; Wallén et al., 2018). It is generally difficult to obtain large numbers of individual animal records on DMI that are required to estimate accurate breeding values for FE (McParland et al., 2014).

Milk production traits and live weight (LW), which are cheap and easy to measure, could potentially be used as reliable predictors of DMI, since they can allow proper accounting for the amount of feed required for production and maintenance (Veerkamp, 1998; Liinamo et al., 2012; VandeHaar et al., 2016). This can be achieved through developing models to predict DMI and gross feed efficiency (GFE, kg energy-corrected milk/kg DMI). Limited efforts have, however, been made to explore the possibility of developing such prediction models in dairy cattle, despite indications that DMI can be predicted reliably from these easy-to-measure traits

(Madilindi et al., 2022). The development of reliable GFE prediction models can also limit the burden of generating DMI data prior to calculating GFE as its major determinant.

Models for predicting GFE can be developed through stepwise regression, by identifying traits that significantly account for variation in GFE. This technique selects independent/explanatory variables for multiple regression models based on their statistical significance (Smith, 2018). Although it has often been criticised for the misapplication of single-step statistical tests to a multi-step procedure, stepwise regression has become popular in cases with many explanatory variables (Ngo, 2012). The method efficiently chooses a relatively small number of explanatory variables from a vast array of possibilities. It is usually assumed that the more the number of possible predictors, the more useful is the stepwise regression (Smith, 2018). Application of this technique presents a good opportunity to develop accurate models for predicting DMI and GFE using traits such as milk production (i.e. milk yield, energy-corrected milk, butterfat, protein, lactose) and live weight. This was demonstrated in a recent study that was carried out to predict DMI in multiparous Holstein cows (Liang et al., 2021).

The current study was carried out to investigate the correlations of milk production traits and LW with DMI and GFE, and subsequently develop the most suitable prediction models for daily DMI and GFE using milk production traits and live weight, in first-parity Holstein cows.

3.2 Material and Methods

3.2.1 Animal management and data collection

The study was conducted at Limpopo Dairies (PTY) LTD farm, Louis Trichardt, South Africa, from 2 November to 11 December 2020. The availability of a feed intake measurement system at this farm mainly motivated its choice for this study. Other dairy farms across South Africa hardly measure cow feed intake due to lack of weighing facilities. The Limpopo dairy farm had a herd with over 800 lactating Holstein cows. Measurements were recorded on a group comprising 100 first-parity cows. Animals were kept under an intensive production system, with conventional cubicle housing in free stall barns. During the experimental period, temperature in the area varied from 18 to 36 °C, with an average of 22 °C per day. Cows were fed a total mixed ration (TMR) *ad libitum* thrice per day (07h30 in the morning, 13h30 in the afternoon and 20h30 in the evening). Feed was disbursed by a feeding truck with an automated feeding scale and animals had free access to water. Residual feed was weighed and discarded daily before the morning feeding. Daily dry matter intake (kg/day) of the group was automatically calculated as feed provided minus feed refusal. All animals were milked thrice a day at 04h00, 13h00, and 20h00. Individual cow milk yield (kg/day) was automatically recorded using the DeLaval's ALPRO System (Tumba, Sweden) and added to the group's milk production (MY, kg/day). Individual cow live weight was measured weekly using the DeLaval's ALPRO System (Tumba, Sweden) weighing scale, after the morning milking session, before the morning feeding.

3.2.2 Sample collection

Daily milk samples were collected for the first-parity group during the afternoon milking session. Samples were collected from Monday to Friday, for a period of six weeks. All milk samples were conserved with bronopol (2-bromo-2-nitropropane-1,3-diol) and then stored at room temperature for <7 days. They were then sent to ARC-Elsenburg Analytical Services, Stellenbosch, South Africa, for determining the percentages of butterfat (BFP), protein (PROP) and lactose (LACP), using a CombiFoss™ F+ (Foss, Hillerød, Denmark), according to manufacturer's protocols.

3.2.3 Traits computation

To standardise milk yield and its components (i.e. butterfat, protein and lactose), daily energy-corrected milk (ECM) yield was calculated according to the following formula (Kirchgebner, 1997):

$$ECM\ (kg/day) = \text{milk yield (kg) x } \frac{(0.39\ \times\ butterfat\% + 0.24\ \times\ protein\% + 0.17\ \times\ lactose\%)}{3.17}$$

Gross feed efficiency (GFE) was calculated as ECM (kg/day) divided by DMI (kg/day). Daily LW (kg/day) was calculated using linear interpolation between two weekly weight measurements. There were 25 measurements of LW and 30 records of daily MY, ECM, BFP, PROP, LACP, butterfat yield (BFY), protein yield (PROY), lactose yield (LACY), DMI and GFE, which were used for correlation analysis. Twenty-five (25) daily records of milk production traits, DMI and GFE as well as measurements of LW remained after deleting milk production traits, DMI and GFE records without corresponding LW measurements. Of these

25 records, 60% were randomly selected for a training data set that was used to develop the models, and the remaining 40% were used as a within-herd validation data set.

3.2.4 Data analysis

3.2.4.1 Correlation coefficients

Pearson correlation coefficients (r) amongst DMI, GFE, LW, MY, ECM, BFP, BFY, PROP, PROY, LACP and LACY, were calculated using the PROC CORR procedure of the Statistical Analysis System (SAS) (version 9.4, SAS Institute, Cary, NC, USA).

3.2.4.2 Development of prediction models

A stepwise regression analysis was performed to select independent traits that met the 0.1500 significance level for entry into the model as well as those accounting for the highest coefficient of determination (R^2), in explaining variation in DMI and GFE. The analysis was conducted using the PROC REG procedures of SAS (version 9.4, SAS Institute, Cary, NC, USA), and the prediction models for DMI and GFE were fitted as follows:

$$Y = \beta_0 + \beta_1 X_1 + \beta_2 X_2 + \beta_3 X_3 + \beta_4 X_4 + \beta_5 X_5 + \beta_6 X_6 + \beta_7 X_7 + \beta_8 X_8 + \beta_9 X_9 + \varepsilon ,$$

Where Y is the dependent trait [daily DMI (kg/day) or GFE], β_0 is the regression intercept, $\beta_1 - \beta_9$ are the regression coefficients, $X_1 - X_9$ are the independent traits [MY (kg/day), ECM (kg/day), BFP (%), PROP (%), LACP (%), BFY (kg/day), PROY (kg/day), LACY (kg/day) and LW (kg/day)], and ε is the residual error term.

3.2.4.3 Within-herd validation

A regression analysis was further performed between actual and predicted DMI and GFE records based on the validation dataset, using the PROC REG procedure of SAS (version 9.4, SAS Institute, Cary, NC, USA). The following fitting statistics were used to assess the robustness and accuracy of the developed prediction models: the R^2 between actual and predicted DMI and GFE values and the root mean squared error (RMSE) from plotting predicted versus actual DMI and GFE.

3.3 Results

3.3.1 Summary statistics

Descriptive statistics for DMI, GFE, milk production and LW are presented in Table 3.1. In this study, each cow consumed an average of 21.91 ± 2.58 kg/day dry matter of a total mixed ration, to produce mean ECM yield of 28.46 ± 3.91 kg/day, which resulted in a GFE of 1.32 ± 0.22 per animal per day. Animals produced MY, BFP and BFY that ranged from 21.78 to 44.73 kg/day, 1.36 to 3.36 % per day and 0.51 to 1.27 kg/day, respectively. Each cow weighed an average weight of 572 ± 15.58 kg.

Table 3.1 Descriptive statistics for dry matter intake, gross feed efficiency, milk production and live weight of first-parity Holstein cows

Traits	N	Mean	Minimum	Maximum	SD
DMI (kg/day)	30	21.91	17.09	25.71	2.58
GFE	30	1.32	0.72	1.78	0.22
MY (kg/day)	30	34.26	21.78	44.73	4.29
ECM (kg/day)	30	28.46	17.94	37.92	3.91
BFP (%)	30	2.81	1.36	3.17	0.35
PROP (%)	30	2.96	1.91	3.39	0.23
LACP (%)	30	4.91	2.96	5.06	0.37
BFY (kg/day)	30	0.95	0.51	1.27	0.14
PROY (kg/day)	30	1.01	0.64	1.36	0.16
LACY (kg/day)	30	1.68	1.05	2.22	0.24
LW (kg/day)	25	572	545	595	15.58

DMI=dry matter intake; BFP=butterfat percent; BFY=butterfat yield; MY=milk yield; ECM=energy-corrected milk; GFE=gross feed efficiency; PROP=protein percent; PROY=protein yield; LACP=lactose percent; LACY=lactose yield, LW=live weight; *N*=number of observations; SD=standard deviation.

3.3.2 Correlation analyses

Pearson's correlation coefficients of milk production traits and LW with DMI and GFE are presented in Table 3.2. DMI was positively associated with MY (0.32, $p < 0.05$) and LW (0.76, $p < 0.0001$), and negatively correlated with BFP (-0.55, $p < 0.01$). On the other hand, GFE had a desirable relationship with MY (0.36, $p < 0.05$), BFP (0.53, $p < 0.0001$) and BFY (0.83, $p <$ 0.0001, but negatively correlated with LW (-0.23, $p > 0.05$).

Table 3.2 Pearson's correlation coefficients of milk production traits and live weight with dry matter intake and gross feed efficiency, in first-parity Holstein cows

Traits	DMI	GFE
MY	0.32*	0.36*
ECM	0.07^{ns}	0.70***
BFP	-0.55**	0.53***
PROP	0.13^{ns}	0.35*
LACP	-0.19^{ns}	0.53**
BFY	-0.21^{ns}	0.83***
PROY	0.31^{ns}	0.49**
LACY	0.18^{ns}	0.61**
LW	0.76***	-0.23^{ns}

DMI=dry matter intake (kg/day); BFP=butterfat percent (%); BFY=butterfat yield (kg/day); MY= milk yield (kg/day), ECM=energy-corrected milk (kg/day), GFE=gross feed efficiency, PROP=protein percent (%); PROY=protein yield (kg/day); LACP=lactose percent (%); LACY=lactose yield (kg/day); LW=live weight (kg/day); ns=not significant at p >0.05; *** =significant at $p < 0.0001$; ** =significant at $p < 0.01$; * =significant at $p < 0.05$.

3.3.3 Developed prediction models

The models that were developed for predicting DMI and GFE, using stepwise regression, are presented in Table 3.3. All the models developed were significant ($p < 0.0001$). Live weight (kg/day) was the best predictor of DMI (kg/day) ($p < 0.0001$), followed by MY (kg/day) ($p < 0.05$). The coefficient of determination significantly increased from 0.66 to 0.79 when MY was added to the DMI prediction model based on LW only. All the other traits did not make any significant contributions ($p > 0.05$); hence, the best model for predicting DMI included only LW and MY, with a corresponding RMSE of 1.05 kg/day. Butterfat yield was the best predictor of GFE ($p < 0.0001$), followed by LW ($p < 0.05$) and MY ($p < 0.001$). A model based on BFY only accounted for 87% of the variation in GFE (i.e. $R^2 = 0.87$). Addition of LW into this model increased R^2 to 0.91, and further inclusion of MY resulted in the best model ($R^2 = 0.98$), with a low corresponding RMSE (0.05).

Table 3.3 Prediction models for DMI and GFE developed by stepwise regression

Explanatory traits	Model	R^2
DMI		
LW	$DMI = -38.09 + 0.106 \text{ x LW}$	0.66
LW, MY	$DMI = -54.21 - 0.192 \text{ x MY} + 0.146 \text{ x LW}$	0.79
GFE		
BFY	$GFE = 0.018 + 1.335 \text{ x BFY}$	0.87
BFY, LW	$GFE = 1.881 + 1.344 \text{ x BFY} - 0.003 \text{ x LW}$	0.91
MY, BFY, LW	$GFE = 4.120 + 0.024 \text{ x MY} + 1.000 \text{ x BFY} - 0.008 \text{ x LW}$	0.98

DMI=dry matter intake (kg/day); BFY=butterfat yield (kg/day); MY=milk yield (kg/day); GFE=gross feed efficiency; LW=live weight (kg/day); all models were significant at $p < 0.0001$; R^2=coefficient of determination.

3.3.4 Within-herd validation of the developed prediction models

Figure 3.1 is a graphical presentation of the regression of DMI predicted from the developed model (PDMI) on actual DMI, for the within-herd validation data set. There was a relatively moderate positive relationship (R^2 = 0.46) between PDMI and actual DMI, with a low root mean square error (RMSE) of 1.46 kg/day. The regression of predicted GFE on actual GFE is presented in Figure 3.2. There was a strong relationship between predicted and actual GFE (R^2 = 0.64) and a low corresponding RMSE (0.13).

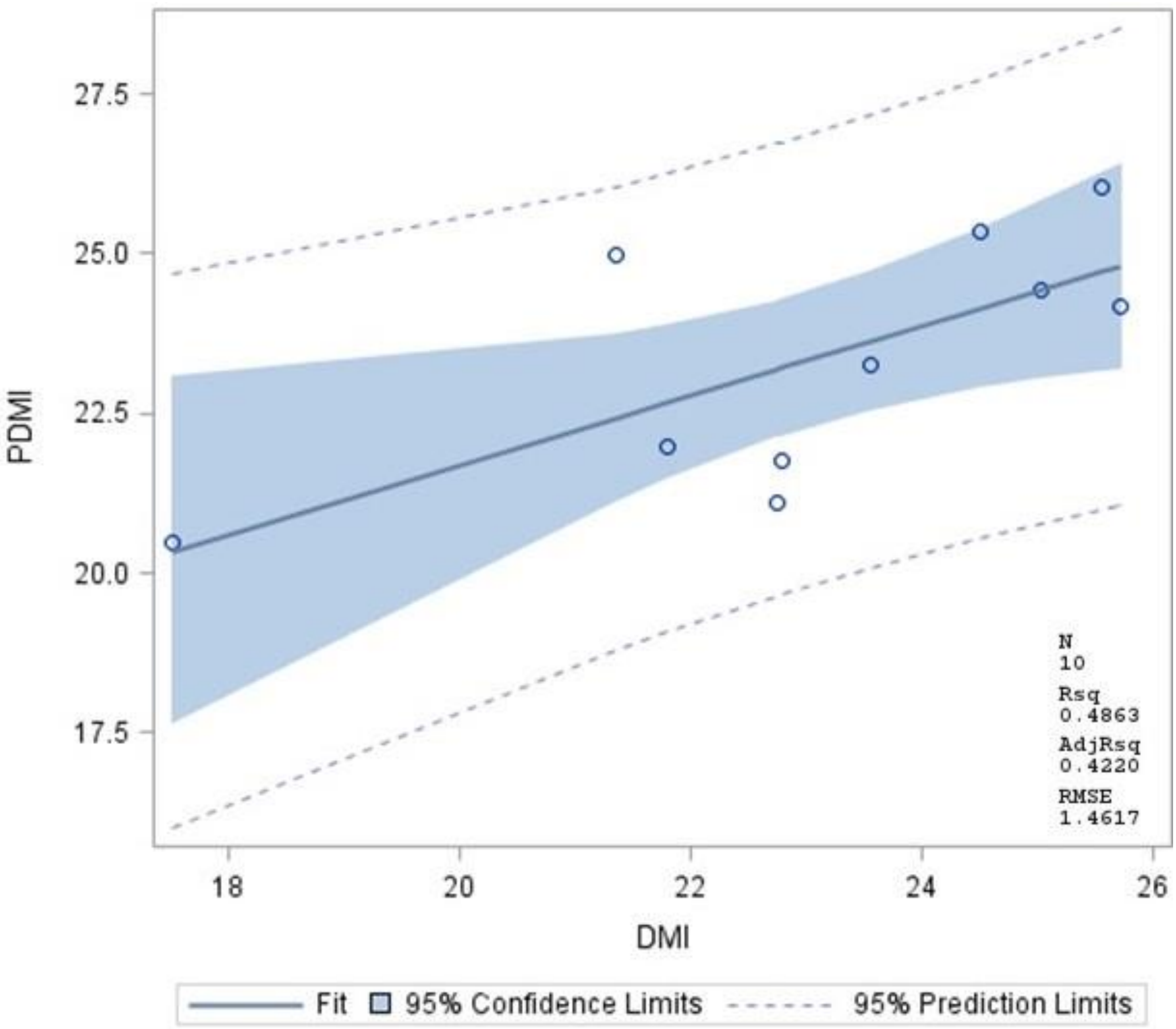

Figure 3.1 Regression of PDMI on actual DMI in first-parity Holstein cows.

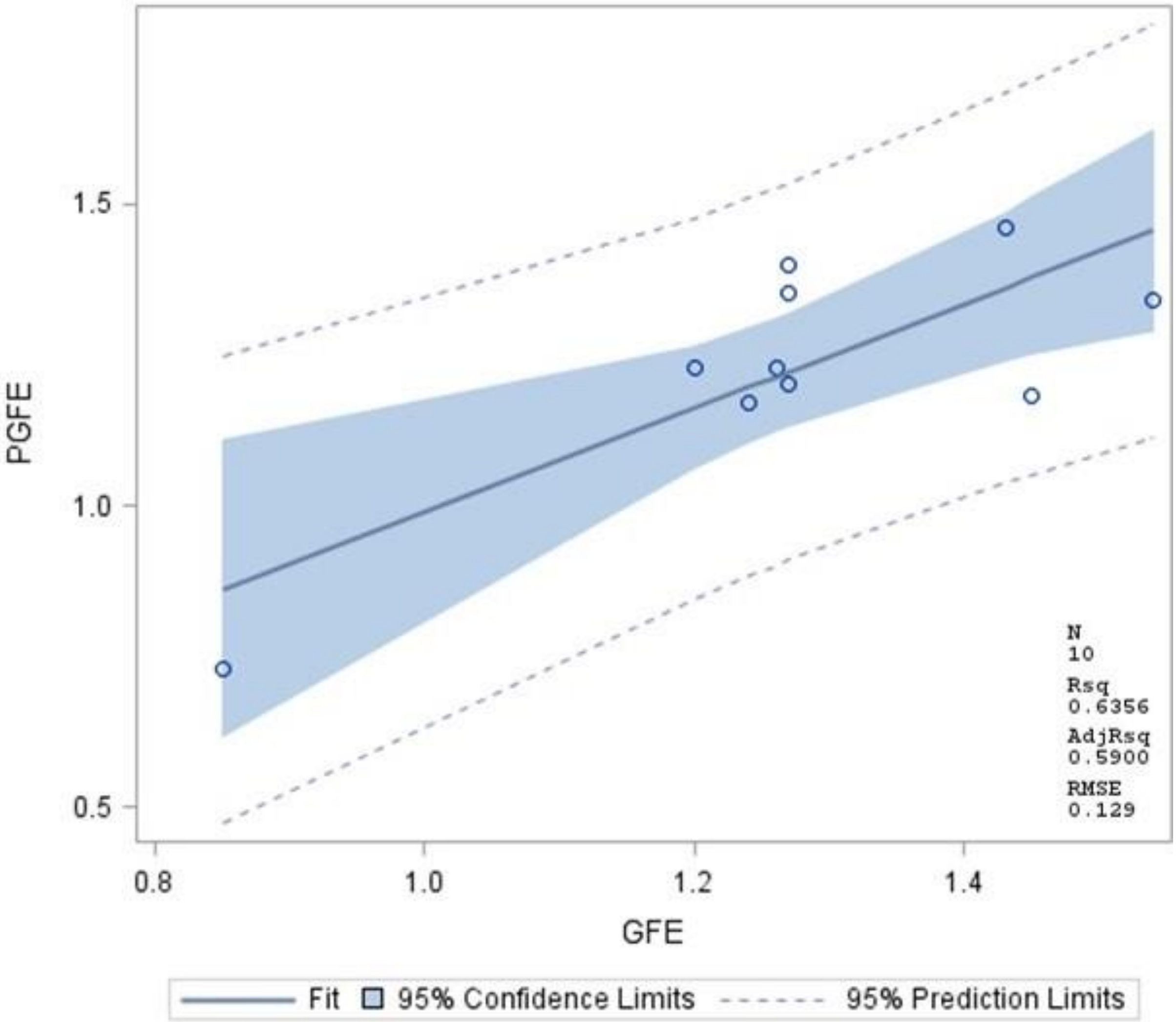

Figure 3.2 Regression of PGFE on actual GFE in first-parity Holstein cows.

3.4 Discussion

Reliable data on individual cow DMI and GFE is key to achieving improvement in the efficiency of feed utilisation in dairy cattle. Availability of such data on a large scale would enable the estimation of accurate breeding values for feed efficiency traits, thereby facilitating their inclusion in the breeding objectives (McParland et al., 2014). Generating large amounts of DMI records through direct measurement is, however, challenging. In the current study, it was hypothesised that milk production traits and live weight, which are easy and cheap to measure, can be used as reliable predictors of DMI and GFE.

3.4.1 Performance statistics for milk production, live weight, DMI and GFE

Each cow in the current study consumed an average of 21.91 kg/day dry matter of a total mixed ration, to produce mean energy-corrected milk and milk yield of 28.46 kg/day and 34.26 kg/day, respectively. This resulted in a gross feed efficiency of 1.32 per animal per day, which is within the expected range for Holstein cows in first lactation (Heinrichs and Ishler, 2016). There is, however, scarcity of information on DMI from studies in a sub-tropical environment with which to compare the results of the current study. Our mean for DMI was, however, lower than that observed in Canadian first-parity Holstein cows (Beard, 2018). This variation could be attributed to various factors including the different environmental conditions where animals were reared, the level of production and genetic merit of the cows, which may highly influence feed intake. A Holstein cow in the heat of the Limpopo Valley, where the current study was carried out, is expected to have much lower intake compared to one in freezing Canada. Maintenance requirements would also be higher for the cow in Limpopo, as it would need more energy to cool its body. Generally, the means for milk production, live weight, DMI and GFE found in this study are within the range for Holstein animals in first-parity (ICAR, 2012; Poncheki et al., 2015; Heinrichs and Ishler, 2016; Krattenmacher et al., 2019).

3.4.2 Correlations between milk production traits, live weight, DMI and GFE

A preliminary step in the development of prediction models was to quantify the phenotypic association of milk production traits and live weight with DMI and GFE, in order to determine those traits that could be the best candidates as predictors for DMI and GFE. Milk yield was moderately and positively associated with DMI (0.32), meaning that increased feed intake led to higher milk production, which is in agreement with findings from other studies (e.g., Ben Meir et al., 2018; Zhang et al., 2020; Liang et al., 2021). This is attributable to more nutrients being available for milk production, after meeting requirements for other physiological functions such as growth and maintenance (Erickson and Kalscheur, 2020). The association between MY and DMI demonstrates that MY could be a useful predictor for DMI. Accordingly, MY has been widely considered alone or together with other traits (e.g. butterfat, protein, lactose contents, LW, mid-infrared spectra of milk, parity and stage of lactation) in most prediction models for DMI in dairy cows (NRC, 2001; Lindgren et al., 2001; Shetty et al., 2017; Lahart et al., 2019; Liang et al., 2021).

Butterfat percent had a moderate antagonistic association with DMI (-0.55), although a previous study reported a poor positive association between these traits in first-parity Holstein cows in Belgium (Zhang et al., 2020). This relationship implies that cows consuming more dry matter produced milk with less butterfat. The biological basis of this relationship is not clear. In extreme cases, too much feed in the cow rumen, particularly rations low in fibre, may cause digestibility problems, which may result in low milk butterfat production (Heinrichs and Jones, 2016). This association between butterfat percent and DMI presented butterfat percent as a candidate predictor in developing our models for predicting DMI. Other studies have also demonstrated the importance of BFP in prediction models for DMI in dairy cows (e.g. Lahart et al., 2019).

Live weight had a strong positive association with DMI (0.76), in concurrence with findings from other studies on first-parity Holstein cows (e.g. Zhang et al., 2020). This relationship has, however, been reported to be moderate in multiparous cows (Zhang et al., 2020; Liang et al., 2021). Thus, heavier animals consume more feed due to their higher requirements for body maintenance, and this has been documented in many studies (Searle et al., 1982; Vallimont et al., 2011; Guinguina et al., 2019). Searle et al. (1982) indicated that LW is one of the factors most closely related to net energy for maintenance. The strong association between LW and DMI observed in the current study points to LW as a major candidate for predicting DMI. Consequently, LW has been widely considered in most prediction models of DMI in dairy cows (NRC, 2001; Lahart et al., 2019; Martin et al., 2021; Liang et al., 2021).

The strong positive relationship observed between BFY and GFE (0.83) implies that cows producing higher quantities of butterfat were more efficient at converting feed into milk. There is, however, scarcity of information on the relationship between these two traits in the literature, with which to compare these findings. Thus, BFY also appeared as a promising predictor of GFE in the development of our prediction models.

A moderate positive association (0.36) was observed between MY and GFE. Comparable results have been reported in Holstein cows (Ben Meir et al., 2018); however, a previous study found a stronger relationship between these two traits (Spurlock et al., 2012). In addition, a long-term study may be beneficial to achieve a strong relationship. This association implies that as MY increases, corresponding gains in feed efficiency are achieved. Milk yield, therefore, came out as another strong potential predictor of GFE.

There was a low antagonistic relationship (-0.23) between LW and GFE, which was however not significant. This negative association is a well-documented phenomenon, and is attributable to the fact that larger cows demand more nutrients for body maintenance, resulting in less feed being available for milk production (Linn et al., 2009; Vallimont et al., 2011; Ben Meir et al., 2018; Guinguina et al., 2019). Thus, LW could contribute towards the prediction of GFE. A recent study by Guinguina et al. (2019) found the inclusion of LW to be useful in models for predicting GFE.

3.4.3 Developed prediction models for DMI and GFE

Reliable prediction of DMI and/or GFE from easy-to-measure traits could assist in generating large quantities of data for the estimation of accurate breeding values. Such predictions can be obtained from basal linear models, with milk production and live weight as independent variables (VandeHaar et al., 2016). These easy-to-measure traits are known to greatly influence feed efficiency, as they are important drivers of feed intake (VandeHaar et al., 2016). It is unclear which trait, between DMI and GFE, can be predicted more reliably than the other from milk production and live weight. In the current study, stepwise regression analyses were performed to develop models for predicting DMI and GFE using milk production traits and live weight, as independent variables, in first-parity Holstein cows.

3.4.3.1 Dry matter intake

Live weight (kg/day) was the best predictor of DMI (kg/day), followed by MY (kg/day) in the present study. This confirms the correlation results of our preliminary analysis, which found these two traits to be good potential predictors of DMI. Combining MY and LW we have achieved better accuracy of prediction, compared to a model with either of the traits only. Previous studies have similarly found MY and LW to be highly correlated with DMI and, thus, included them in prediction models for DMI (Holter et al., 1997; NRC, 2001; Lahart et al., 2019; Liang et al., 2021; Martin et al., 2021). These two variables are the major determinants of the cow’s total nutrient requirements; hence, they have large influence on DMI. Our best model for predicting DMI had a greater prediction power (R^2 of 0.79) prior validations, than the one recently developed from multiparous Holstein data in China (R^2 of 0.46) (Liang et al., 2021). A high prediction accuracy (R^2 of 0.71) for DMI, was also obtained from a model including MY, LW and mid-infrared (MIR) spectra data, in a multiparous American Holstein cattle population (Dórea et al., 2018). Differences in the methods used to measure DMI, model development approaches, milk production traits considered, parity and stage of lactation may be responsible for the disparity in accuracy of prediction between studies. Based on the magnitude of the R^2 value, our model may be considered sufficiently reliable for application to obtain large quantities of DMI data at low cost. High accuracy of phenotypes may be dispensed with as a requirement for obtaining accurate estimated breeding values (EBVs) if large quantities of phenotypic records are obtainable (Calus et al., 2013; McParland and Berry, 2016). Given the fact that a significantly high number of the South African Holstein cattle population is under national milk recording and improvement scheme (NMRIS, 2020), the models developed in the current study provide an opportunity to generate large quantities of DMI data, which can be utilised to produce high accuracy EBVs for feed efficiency. There is, however, a need to determine the genetic variability of the predicted DMI, so as to determine the potential to improve it through selection.

3.4.3.2 Gross feed efficiency

In the present study, butterfat yield (kg/day) was the best predictor of GFE, followed by LW (kg/day) and MY (kg/day). This supports the results of our preliminary analysis (i.e. correlations), which established these three traits to be good potential predictors of GFE. A model including BFY, MY and LW achieved the best accuracy of prediction, compared to one with only one of these traits. These traits have also been found to be associated with GFE and, therefore, good predictor traits for GFE in several other studies (Linn et al., 2009; Vallimont et al., 2011; Ben Meir et al., 2018; Guinguina et al., 2019). Our best model for predicting GFE had an exceptionally stronger prediction power (R^2 = 0.98) compared to the previously developed model from multiparous Holstein data (R^2 = 0.76) (Guinguina et al., 2019). Beard (2018) developed models with much lower prediction ability (R^2 = 0.45) using primiparous Canadian Holstein data, including milk yield, milk components and live weight only. The disparity in prediction power among the different studies may be attributed to variation in methods used to measure DMI, parities considered and approaches used to develop the models. The stage of lactation at which DMI is measured may also influence accuracy of prediction (Lahart et al., 2019). There are limited studies on primiparous cows in the literature. Given its high prediction power (i.e. high coefficient of determination), our best model could be applied to generate large quantities of reliable GFE data at low cost, which can be used to estimate accurate EBVs for GFE. It is, however, necessary to first determine the genetic variability of this predicted trait, in order to determine the extent to which it is under genetic control.

3.4.4 Within-herd validation of DMI and GFE prediction models

An assessment of the robustness and accuracy of the models developed for predicting DMI and GFE from milk production and live weight was carried through within-herd validation of predicted data. There were no external data available to carry out such an analysis.

3.4.4.1 Validation of DMI prediction model

Validation of the model for predicting DMI that included MY and LW only yielded a moderate R^2 and low RMSE, indicating modest robustness and accuracy. This prediction power was, however, relatively higher compared to values observed by Liang et al. (2021) in a study on multiparous Holstein cattle. Interestingly though, the model developed by Liang et al. (2021) included dry matter intake of the first 2 hours after feeding, in addition to MY and LW. On the other hand, Lahart et al. (2019) developed models that predicted DMI with milk production traits (MY, fat percent and protein percent) and LW as well as stage of lactation and parity of grazing Irish Holstein-Friesian and Jersey cross-bred cattle. Adding milk MIR spectra data to these prediction models resulted in a slightly improved prediction power (Lahart et al., 2019). Similarly, Dórea et al. (2018) predicted DMI from milk yield, body weight and days in milk of multiparous American Holstein cattle with a strong prediction power, which improved with the addition of milk MIR spectra data. Models developed from the different studies are bound to vary in their ability to predict DMI largely due to differences in the predictor traits included, methods used to measure DMI and validate predicted DMI, as well as factors such as breed, parity, stage of lactation and production system (Dórea et al., 2018; Lahart et al., 2019; Liang et al., 2021). Utilisation of additional easy-to-measure traits such as milk MIR spectra and days in milk may be useful in improving the accuracy of predicting DMI, as indicated by some previous studies (Shetty et al., 2017; Dórea et al., 2018; Wallén et al., 2018; Lahart et al., 2019). It might also be worthwhile to explore other prediction and validation methods such as the partial least squares approach and artificial neural networks (Felipe et al., 2015; Dórea et al., 2018).

3.4.4.2 Validation of GFE prediction model

Studies on the prediction of GFE are generally scarce in the literature. The model that we developed for predicting GFE from BFY, LW and MY had a reasonably strong prediction ability, as indicated by a high R^2 and small RMSE. This was confirmed by the results of within-herd validation, despite a slight inconsistence in the relative magnitude of the R^2 and RMSE values. Guinguina et al. (2019) obtained comparable results, using energy-corrected milk, live weight and estimated dry matter digestibility to predict GFE. In another study on primiparous Canadian Holstein cattle, prediction of weekly feed intake conversion efficiency from milk yield, milk components and live weight yielded a moderate prediction ability, with a much higher RMSE than in the current study (Beard, 2018). There is scope to improve the model for predicting GFE developed in the current study by utilising data from novel technologies, such as milk MIR spectra. Extensive research has demonstrated that milk MIR spectra data can considerably improve the performance of models for predicting feed efficiency traits such DMI, residual feed intake and energy intake in dairy cows (McParland et al., 2014; Shetty et al., 2017; Dórea et al., 2018; Wallén et al., 2018; Lahart et al., 2019). The application of other model development approaches, such as partial least squares and artificial neural networks, also warrants investigation for better prediction of GFE (Felipe et al., 2015; Dórea et al., 2018).

3.4.5 Limitations of the study and recommended future work

The current study developed models for predicting DMI and GFE utilising data of first-parity Holstein cows, and achieved reasonable prediction accuracies, as determined by within-herd validation. External (across-herd) validation, which examines whether a prediction model can function outside of the dataset used to create the model was, however, not performed in this study. Such validation is essential in ensuring that a model is robust enough to achieve the same power of prediction in other populations (Shetty et al., 2017; Lahart et al., 2019). It is also not clear if the models developed in the current study can be reliably extrapolated to multi-parity cows. Thus, further studies are required to determine if the models developed in this study are applicable in other herds, multi-parity cows, breeds and/or other dairy production systems. Such knowledge is a prerequisite to the wide application of these models in different environments. Furthermore, it is important to determine the genetic variation of the predicted DMI and GFE phenotypes, in order to assess their potential for improvement through selection. Further research is also warranted to determine whether there are genes or parts of the genome that are associated with these predicted traits. Such knowledge may assist in implementing marker-assisted selection, by identifying animals that utilise feed efficiently through DNA analysis.

3.5 Conclusion

Results of the current study suggest that daily DMI and GFE can be predicted reliably for first-parity Holstein cows, using models comprising of milk production traits and live weight. The prediction models developed in the study may be used to generate large quantities of records of individual cow DMI and GFE, predicted from these easy-to-measure and routinely recorded traits. Provided these predicted traits exhibit considerable genetic variation, such data could be used to estimate accurate EBVs, thus facilitating genetic improvement of feed efficiency through selection. Further research is, however, required to validate these prediction models with external data, as well as extending the analyses to multi-parity cows.

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Chapter 4

Predicting gross feed efficiency from milk components and live weight in multiparous Holstein cows

Abstract

The primary objective of this study was to develop and validate models for predicting gross feed efficiency in multiparous Holstein cows, using milk components and live weight (LW). Thirty daily measurements of dry matter intake (DMI) and milk production traits (milk yield (MY), energy-corrected milk (ECM), butterfat yield (BFY), protein yield (PROY), lactose yield (LACY), butterfat percent (BFP), protein percent (PROP), lactose percent (LACP), and 25 daily live weight (LW) records from a group of 110 intensively-fed multiparous Holstein cows, in lactations 2 to 6, were used. Gross feed efficiency (GFE) was computed as kg ECM divided by kg DMI. Correlations (r) of the milk production traits and LW with GFE were estimated first, in order to identify the most potential predictors of GFE. A forward stepwise regression analysis was then applied to develop models to predict GFE from LW, MY, ECM, BFY, PROY, LACY, BFP, PROP and LACP. Within-herd validation of the models was further conducted, by performing regression analysis between actual and predicted GFE records based on the validation dataset. Means for DMI, ECM, butterfat yield (BFY) and LW were 26.24 ± 1.80 kg/day, 40.59 ± 3.82kg/day, 1.49 ± 0.16 kg/day and 680 ± 20.57 kg/day, respectively. Mean GFE was 1.55 ± 0.16. Gross feed efficiency had positive correlations with BFY (r = 0.82, $p < 0.0001$), ECM (0.71, $p < 0.0001$), BFP (0.63, $p < 0.001$), MY (0.53, $p < 0.01$) and LW (0.05, $p > 0.05$), and negative association with LACP (-0.13, $p > 0.05$). Butterfat yield was the best predictor for GFE, and a model comprising of BFY only predicted GFE with a high level of reliability [R^2 = 0.80; root mean squared error = 0.09]. The best model for predicting GFE was: GFE = 0.4134 + 0.7594 x BFY (kg/day). Within-herd validation of this model revealed a relatively moderate relationship between actual and predicted GFE (R^2 = 0.54) and a low RMSE (0.06), suggesting its potential use to predict GFE in intensively-fed multi-parous Holstein cows. Large quantities of data on individual cow GFE can be generated at a low cost, utilising this model, thus providing an opportunity to improve feed efficiency through selection.

Keywords: Association, basal model, feed efficiency, multi-parous, stepwise analysis

4.1 Introduction

Feed efficiency is an extremely important trait in dairy cattle. Cows that convert feed into milk efficiently are more profitable, as they reduce feed costs (Miglior et al., 2017; Heida et al., 2021). Improved dairy cow feed efficiency also results in a lower carbon footprint by the dairy industry (de Haas et al., 2017; Garnsworthy et al., 2019; Olijhoek et al., 2020). Thus, genetic selection for better feed efficiency may contribute both economic and environmental benefits (de Haas et al., 2017; Heida et al., 2021). A major challenge in achieving such selection is quantifying dry matter intake (DMI) of lactating cows, which is a major variable required to calculate feed efficiency traits. Measurement of dry matter intake is labour-intensive and costly, especially on commercial herds or outside a research environment (Brito et al., 2020). Consequently, a lack of records on daughters of progeny-tested bulls has been a major obstacle hampering the inclusion of feed efficiency in selection programmes (Manzanilla-Pech et al., 2017; Wallén et al., 2018; Brito et al., 2020).

Large quantities of data on GFE of individual cows are a prerequisite to achieving accurate selection and, hence, significant genetic improvement (McParland et al., 2014; Seymour et al., 2019). This could be achieved by predicting feed efficiency phenotypes from easy-to-measure and widely-recorded traits (Berry and Crowley, 2013; Manzanilla-Pech et al., 2016, 2017; Zhang et al., 2020; Madilindi et al., 2022a). It has been noted in previous research that milk production and live weight allow proper accounting of the amount of feed required for production and maintenance (Liinamo et al., 2012; VandeHaar et al., 2016; Manzanilla-Pech et al., 2017; Zhang et al., 2020).

Recently, Madilindi et al. (2022b) developed models that could reliably predict daily DMI and GFE from milk yield, butterfat yield and live weight (LW) in primiparous Holstein cows. This presents an opportunity to generate large quantities of GFE data, which could be used to implement genetic evaluation at a low cost (Madilindi et al., 2022b). Due to a variety of physiological changes occurring in the cow between the first and later lactations, it is not clear whether these models could be extrapolated to multiparous cows (Madilindi et al., 2022b). Hence, it was deemed necessary to develop appropriate prediction models for multiparous cows.

The present study was, therefore, carried out to develop and validate prediction models for daily GFE, using milk production traits and live weight, in multiparous South African Holstein cows.

4.2 Material and Methods

4.2.1 Animal management and data collection

Multiparous cows in the same herd described in Chapter 3 was used for the current study. Although they were managed the same, the multiparous group was on a higher plane of nutrition. Management of animals and recording of data were as described in section 3.2.1 of Chapter 3. Data were recorded on a group comprising 110 multi-parous Holstein cows.

4.2.2 Sample collection

Sample collection was as described in section 3.2.2 of Chapter 3. Milk samples were collected daily from a group of 110 multiparous Holstein cows, in lactations 2 to 6, during the afternoon milking session.

4.2.3 Traits recorded

Energy-corrected milk (ECM), gross feed efficiency (GFE) and live weight (LW) were computed as described in section 3.2.3 of Chapter 3. Collected data comprised of 30 records on daily milk production traits (milk yield (MY), ECM, butterfat percent (BFP), protein percent (PROP), lactose percent (LACP), butterfat yield (BFY), protein yield (PROY), lactose yield (LACY)), DMI and GFE, and 25 measurements of LW. Twenty-five daily records of milk production traits, DMI and GFE as well as measurements of LW remained after deleting milk production traits, DMI and GFE records without corresponding LW measurements. Of these 25 records, 60% were randomly selected for a training data set that was used to develop the models, and the remaining 40% were used as a within-herd validation data set.

4.2.4 Data analysis

4.2.4.1 Correlation coefficients

Correlations of MY, ECM, BFY, PROY, LACY, BFP, PROP, LACP and LW with GFE were computed as described in section 3.2.4.1 of Chapter 3.

4.2.4.2 Development of prediction model

The model to predict GFE from milk components and live weight was developed by a stepwise regression approach, as described in section 3.2.4.2 of Chapter 3.

4.2.4.3 Within-herd validation

Validation for robustness and accuracy of the model that was developed to predict GFE from milk components and live weight was carried out by regressing actual GFE on predicted GFE, as described in section 3.2.4.3 of Chapter 3.

4.3 Results

4.3.1 Descriptive statistics

Summary statistics for DMI, GFE, milk components and LW are presented in Table 4.1. Each cow consumed an average of 26.24 ± 1.80 kg dry matter of a total mixed ration, to produce an average ECM yield of 40.59 ± 3.82 kg, per day. This resulted in a GFE of 1.55 ± 0.16 per animal per day. Butterfat yield (BFY) per cow varied from 1.27 to 2.07 kg/day. Cow live weight ranged from 648 to 708 kg, with a mean of 681 ± 20.57 kg.

Table 4.1 Summary statistics for dry matter intake, gross feed efficiency, milk components and live weight of multi-parous Holstein cows

Traits	N	Mean	Minimum	Maximum	SD
DMI (kg/day)	30	26.24	21.42	28.75	1.80
GFE	30	1.55	1.33	2.01	0.16
MY (kg/day)	30	44.81	40.61	63.57	4.01
ECM (kg/day)	30	40.59	35.96	56.92	3.82
BFP (%)	30	3.32	2.84	4.10	0.24
PROP (%)	30	3.05	2.90	3.30	0.10
LACP (%)	30	4.94	4.86	5.03	0.05
BFY (kg/day)	30	1.49	1.27	2.07	0.16
PROY (kg/day)	30	1.37	1.20	1.95	0.14
LACY (kg/day)	30	2.21	2.01	3.09	0.19
LW (kg/day)	25	681	648	708	20.57

DMI=dry matter intake; BFP=butterfat percent; BFY=butterfat yield; MY=milk yield; ECM=energy-corrected milk; GFE=gross feed efficiency; PROP=protein percent; PROY=protein yield; LACP=lactose percent; LACY=lactose yield; LW=live weight; N=number of observations; SD=standard deviation.

4.3.2 Correlations

Table 4.2 presents Pearson's correlation coefficients of milk production traits and LW with GFE. Gross feed efficiency had high and positive correlations with BFY (0.82, $p < 0.0001$) and ECM (0.71, $p < 0.0001$). It had moderate correlations with BFP (0.63, $p < 0.001$), MY (0.53, $p < 0.01$) and PROY (0.47, $p < 0.001$) and a low correlation with LACP (-0.13, $p > 0.05$). There was, however, poor correlation of GFE with LW (0.05, $p > 0.05$).

Table 4.2 Pearson's correlation coefficients of milk production traits and live weight with gross feed efficiency, in multiparous Holstein cows

Trait	**GFE**
MY	0.53*
ECM	0.71***
BFP	0.63**
PROP	0.03^{ns}
LACP	-0.13^{ns}
BFY	0.82***
PROY	0.47**
LACY	0.53**
LW	0.05^{ns}

BFP=butterfat percent (%); BFY=butterfat yield (kg/day); MY=milk yield (kg/day); ECM=energy-corrected milk (kg/day); GFE=gross feed efficiency; PROP=protein percent (%); PROY=protein yield (kg/day); LACP=lactose percent (%); LACY=lactose yield (kg/day); LW=live weight (kg/day); ns=not significant at p >0.05; ***=significant at p < 0.0001; **=significant at p < 0.01; *=significant at p < 0.05.

4.3.3 Developed prediction model

The model developed comprised of butterfat yield (BFY) (kg/day) as the only predictor of GFE ($p < 0.0001$), and had a coefficient of determination (R^2) of 0.80 and a low residual mean square error (RMSE, 0.09). Other predictor traits did not make significant contributions ($p > 0.05$) to the model. The model developed to predict GFE was:

$$pGFE = 0.4134 + 0.7594 \times BFY(kg/day)$$

4.3.4 Within-herd validation of the developed prediction model

The regression of predicted GFE (pGFE) on actual GFE, is presented in Figure 4.1, for the within-herd validation data set. The relationship between predicted and actual GFE was moderate (R^2 = 0.54), with a low RMSE (0.06).

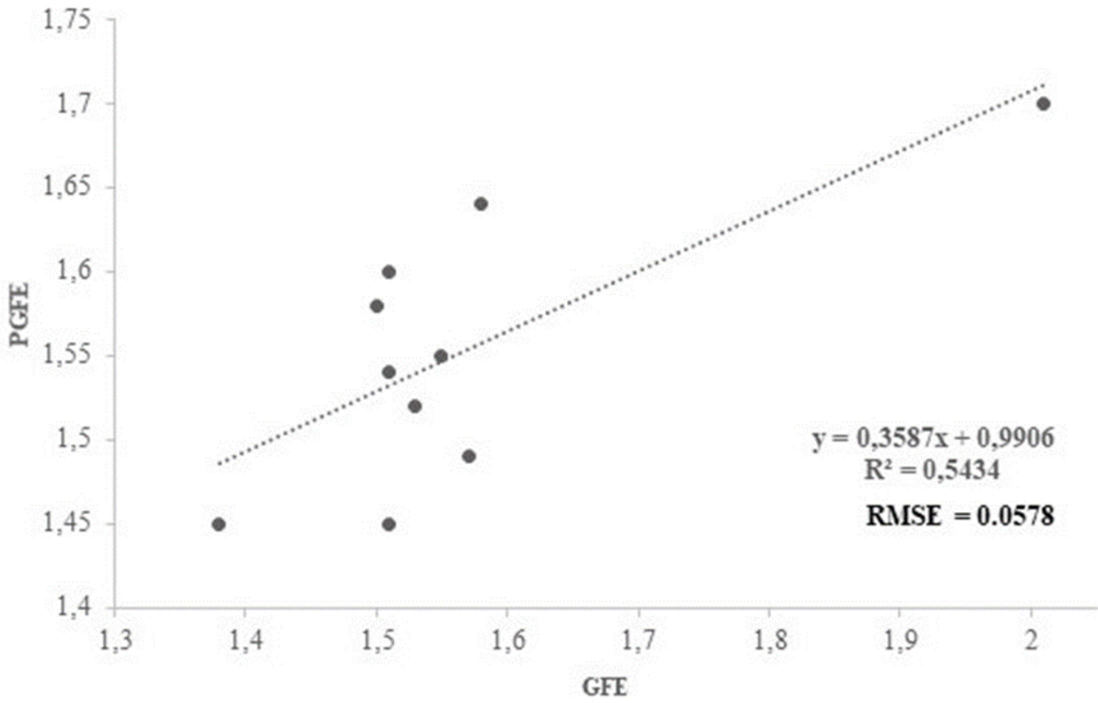

Figure 4.1 Regression of pGFE on actual GFE in multiparous Holstein cows.

4.4 Discussion

Scarcity of data on individual cow DMI is the main challenge to achieving genetic improvement of feed efficiency in dairy cows (Connor, 2015; Brito et al., 2020). In this study, it was hypothesised that milk components and live weight, which are easy-to-measure traits, can be used as reliable predictors of GFE in multiparous cows. Realisation of this hypothesis would make it possible to achieve accurate selection for feed efficiency without having to directly measure individual cow DMI.

4.4.1 Performance statistics for milk production, live weight, DMI and GFE

In this study, an individual cow consumed an average of 26.24 ± 1.80 kg dry matter of a total mixed ration to produce an average of 40.59 ± 3.82 kg of ECM, per day. This translates to a GFE of 1.55 ± 0.16 per cow, which is comparable to values reported in other studies elsewhere, for multiparous Holstein cows (Heinrichs and Ishler, 2016; Becker et al., 2022).

4.4.2 Correlations of milk production traits and live weight with GFE

An initial step in developing the prediction models was to identify the most prospective predictors of GFE by estimating phenotypic correlations of milk production traits and live weight with GFE. The fairly high positive correlation (0.71) observed between ECM and GFE implies that cows producing higher yields of ECM are more efficient convertors of feed into milk. This concurs with results from a previous study on Canadian Holstein cows (Manafiazar et al., 2016); however, Ben Meir et al. (2018) found a less strong relationship (0.33) between the two traits in Israeli Holstein cows. Thus, ECM is likely to serve as a good predictor for GFE. Similar findings were made by Guinguina et al. (2019), who went on to develop a prediction model for GFE that included ECM, live weight and estimated faecal dry matter output.

The strong positive association between BFY and GFE (0.82) observed in this study supports results from an earlier study on first-parity South African Holstein cows (Madilindi et al., 2022b). Moreover, BFY came out as the most potential predictor of GFE, also in agreement with Madilindi et al. (2022b).

Other production traits such as BFP (0.63), MY (0.53) and PROY (0.47) had moderate correlations with GFE, which concurs with other studies (Ben Meir et al., 2018, Madilindi et al., 2022b). Thus, these traits are potentially good predictors of GFE. This finding is supported by a recent study that developed a model for predicting nitrogen use efficiency which included milk, protein and butterfat content, in Chinese Holstein cows (Shi et al., 2023).

The association between LW and GFE was poor (0.05) and insignificant, in consensus with other previous studies that, however, reported negative correlations (Manafiazar et al., 2016; Ben Meir et al., 2018; Madilindi et al., 2022b). An antagonistic association has been widely observed between LW and GFE, which is attributable to the fact that larger cows demand more nutrients for body maintenance, resulting in less feed being available for milk production (Linn et al., 2009; Vallimont et al., 2011; Ben Meir et al., 2018; Guinguina et al., 2019). Hence, LW has been included in models for predicting GFE in other studies (Guinguina et al., 2019; Madilindi et al., 2022b).

4.4.3 Developed model for predicting GFE

Milk components and live weight are easy-to-measure traits that are key drivers of feed intake and, therefore, major determinants of feed efficiency in dairy cows (VandeHaar et al., 2016; Madilindi et al., 2022a). They can, therefore, potentially serve as good predictors of feed efficiency (Madilindi et al., 2022a). In this study, stepwise regression analyses were carried out to develop a basal linear model for predicting GFE, based on milk components and live weight as independent traits, in multiparous Holstein cows. Butterfat yield (kg/day) was the best predictor of GFE, as expected from the high correlation observed between BFY and GFE in preliminary analysis. It was, in fact, the only trait that made a significant contribution to the prediction of GFE. The prediction model for GFE developed, therefore, only comprised of BFY. Other milk components, as well as live weight, have however been included in prediction models for GFE developed in previous studies (Guinguina et al., 2019; Madilindi et al., 2022b). Our best model for predicting GFE had a stronger prediction power (R^2 = 0.80) prior validations, compared to other models developed previously from multiparous Holstein data (R^2 = 0.76) (Guinguina et al., 2019). This prediction power was, however, lower than the value of 0.98 obtained for models developed recently for first-parity Holstein cows (Madilindi et al., 2022b). The models developed by Madilindi et al. (2022b), however, included BFY, milk yield and live weight. Besides disparity in traits and model development approaches applied, factors such as parities and stages of lactation considered, may account for the variance in prediction power among studies (Guinguina et al., 2019; Lahart et al., 2019; Martin et al., 2021; Madilindi et al., 2022b; Shi et al., 2023). The high prediction power obtained with our best model suggests that this model could be applied reliably to produce large quantities of GFE phenotypes, at a low cost. Such data could be used to obtain estimated breeding values for GFE with high accuracy. It is, however, necessary to assess the extent to which this predicted GFE is under genetic influence, in order to determine its suitability as a selection criterion.

4.4.4 Within-herd validation of GFE prediction model

A goodness of fit linear regression of predicted GFE (pGFE) on actual GFE from the same herd was conducted, in order to assess robustness and accuracy of the developed model. Unfortunately, there were no data available to conduct an external (across-herd) validation. A fairly moderate R^2 value (0.54) and a low RMSE (0.06) were obtained, suggesting reasonable robustness and accuracy of the model. Beard (2018) obtained a comparable prediction ability, with a model comprising milk yield, milk components and live weight, and using first-parity Canadian Holstein data. However, an appreciably better prediction ability was obtained recently with a model to predict GFE from BFY, milk yield and live weight, using first-parity South African Holstein data (Madilindi et al., 2022b). Use of more predictor traits, which could have accounted for more of the variation in GFE, may explain the better prediction ability achieved by Madilindi et al. (2022b).

The use of data from novel technologies, such as milk mid-infrared spectra, may help to improve the performance of the model developed in the current study, as demonstrated in previous studies on prediction of other feed efficiency traits in dairy cows such as dry matter intake, residual feed intake, energy intake and nitrogen use efficiency (McParland et al., 2014, 2016; Shetty et al., 2017; Dórea et al., 2018; Wallén et al., 2018; Lahart et al., 2019; Shi et al., 2023). In addition, exploring other prediction and validation methods such as the partial least squares approach and artificial neural networks might assist to improve the performance of the prediction models (Felipe et al., 2015; Dórea et al., 2018; Salleh et al., 2023; Shi et al., 2023).

4.5 Conclusion

A model that can reliably predict daily GFE, using butterfat yield only, was developed for multiparous Holstein cows in the current study. This model can, therefore, be applied to generate large quantities of individual cow GFE data, at a low cost. If the predicted GFE expresses genetic variation, the data so generated could be used to achieve accurate selection for feed efficiency. Across-herd validation of this prediction model is, however, important before its widespread application.

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Chapter 5

Genetic parameters for predicted gross feed efficiency and its association with energy-corrected milk in South African Holstein cattle

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Abstract

Genetic parameters for daily predicted gross feed efficiency (pGFE) and energy-corrected milk (ECM) in the first three parities of South African Holstein cattle were estimated by repeatability animal models. Data comprised of 11,068 test-day milk production records of 1,575 Holstein cows that calved between 2009 and 2019. Heritability estimates for pGFE were 0.12 ± 0.06, 0.09 ± 0.04 and 0.18 ± 0.05 in early, mid and late lactation, respectively. Estimates were moderate for primiparous (0.21 ± 0.05) and low for multiparous (0.10 ± 0.04) cows. Heritability and repeatability across all lactations were 0.14 ± 0.03 and 0.37 ± 0.03, respectively. Genetic correlations between pGFE in different stages of lactation ranged from 0.87 ± 0.24 (early and mid) to 0.97 ± 0.28 (early and late), while a strong genetic correlation (0.90 ± 0.03) was found between pGFE and ECM, across all lactations. The low to moderate heritability estimates for pGFE suggest potential for genetic improvement of the trait through selection, albeit with a modest accuracy of selection. The high genetic correlation of pGFE with ECM may, however, assist to improve accuracy of selection for feed efficiency by including both traits in multi-trait analyses. These genetic parameters may be used to estimate breeding values for pGFE, which will enable the trait to be incorporated in the breeding objective for South African Holstein cattle.

Keywords: Predicted feed efficiency, genetic improvement, lactation stage, repeatability model

5.1 Introduction

The dairy industry is increasingly under pressure to improve feed efficiency, due to the need to maintain herd profitability in an era of increasing feed costs, as well as growing concerns to safeguard the environment (Connor, 2015; Miglior et al., 2017; Løvendahl et al., 2018; Krattenmacher et al., 2019; Madilindi et al., 2022a). Gross feed efficiency (GFE) is an important trait in dairy production that provides valuable information about the efficiency of lactating cows to utilise feed. It is measured as the ratio between kilograms of milk or energy-corrected milk produced and kilograms of dry matter intake (DMI) (Chesnais et al., 2016).

Dry matter intake is a major component of feed efficiency traits, including GFE (Connor, 2015; Chesnais et al., 2016; Madilindi et al., 2022a). Direct measurement of DMI from individual lactating cows is generally difficult, and may be achievable only in research stations or appropriately-equipped commercial herds, under a total mixed ration-feeding system (Manzanilla-Pech et al., 2014; de Haas et al., 2015; Li et al., 2018; Krattenmacher et al., 2019). It is thus difficult to obtain DMI data directly from lactating cows on a large scale (Miglior et al., 2017; Madilindi et al., 2022a), which presents a serious challenge to selection for feed efficiency.

Due to scarcity of data on feed intake, there is a paucity of information on the genetic attributes of GFE in dairy cows (Spurlock et al., 2012; Köck et al., 2018). A study by Spurlock et al. (2012) described GFE as being moderately heritable in American Holstein cows, with estimates of 0.20 ± 0.12 in mid lactation and 0.32 ± 0.13 in early lactation, from random regression model analyses. Heritability estimates for GFE over the entire lactation were also moderate in primiparous (0.47 ± 0.23) and multiparous (0.43 ± 0.25) cows, with an overall estimate of 0.32 ± 0.13 across all lactations (Spurlock et al., 2012). On the other hand, Köck et al. (2018) reported a low heritability estimate (0.12 ± 0.04) for GFE across all lactations of Austrian Holstein cattle, based on a linear animal model. Spurlock et al. (2012) further observed a strong genetic correlation (0.96 ± 0.18) between GFE in early and mid-lactation. The number of cows used in this study was, however, relatively small (227 and 175, respectively), for multiparous and primiparous cows (Spurlock et al., 2012). In addition, the genetic parameter estimates were based only on the first half of lactation, leaving a gap in knowledge about the latter half of lactation. Although the findings by Spurlock et al. (2012) and Köck et al. (2018) suggest that GFE exhibits sufficient genetic variation to warrant genetic improvement through selection, there is a need to validate these results using larger data sets, and looking at all the stages of lactation.

In an attempt to address the challenge of recording feed efficiency data, several studies have developed models to predict DMI, energy intake and residual feed intake from easy-to-measure traits such as milk production, live weight, mid-infrared spectral data, considering environmental factors such as lactation stage (NRC, 2001; McParland et al., 2014; Shetty et al., 2017; Lahart et al., 2019; Liang et al., 2021). Such models could make it possible to generate large quantities of feed efficiency data, across the whole lactation, at a low cost. Provided they vary genetically, such predicted traits may thus serve as appropriate selection criteria for feed efficiency. Predicted feed efficiency traits appear to exhibit different genetic variation from the actual measured traits, with varying heritability estimates being obtained among studies (Krattenmacher et al., 2019; Zhang et al., 2020). Moreover, genetic parameter estimates for predicted feed efficiency traits are generally scarce, and their application is still limited.

Madilindi et al. (2022b) developed models to predict daily GFE from live weight and milk components in primiparous South African Holstein cows. Dry matter intake was predicted reliably by a model consisting of only live weight (LW) and milk yield (MY) ($R^2 = 0.79$; root mean squared error (RMSE) = 1.05 kg/day), while a model that comprised butterfat yield, MY and LW had the highest ability to predict GFE ($R^2 = 0.98$; RMSE = 0.05) (Madilindi et al., 2022b). This presents a big promise to generate large quantities of data of individual cow DMI and GFE at a low cost, which can be used to implement genetic improvement of feed efficiency. It is, however, essential to first assess the extent to which these predicted traits are under genetic control, and also estimate the genetic parameters for carrying out the requisite genetic evaluation.

The aim of this study was, therefore, to estimate genetic parameters for gross feed efficiency predicted from milk components and its relationship with energy-corrected milk, across the first-three lactations of South African Holstein cattle.

5.2 Materials and Methods

5.2.1 Data

Test-day records and pedigree data of cows from nine intensively-fed Holstein herds, participating in the South African National Milk Recording and Improvement Scheme, were obtained from the Integrated Registration and Genetic Information System of South Africa (http://www.intergis.agric.za/). Records for the period 2009 to 2019 were considered.

5.2.2 Energy-corrected milk

Energy-corrected milk (ECM) yield (kg/day) was calculated from test-day milk yield (kg/day), protein (%), butterfat (%) and lactose percent (%), using Equation 5.1, according to Kirchgeßner (1997).

$$ECM\ (kg/day) = \text{milk yield (kg) x } \frac{(0.39 \text{ x butterfat \% } + 0.24 \text{ x protein \% } + 0.17 \text{ x lactose \%})}{3.17} \quad [5.1]$$

5.2.3 Prediction of gross feed efficiency

Prediction models for GFE were developed prior to this study, for primiparous (Madilindi et al. 2022b) and multiparous Holstein cows (Madilindi et al. unpublished). Due to the unavailability of live weight data, the prediction model based on test-day butterfat yield (BFY) (kg/day), which was the third best for primiparous cows, was used to predict GFE in the current study. The prediction model based on test-day BFY (kg/day), which was the best model for multiparous cows, was also used to predict GFE. Equation 5.2 was used for primiparous cows, whereas Equation 5.3 was used for multiparous cows. These models had coefficients of determination (R^2) of 0.87 and 0.80, respectively. Gross feed efficiency was calculated as the ratio between ECM (kg/day) and DMI (kg/day).

$$pGFE = 0.018 + 1.335 \times BFY\ (kg/day) \quad [5.2]$$

$$pGFE = 0.413 + 0.759 \times BFY\ (kg/day) \quad [5.3]$$

5.2.4 Data preparation and editing

The original data set consisted of 13,332 first to third lactation test-day records of 1,927 Holstein cows. Age of the cow at calving was restricted to the ranges of 20 to 36, 30 to 54 and 40 to 66 months for first, second and third lactation, respectively, so as to exclude outliers (Mostert et al., 2006; Dube et al., 2008). Test-day milk yields of <3.0 kg or >99.9 kg, protein percent of <1% or >7%, butterfat percent of <1.5% or >9%, and lactose percent of <4.2% or >5.2% were considered as outliers and excluded. Only test-day records falling between 10 and 305 days in milk (DIM) were included. Each lactation was divided into early (10-100 DIM), mid (101-200 DIM) and late (201-305 DIM) stages. Each animal had a minimum of two ECM and pGFE observations per stage of lactation. The pedigree was built around animals with ECM and pGFE records, and was traced back to four generations. The final data set, after editing, comprised of 11,068 test-day records of 1,575 cows from eight herds. The structure of the final data set used to estimate (co)variance components for ECM and pGFE is presented in Table 5.1.

Table 5.1 Structure of the data set used to estimate variance components for daily-predicted gross feed efficiency and energy-corrected milk in the first three parities of South African Holstein cattle

Lactation period	Number of Animals	Number of Dams	Number of Sires
Lactation stage			
Early	803	688	229
Mid	1198	987	300
Late	1131	641	286
Entire-lactation			
Primiparous	1069	909	251
Multiparous	1012	848	257
All lactations	1575	1263	355

5.2.5 Statistical analysis

Descriptive statistics for pGFE and ECM were calculated using the Proc Means procedure of the Statistical Analysis System (version 9.4, SAS, Institute, Carry, NC, USA). Non-genetic factors influencing pGFE and ECM, which required to be fitted in the models for (co)variance components estimation, were also determined using the General Linear Models procedure of the Statistical Analysis System (version 9.4, SAS, Institute, Carry, NC, USA). These effects included age of cow at calving, lactation stage, parity and herd-test-day.

Bivariate analyses were carried out to estimate (co)variance components, as well as heritability and repeatability, for pGFE and ECM, within stages of lactation, for the entire first lactation (primiparous), entire second and third lactations (multiparous), and all entire lactations pooled together. All the analyses were conducted by the restricted maximum likelihood (REML) procedure of the ASReml 4.2 software (Gilmour et al., 2021). Genetic and phenotypic correlations were estimated for pGFE between stages of lactation and among lactations, as well as between pGFE and ECM within stages of lactation and across lactations. The following repeatability animal models were fitted:

$$\begin{bmatrix} y_1 \\ y_2 \end{bmatrix} = \begin{bmatrix} X_1 & 0 \\ 0 & X_1 \end{bmatrix} \begin{bmatrix} b_1 \\ b_2 \end{bmatrix} + \begin{bmatrix} Z_1 & 0 \\ 0 & Z_2 \end{bmatrix} \begin{bmatrix} u_1 \\ u_2 \end{bmatrix} + \begin{bmatrix} W_1 & 0 \\ 0 & W_2 \end{bmatrix} \begin{bmatrix} pe_1 \\ pe_2 \end{bmatrix} + \begin{bmatrix} e_1 \\ e_2 \end{bmatrix},$$

where y_1 and y_2 are vectors of test-day observations for pGFE or ECM; X_1 and X_2 are incidence matrices relating fixed effects to observations; b_1 and b_2 are vectors of fixed effects; Z_1 and Z_2 are incidence matrices relating random animal additive genetic effects to observations; u_1 and u_2 are vectors of animal additive genetic effects; W_1 and W_2 are incidence matrices relating random permanent environmental effects to observations; pe_1 and pe_2 are vectors of permanent environmental effects; e_1 and e_2 are vectors of residual effects.

Animal additive genetic effects (a) were assumed to have the distribution $N \sim (0, A\sigma_a^2)$, where A is the additive genetic relationship matrix and σ_a^2 is the animal additive genetic variance. Permanent environmental effects (pe) were assumed to be distributed with $N \sim (0, I\sigma_{pe}^2)$, where I is an identity matrix, σ_{pe}^2 is the variance due to permanent environmental effects and cov $(a, pe) = 0$. Residual effects (e) were assumed to be distributed with $N \sim (0, I\sigma_e^2)$, where I is an identity matrix, σ_e^2 is the residual variance and cov $(a, e) = 0$.

The (co) variance matrix for random effects in the models was as follows:

$$\mathrm{Var} \begin{bmatrix} a \\ pe \\ e \end{bmatrix} = \begin{bmatrix} A\sigma_a^2 & 0 & 0 \\ 0 & I\sigma_{pe}^2 & 0 \\ 0 & 0 & I\sigma_e^2 \end{bmatrix}$$

Genetic trend for pGFE, for all the lactations combined, was estimated by plotting average estimated breeding values (EBVs) by year of birth. The EBVs were estimated by the Best Linear Unbiased Prediction method (Henderson, 1984) using the ASReml 4.2 (Gilmour et al., 2021).

5.3 Results

5.3.1 Descriptive statistics

Means and coefficients of variation (CV) for daily pGFE and ECM, by stage of lactation and for entire-lactations, are presented in Table 2. Mean daily pGFE ranged from 1.20 in late lactation to 1.39 in early lactation, with an overall mean of 1.25. Both primiparous and multiparous cows had a mean daily pGFE of 1.26. Mean ECM varied from 25.78 kg/day in late lactation to 29.67 kg/day in early lactation. Multiparous cows produced an average of 2.62 kg/day of ECM more than the primiparous cows, and the overall mean for ECM across lactations was 27.68 kg/day. Predicted GFE showed higher variation in multiparous (CV=23.02%) than in primiparous (CV=17.46%) cows. Energy-corrected milk yield was slightly more variable in late (CV=34.14%) than in early (CV=28.08%) lactation.

Table 5.2 Summary statistics for daily-predicted gross feed efficiency and energy-corrected milk by stage of lactations, parity and entire first three lactations of South African Holstein cows

Items		**Traits**	**Mean**	**CV (%)**
Lactation stage				
	Early	pGFE	1.39	19.08
		ECM, kg/day	29.67	28.08
	Mid	pGFE	1.25	20.00
		ECM, kg/day	28.08	29.95
	Late	pGFE	1.20	21.67
		ECM, kg/day	25.78	34.14
Entire-lactation				
	Primiparous	pGFE	1.26	17.46
		ECM, kg/day	26.58	29.95
	Multiparous	pGFE	1.26	23.02
		ECM, kg/day	29.20	31.16
	All lactations	pGFE	1.25	20.80
		ECM, kg/day	27.68	31.14

pGFE=predicted gross feed efficiency; ECM=energy-corrected milk; CV=coefficient of variation.

5.3.2 Heritability and repeatability estimates

5.3.2.1 Within lactation stage

Estimates of heritability for daily pGFE and ECM within stages of lactation are shown in Table 4.3. The heritability of pGFE was low to moderate, ranging from 0.09 ± 0.04 in mid lactation to 0.18 ± 0.05 in late lactation. Estimates were low for ECM, varying from 0.12 ± 0.04 in mid lactation to 0.15 ± 0.05 in late lactation.

Table 5.3 Heritability estimates (± se) for daily-predicted gross feed efficiency and energy-corrected milk within stages of lactation in South African Holstein cattle

Lactation stage	**pGFE**	**ECM**
Early	0.12 ± 0.06	0.13 ± 0.06
Mid	0.09 ± 0.04	0.12 ± 0.04
Late	0.18 ± 0.05	0.15 ± 0.05

pGFE=predicted gross feed efficiency; ECM=energy-corrected milk.

5.3.2.2 Entire lactations

Table 5.4 presents estimates of heritability and repeatability for pGFE and ECM for entire-lactations. The heritability of pGFE was low (0.10 ± 0.04) for multiparous (combined second and third lactations) and moderate (0.21 ± 0.05) for primiparous (first-lactation) cows. Heritability estimates for ECM were also low (0.09 ± 0.04) for multiparous and moderate (0.17 ± 0.05) for primiparous cows. Overall estimates of heritability for pGFE and ECM across all three lactations were low and identical (0.14 ± 0.03). Corresponding estimates of repeatability were mostly moderate, and ranged between 0.42 ± 0.02 for pGFE in multiparous and 0.52 ± 0.02 for ECM in primiparous cows. Repeatability estimates for all the lactations combined were also moderate at 0.37 ± 0.01 and 0.40 ± 0.01 for pGFE and ECM, respectively.

Table 5.4 Heritability and repeatability estimates for predicted gross feed efficiency and energy-corrected milk for entire-lactations of primiparous and multiparous South African Holstein cows

	pGFE		**ECM**	
Lactation	$h^2 \pm$ se	$r \pm$ se	$h^2 \pm$ se	$r \pm$ se
First	0.21 ± 0.05	0.45 ± 0.02	0.17 ± 0.05	0.52 ± 0.02
Second and third	0.10 ± 0.04	0.42 ± 0.02	0.09 ± 0.04	0.47 ± 0.02
All	0.14 ± 0.03	0.37 ± 0.01	0.14 ± 0.03	0.40 ± 0.01

pGFE=predicted gross feed efficiency; ECM=energy-corrected milk; h^2=heritability; r=repeatability; se=standard error.

5.3.3 Genetic and phenotypic correlations

5.3.3.1 Correlations for pGFE between stages of lactation

Estimates of genetic and phenotypic correlations among daily pGFE in different stages of lactation are presented in Table 5.5. Genetic correlations were all positive and high, ranging from 0.87 ± 0.24 between early and mid-lactation to 0.97 ± 0.28 between early and late lactation. Phenotypic correlations were also positive but moderate, varying from 0.40 ± 0.03 between early and late lactation to 0.44 ± 0.02 between mid and late lactation.

Table 5.5 Genetic (upper diagonal) and phenotypic (lower diagonal) correlations for predicted gross feed efficiency between stages of lactation in South African Holstein cattle

Lactations stage	**Early**	**Mid**	**Late**
Early		0.87 ± 0.24	0.97 ± 0.28
Mid	0.42 ± 0.03		0.94 ± 0.12
Late	0.40 ± 0.03	0.44 ± 0.02	

5.3.3.2 Correlations between pGFE in primiparous and multiparous cows

The genetic correlation between pGFE in primiparous and multiparous cows was strong and positive (0.99 ± 0.21). On the other hand, the phenotypic correlation was low (0.27 ± 0.03).

5.3.3.3 Correlations between pGFE and ECM

Table 5.6 contains genetic correlation estimates between pGFE and ECM within stages of lactation and across all the three lactations. Correlations within stages of lactation were considerably strong and favorable, ranging from 0.90 ± 0.05 in mid lactation to 0.99 ± 0.02 in early lactation. The genetic correlation across all lactations was also high and favourable (0.90 ± 0.03).

Table 5.6 Genetic correlations between daily predicted gross feed efficiency and energy-corrected milk within stages of lactation and across lactations in South African Holstein cattle

Lactation stage	r_g ± se
Early	0.99 ± 0.02
Mid	0.90 ± 0.05
Late	0.91 ± 0.04
All lactations	0.90 ± 0.03

r_g=genetic correlation; se=standard error.

5.3.4 Genetic trend

Genetic trend for daily pGFE, for cows born between 2007 and 2017, is presented in Figure 5.1. There was a marginal increase in mean estimated breeding value (EBV) for daily pGFE from -0.02 in 2007 to 0.04 in 2017, representing a rate of increase of 0.0058 per year during the 10-year period.

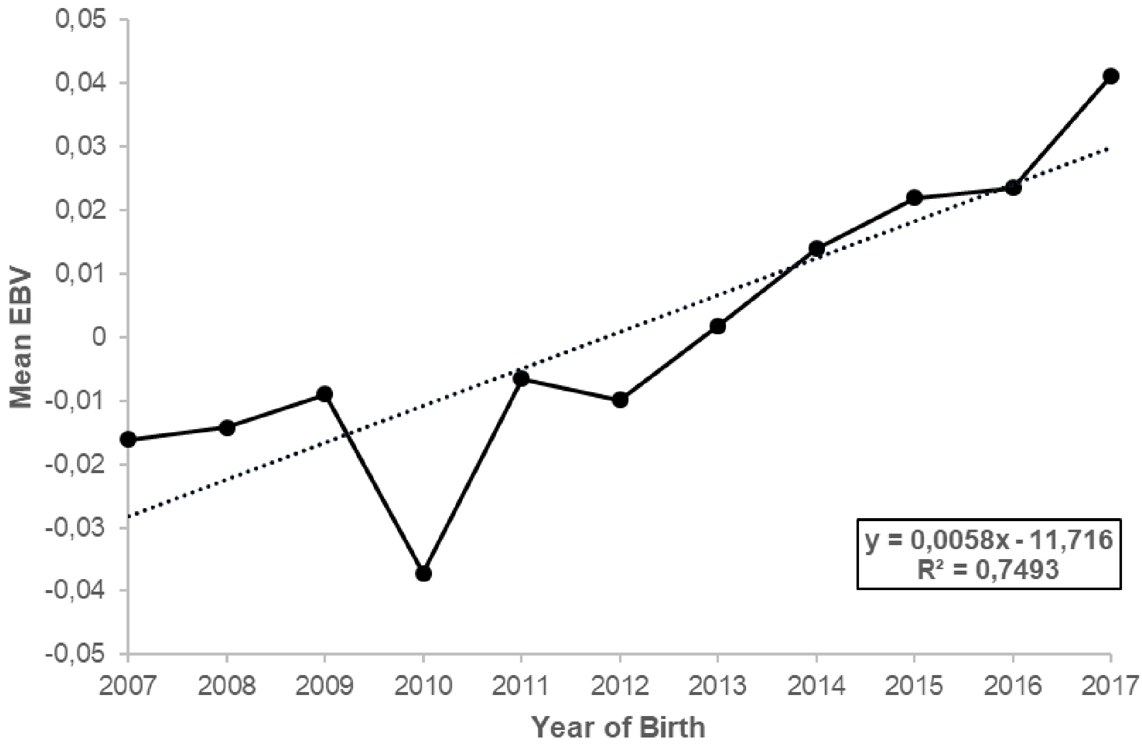

Figure 5.1 Genetic trend for daily-predicted gross feed efficiency in South African Holstein cattle.

5.4 Discussion

5.4.1 Phenotypic means for pGFE and ECM

Gross feed efficiency (GFE) is an exceptionally important trait in dairy production, due to its impact on profitability and environmental sustainability. Energy-corrected milk is a major predictor trait for GFE, and is also of great economic importance. Besides genetic variation between populations, differences in measurement or prediction methods may account for discrepancies in mean GFE among studies (Köck et al., 2018; Tarekegn et al., 2021; Becker et al., 2022). On the other hand, mean ECM is based on yield of milk, which is invariably measured directly, using standard measuring devices (Kirchgeßner, 1997).

Previous studies (Bach et al., 2006; Ishler and Heinrichs, 2016) reported relatively higher mean values for actual GFE than those obtained for pGFE in the current study. However, the observation that cows were more efficient in early compared to later stages of lactation concurs with earlier research on intensively-fed Holstein cows elsewhere (Bach et al., 2006; Ishler and Heinrichs, 2016). As expected from the normal lactation curve, higher daily yields of ECM were also produced in early than later lactation stages. It has been noted that cows in early lactation are more feed efficient because they mostly utilise their body reserves to derive energy for milk production, which causes an artificial increase in gross feed efficiency (Ishler and Heinrichs, 2016; Ledinek et al.. 2019). On the other hand, late-lactation cows will be gaining weight; thus lowering their calculated gross feed efficiency. The reduced gross feed efficiency in late lactation should, however, not be viewed negatively because cows need to regain body weight in late lactation, in order to have adequate body reserves for the next lactation. Exceptionally high gross feed efficiency in early lactation may, however, indicate that cows are losing too much weight, which might lead to metabolic disorders (Ishler and Heinrichs, 2016; Ledinek et al., 2019).

Mean daily pGFE in first lactation was lower than values for actual GFE observed in other recent studies, despite mean daily ECM yields being comparable (Byskov et al., 2017; Li et al., 2018; Krattenmacher et al., 2019). Although mean daily pGFE was the same (1.26) for primiparous and multiparous cows, multiparous cows produced an average of 2.62 kg/day more ECM. Spurlock et al. (2012) also observed similar means for actual GFE of primiparous and multiparous American Holstein cows. The overall mean for daily pGFE across lactations was lower compared to values reported recently for actual GFE in Austrian, German and Swedish Holstein cattle (Köck et al., 2018; Tarekegn et al., 2021; Becker et al., 2022). Cows in the present study also produced relatively lower daily ECM on average than Austrian, German and Swedish Holstein cattle (Köck et al., 2018; Tarekegn et al., 2021; Becker et al., 2022).

5.4.2 Heritability estimates for pGFE and ECM

5.4.2.1 Heritability estimates for pGFE

A central objective of the current study was to assess the extent to which pGFE exhibits genetic variation and, hence, determine its suitability as a selection criterion for feed efficiency. The heritability estimates for pGFE within stages of lactation and across lactations were low to moderate, indicating scope for modest genetic improvement through selection. Late lactation had the second highest heritability, with the estimate for early lactation being marginally higher than that for mid lactation. This is consistent with the observation that residual error variance for daily production is lower in late lactation, which results in higher heritability estimates (Meseret and Negussie, 2017; Buaban et al., 2020; Wahinya et al., 2020; Tarekegn et al., 2021).

Spurlock et al. (2012) also observed moderate albeit larger heritabilities for actual GFE in the first half of lactation, and a higher estimate in early compared to mid-lactation, in a study on American Holstein cattle. In further agreement with Spurlock et al. (2012), heritability was higher in primiparous than multiparous cows, which could be due to the higher residual error variance in multiparous cows. Spurlock et al. (2012) analysed actual measured GFE in the first and second halves of lactation, which may partially explain the disparity in the magnitude of estimates from those of the current study. Additionally, Spurlock et al. (2012) used random regression models, which are better at modelling genetic and environmental variances along the lactation trajectory than repeatability models (Dzomba et al., 2010).

The heritability estimate for pGFE across lactations falls within the range of 0.10 ± 0.03 to 0.18 ± 0.03 obtained for actual GFE in Austrian dairy cattle (Köck et al., 2018). However, since this estimate is comparatively lower than the value observed for the late lactation stage, strategic selection based on measurements recorded only in late lactation may be more effective than considering the entire lactation. Due to the higher heritability of pGFE in primiparous compared to multiparous cows, selection considering first parity records only also appears to be justifiable. Thus, stage of lactation and parity should be taken into consideration when incorporating pGFE in the selection objective.

5.4.2.2 Heritability estimates for ECM

Energy-corrected milk is an important component of the complex feed efficiency trait; hence, knowledge of its genetic attributes is essential to the inclusion of GFE in the selection objective. The heritability of ECM yield has been fairly studied in recent years, mainly based on first lactation records, and most of the estimates obtained were moderate (e.g. Manzanilla-Pech et al., 2014; Li et al., 2018; Krattenmacher et al., 2019). In general, these estimates are larger than the low values obtained in the current study. Manzanilla-Pech et al. (2014) found relatively larger values (>0.19), with higher estimates in mid compared to early and late lactation, in Dutch Holstein cattle. On the contrary, we observed higher estimates in late than mid and early lactation. Higher heritability estimates, which were larger in early than mid and late lactation, have also been reported in first-parity Holstein populations elsewhere (Li et al., 2018; Krattenmacher et al., 2019). Thus, there appears to be no consistency among studies on the relative magnitude of heritability of ECM by stage of lactation.

Disparities in the heritability of milk production traits between parities is well documented in the literature (e.g. Haile-Mariam and Pryce, 2017; Meseret and Negussie, 2017; Buaban et al., 2020; Tarekegn et al., 2021). In the current study, we obtained higher heritabilities for ECM in primiparous compared to multiparous cows, which is in agreement with Spurlock et al. (2012). Spurlock et al. (2012), however, found much larger estimates (>0.24) using random regression models.

A low heritability estimate for ECM across the first three lactations was also observed by Köck et al. (2018) in Austrian Holstein cattle, and suggests selection should be based on parity.

5.4.3 Genetic correlations and repeatability estimates for pGFE and ECM

5.4.3.1 Genetic correlations for pGFE

Genetic correlations between pGFE in different stages of lactation were estimated to determine if selection applied in one stage will result in improvement along the entire lactation. These correlations were positive and substantially large, supporting earlier findings by Spurlock et al. (2012) who observed a genetic correlation of 0.96 ± 0.18 between early and mid-lactation, for actual GFE in American Holstein cattle. These results suggest that pGFE in different stages of lactation is essentially an expression of the same trait. This further supports the idea to base selection only on data recorded in late lactation.

The genetic correlation between pGFE in primiparous and multiparous cows was also positive and extremely high (close to unity). It means pGFE in primiparous and multiparous cows may be under the influence of the same or linked genes. The observed correlation suggest that selection for pGFE based on first lactation data will result in improvement in later lactations. Such an approach is further justified by our finding that the heritability of pGFE is higher in primiparous than multiparous cows.

5.4.3.2 Correlations between pGFE and ECM

Knowledge of the genetic correlations between pGFE and ECM may assist in improving accuracy of selection of pGFE, as well as incorporating it in the selection objective. These estimates were all positive and substantially high (>0.90), within stages of lactation and across parities, confirming earlier findings by Köck et al. (2018) who reported strong positive genetic correlations between actual GFE and ECM across lactations in Australian Holstein cattle. Spurlock et al. (2012) also noted that improved GFE was closely associated genetically with increased ECM yield throughout the first half of lactation in American Holstein cattle. These results indicate that the two traits may be under the influence of the same or linked genes, and selection for higher ECM yield is likely to result in a correlated improvement in pGFE. More importantly, accuracy of selection for pGFE can be increased through multiple-trait analysis including ECM.

5.4.3.3 Repeatability estimates for pGFE and ECM

Repeatability was estimated to assess the extent to which repeated measures of pGFE and ECM across lactations are under the influence of permanent effects. Repeatability was moderate (0.37 ± 0.01 to 0.52 ± 0.02) for both pGFE and ECM, in agreement with a previous study by Köck et al. (2018) on Austrian Holstein cattle. Much higher repeatability estimates for ECM (>0.75) were, however, reported in recent studies on first lactations of Holstein cattle populations elsewhere (Byskov et al., 2017; Krattenmacher et al., 2019). It therefore appears that pGFE and ECM in first lactation is a fairly reliable indicator of performance in later lactations. Thus, culling decisions on pGFE or ECM may be made using only first lactation data.

5.4.4 Genetic trend for predicted gross feed efficiency

Genetic trend for pGFE, across all lactations, was ascertained to assess if there have been any changes in genetic merit for the trait in recent years, in the South African Holstein cattle population. Such a change may occur as a correlated response to selection for other traits with which it is genetically correlated. There has been sustained genetic selection for yield traits in the South African Holstein cattle population (Ramatsoma et al., 2014), which has unfortunately resulted in a correlated deterioration in functional traits (Banga et al., 2014). The current study found a marginal increase in genetic merit for daily pGFE over the period 2007-2017, which may also be a correlated response to selection for yield traits. This is plausible, given the high positive genetic correlation that we observed between pGFE and ECM. Other researchers (Spurlock et al., 2012; Köck et al., 2018) also noted a correlated genetic improvement of actual GFE due to an increase in milk production traits and a decrease in live weight. Thus, the exclusive focus on selection for yield traits in South African Holstein cattle has, fortunately, not been detrimental to feed efficiency. There is, however, a need to achieve more meaningful genetic improvement of feed efficiency by including it in the breeding objective.

5.5 Conclusion

Results of this study indicate that daily gross feed efficiency predicted from milk components exhibits modest genetic variation, with the highest heritability being in first-parity, and in late lactation. High genetic correlations among pGFE in different stages of lactation indicate that records of pGFE along the lactation trajectory can be considered as repeated measures of the same trait. Hence, selection for pGFE based on late lactation records only seems reasonable, as it would achieve the highest accuracy of selection while improving the trait across the whole lactation. Higher heritability of pGFE in primiparous compared to multiparous cows, coupled with high genetic correlations between these lactations, justifies selection on first lactation records only. There appears to be scope for improving accuracy of selection for feed efficiency through multiple-trait analysis including ECM, due to the high genetic correlation between the two traits. Genetic trends show a slight increase in the genetic merit for pGFE in South African Holstein cattle in recent years, which may be a correlated response to selection for higher milk yield or other correlated traits. There is, however, a need to achieve significant improvement in the genetic merit of feed efficiency, in order to achieve profitable and environmentally sustainable dairy production systems. The genetic parameters obtained in the current study can be applied to estimate EBVs for pGFE, which may be used to achieve such improvement. Further enhancements to the selection programme could be effected through the application of random regression modelling, as well as identification of markers or genes influencing feed efficiency.

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Chapter 6

Genetic analysis of predicted dry matter intake and gross feed efficiency in South African Holstein cows

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Abstract

Genetic parameters were estimated for dry matter intake and gross feed efficiency predicted from milk components in the first three parities of South African Holstein cattle. Test-day data from the South African National Milk Recording Scheme were used to predict dry matter intake (pDMI) from milk yield. Predicted gross feed efficiency (pGFE) was then calculated from pDMI and energy-corrected milk (ECM). Variance components and genetic parameters were estimated by a repeatability animal model using the ASReml program. Heritability estimates ranged from 0.05 ± 0.02 for pGFE in mid lactation to 0.13 ± 0.03 for pDMI in late lactation. Overall estimates of heritability across parities were 0.08 ± 0.02 and 0.13 ± 0.02 for pGFE and pDMI, respectively. Genetic correlations between pDMI and pGFE were moderate and negative in early (-0.42 ± 0.24) and mid lactation (-0.20 ± 0.24), and low and positive in late lactation (0.05 ± 0.17). There was a decrease in genetic correlation between pDMI and pGFE with increase in parity, from 0.26 ± 0.16 to -0.09 ± 0.17. The low heritability estimates for pDMI and pGFE indicate low accuracy of selection for these traits in South African Holstein cattle. This can, however, be improved through multi-trait analyses including both traits and others that are correlated.

Keywords: Feed efficiency, genetic variation, genetic improvement, repeatability animal model

6.1 Introduction

Feed is a major cost in dairy production; hence, increased feed efficiency is key to achieving sustainable improvements in herd profitability. Better efficiency of feed utilisation is also associated with a reduction of major greenhouse gas emissions and, therefore, may contribute towards mitigating climate change (Connor, 2015). Thus, genetic improvement of feed efficiency could be a solution to increasing environmental sustainability and herd profitability of the dairy industry (Berry et al., 2015).

Genetic selection for feed efficiency is a challenging task that requires the phenotypic measurement of many animals in order to accurately predict the genetic merit of each animal for the trait. Generally, it is costly and difficult to measure dry matter intake (DMI) directly in lactating cows, in order to calculate gross feed efficiency (GFE). This challenge may, however, be overcome through selection on DMI and GFE predicted from routinely measured milk production traits (Zhang et al., 2020; Madilindi et al., 2021). A major prerequisite to the effective use of such predicted traits as selection criteria is that they should exhibit genetic variation. Hence, the primary aim of this study was to estimate genetic (co)variances and related parameters for predicted dry matter intake and gross feed efficiency in South African Holstein cattle. Such parameters could provide the basis for achieving genetic improvement of feed efficiency in this population.

6.2 Materials and Methods

6.2.1 Data

Data were from 568 herds participating in the South African National Milk Recording Scheme, and were extracted from the Integrated Registration and Genetic Information System of South Africa. The original data set consisted of 1,739,261 test-day records of 140,345 South African Holstein cows that calved between 2009 and 2019. Only the first three parities were considered, consisting of 440,062 test-day records of 62,695 cows, after data editing.

6.2.2 Prediction of dry matter intake and gross feed efficiency

Firstly, test-day milk yield (kg/day) was used to calculate daily-predicted dry matter intake (pDMI) (kg/day) per cow, based on the simple regression prediction Equation 6.1, developed by Lindgren et al. (2001). Preliminary analysis using South African Holstein data had found this equation to be reliable, as indicated by an R^2 value of 0.76.

$$pDMI\ (kg/day) = 5.7 + 0.43 \times Milk\ (kg/day) \qquad [6.1]$$

Next, energy-corrected milk (ECM) yield (kg/day) per cow was calculated from test-day milk yield (kg/day), protein percent (%), butterfat percent (%) and lactose percent (%), using Equation 6.2, according to Kirchgeßner (1997).

$$ECM\ (kg/day) = \text{milk yield (kg) x } \frac{(0.39 \text{ x butterfat \% } + 0.24 \text{ x protein \% } + 0.17 \text{ x lactose \%})}{3.17} \qquad [6.2]$$

Predicted gross feed efficiency (pGFE) per cow was subsequently calculated, using Equation 6.3:

$$pGFE = \frac{\text{ECM (kg/day)}}{\text{pDMI (kg/day)}} \qquad [6.3]$$

6.2.3 Statistical analysis

Variance components, heritability, and repeatability for pDMI and pGFE were estimated by ASReml 4.2. (Gilmour et al., 2021) using a repeatability animal model (Equation 6.4):

$$y_{jklmn} = \mu + HTD_j + LS_k + P_l + \beta ACC_{jklmn} + a_{jklmn} + p_{jklmn} + e_{jklmn,} \qquad [6.4]$$

where y_{jklmn} is an observation of pDMI or pGFE; μ is the overall mean; HTD_j is the fixed effect of herd-test-day contemporary group; LS_k is the fixed effect of lactation stage (k = early lactation (10-100 days in milk (DIM)), mid lactation (101-200 DIM), and late lactation 201-305 DIM); P_l is the fixed effect of parity (l =1 to 3); ACC_{jklmn} is age of cow at calving; β_{jklmn} is a linear regression coefficient on age of cow at calving; a_{jklmn} is the random animal additive genetic effect with var (a) ~distribution $N(0,\mathbf{A}\sigma^2_a)$, where σ^2_a is the additive genetic variance and **A** is the relationship matrix; p_{jklmn} is the random permanent environmental effect of the animal with distribution $N(0,\mathbf{I}\sigma^2_p)$, where σ^2_p is the permanent environmental variance; e_{jklmn} is the random residual effects with distribution $N(0,\mathbf{I}\sigma^2_e)$, where σ^2_e is the residual variance and **I** is an identity matrix.

Bivariate analyses were carried out to estimate genetic correlations between pDMI and pGFE within and across lactation stages as well as parities.

6.3 Results

Estimates of heritability and genetic correlations for pDMI and pGFE by stage of lactation are presented in Table 6.1. Heritabilities ranged from 0.05 ± 0.02 for pGFE in mid lactation to 0.13 ± 0.03 for pDMI in late lactation. The heritability estimates of pDMI tended to increase with stage of lactation. No trend of heritability estimates for pGFE was observed among lactation stages. Genetic correlations between pDMI and pGFE varied from -0.42 ± 0.24 in early to 0.05 ± 0.17 in late lactation.

Table 6.1 Heritability estimates (diagonals) and genetic correlations (off diagonals) for daily-predicted dry matter intake and gross feed efficiency within lactation stage in South African Holstein cattle

	Early		Mid		Late	
Traits	pDMI	pGFE	pDMI	pGFE	pDMI	pGFE
pDMI	**0.07 ± 0.02**	-0.42 ± 0.24	**0.09 ± 0.02**	-0.20 ± 0.24	**0.13 ± 0.03**	0.05 ± 0.17
pGFE		**0.08 ± 0.02**		**0.05 ± 0.02**		**0.09 ± 0.02**

pDMI=predicted dry matter intake; pGFE=predicted gross feed efficiency.

Table 6.2 contains estimates of heritability and genetic correlations for pDMI and pGFE within parity. Heritability estimates ranged from 0.07 ± 0.02 for pGFE in both first and third-parity to 0.14 ± 0.03 for pDMI in third-parity. There was a slight increase in heritabilities of pDMI with increase in parity. No trend of heritability estimates for pGFE was observed across parities. Overall estimates across parities were 0.08 ± 0.02 and 0.13 ± 0.02, respectively, for pGFE and pDMI. Repeatability estimates of 0.26 ± 0.01 and 0.41 ± 0.01 were obtained across lactations, respectively, for pGFE and pDMI. Genetic correlations between pDMI and pGFE varied from -0.09 ± 0.17 in third-parity to 0.26 ± 0.16 in first-parity.

Table 6.2 Heritability estimates (diagonals) and genetic correlations (off diagonals) for daily-predicted dry matter intake and gross feed efficiency within first-three parities in South African Holstein cattle.

	Parity 1		Parity 2		Parity 3	
Traits	pDMI	pGFE	pDMI	pGFE	pDMI	pGFE
pDMI	**0.11 ± 0.03**	0.26 ± 0.16	**0.12 ± 0.03**	0.11 ± 0.16	**0.14 ± 0.03**	-0.09 ± 0.17
pGFE		**0.07 ± 0.02**		**0.10 ± 0.02**		**0.07 ± 0.02**

pDMI=predicted dry matter intake; pGFE=predicted gross feed efficiency.

6.4 Discussion

Heritabilities for pDMI and pGFE were generally low within lactation stages. The heritability estimates of pDMI slightly increased with stage of lactation, implying that accuracy of selection for this trait may depend on the lactation stage in which selection is applied. Tarekegn et al. (2021) similarly reported an increase in heritability estimates for measured daily DMI with lactation week. No trend of heritability estimates for pGFE was observed among lactation stages in the current study. However, a decrease in the heritability estimate for GFE with increase in lactation stage was observed previously by Spurlock et al. (2012). These discrepancies may be a reflection of differences in the methods used to measure the traits. The genetic correlations between pDMI and pGFE was inexplicably negative in early and mid-lactations, and positive in late lactation. There were, unfortunately, no estimates available in the literature with which to compare these results. The relatively high genetic correlation in early lactation may assist in increasing accuracy of selection, if the two traits are included in a multi-trait analysis.

Heritability estimates for pDMI and pGFE were low within first-three parities. A slight increase in heritabilities of pDMI with increase in parity was observed. This indicates that accuracy of selection for pDMI may depend on the parity in which selection is applied. Recently, Zhang et al. (2020) reported heritability estimates comparable with those obtained in the current study for pDMI in the first-two parities, although the estimate for the first parity was higher than for the second. No trend of heritability estimates for pGFE was observed across parities in our study. Spurlock et al. (2012) however reported higher heritability estimates for actual GFE in primiparous (0.47) compared to multiparous (0.43) cows, although their estimates were much larger than those found in the current study. The inconsistency in estimates of heritability for DMI and GFE among studies could be attributable to discrepancies in the measurement/prediction methods as well as stages of lactation during which measurements were taken. Moderate repeatability estimates were obtained across lactations, implying that first lactation records on pDMI can fairly predict pDMI in later lactations. Genetic correlation between pDMI and pGFE decreased with increase in parity in the current study. This may mean that increased accuracy of selection through multiple-trait analysis of the two traits would be more effective with first lactation data. Genome-wide association studies may be warranted to validate these results.

6.5 Conclusion

Results of the current study show that there is low genetic variation in DMI and GFE predicted from milk components, which implies low accuracy of selection. Moderate genetic correlations between the traits, however, may be used to increase accuracy of selection in multi-trait analyses. Variation in pDMI appears to slightly vary with parity and stage of lactation; thus, lactation stage-specific and parity-specific selection may be required. Further research may be required to identify genomic regions, and subsequently genes, associated with these predicted feed efficiency traits, for possible marker-assisted selection, which might accelerate genetic improvement.

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Chapter 7
General Discussion, Conclusions and Recommendations

7.1 General Discussion

Improving feed efficiency has become a major goal in dairy production globally, mainly due to the growing need to maintain herd profitability as well as achieve environmental sustainability. Developing genetic solutions to improve feed efficiency presents a cost effective and sustainable strategy towards attaining this goal. Difficulty in measuring dry matter intake on individual lactating cows, for calculating feed efficiency traits has, however, been a big challenge to genetic improvement of feed efficiency. There has generally been a lack of sufficient quantities of data on dry matter intake, which are required to estimate accurate breeding values for gross feed efficiency, thus hindering its inclusion in selection objectives. Previous research has, however, indicated the possibility of predicting feed efficiency phenotypes from easily measured traits. To this end, this study was carried out to investigate the possibility of estimating genetic merit for feed efficiency in South African Holstein cattle using live weight and milk components as predictor traits. This was carried out by developing models for predicting dry matter intake and gross feed efficiency from on-farm recorded data on feed intake, cow live weight and milk components. The prediction models were validated, followed by estimation of genetic parameters among the predicted traits. Accurate prediction of genetically variable feed efficiency phenotypes would pave the way for incorporating feed efficiency into the selection objective.

7.1.1 Developed models for dry matter intake and gross feed efficiency

The first step of the study was to develop and validate models to predict dry matter intake and gross feed efficiency using live weight and milk components. The best potential predictor traits were determined first by estimating their correlations with dry matter intake and feed efficiency. Stepwise regression analysis was subsequently applied to develop the best prediction models. This approach has been used to develop reliable prediction models in several previous studies. The most reliable prediction models developed were significant, with live weight and butterfat yield being the best predictors for dry matter intake and gross feed efficiency, respectively. Live weight alone accounted for about 66% of the variation in dry matter intake, which is expectable given the close relationship between the animal's maintenance requirements and its body weight. Similarly, butterfat is the milk component with the highest energy requirement for synthesis; hence its outstanding ability to predict gross feed efficiency. The predictive abilities of the models developed were generally moderate to remarkable, with relatively low prediction errors; and they were comparable to or better than those obtained in other previous studies. This implies that the predicted traits are likely to perform well as selection criteria for feed efficiency. The developed models present an opportunity to produce large quantities of dry matter intake and gross feed efficiency phenotypes on individual cows, at a low cost. Provided that such phenotypes exhibit reasonable genetic variation, this suggests scope for utilising them to achieve genetic improvement in feed efficiency in the South African Holstein cattle population.

7.1.2 Genetic parameter estimates for energy-corrected milk, predicted dry matter intake and gross feed efficiency

In order for them to be useful selection criteria, predicted dry matter intake and gross feed efficiency phenotypes should express genetic variation in the population under selection. Accordingly, it was necessary to estimate genetic parameters for predicted dry matter intake and gross feed efficiency. Relationships between these traits and energy-corrected milk were also estimated, in order to explore the possibility of using the latter to improve accuracy of selection through multiple trait analyses. Heritability for the predicted phenotypes ranged from low to moderate, and varied with stage of lactation and parity. These results suggest that the predicted traits can justifiably be used as selection criteria for feed efficiency. Selection based on these traits should, however, be strategic and target the stage of lactation and parity exhibiting the highest genetic variation, in order to maximise rates of genetic gain. Energy-corrected milk had an exceptionally strong genetic correlation with predicted gross feed efficiency, indicating that it can be used to improve accuracy of selection by including it in multiple trait analysis with predicted gross feed efficiency. Estimated genetic trends for predicted gross feed efficiency showed a marginal improvement over a 10-year period, which may be a correlated response to selection for milk production. However, direct selection using the genetic parameters estimated in the current study is likely to achieve more meaningful rates of genetic improvement of feed efficiency in the South African Holstein cattle population.

7.2 Conclusions

Daily dry matter intake (kg/day) and gross feed efficiency in South African Holstein cows can be predicted reliably from milk and butterfat yields, and live weight, using models developed in the current study. The predicted traits exhibit modest genetic variation, indicating their suitability as selection criteria for feed efficiency in the population. Thus, there is potential to genetically improve feed efficiency in South African Holstein cattle by generating large quantities of feed efficiency phenotypes (i.e. predicted DMI and GFE) from easy-to-measure traits (live weight and milk components) and using these to estimate breeding values. These phenotypes may also be used to implement genomic selection for feed efficiency, resulting in higher rates of genetic change.

7.3 Recommendations

The following recommendations may be made, based on the results of the current study.

7.3.1 Practical application of results

7.3.1.1 Application of developed prediction models

Viability of dairy farming in South Africa is under severe threat from consistently escalating feed costs, which has led to a drastic decline in producer numbers. This poses a serious challenge to food security in the country, and the whole sub-region. There is also a heightened need to reduce greenhouse gas emissions in dairy herds globally. Given the fact that there is routine recording of daily milk production and composition data in South Africa, the models developed in this study offer a great opportunity to generate large numbers of predicted dry matter intake and gross feed efficiency data. These data can be used to produce accurate estimated breeding values for feed efficiency, which will help to address the serious challenges faced by the dairy industry. For example, predicted dry matter intake is used in the Iranian Holstein genetic evaluation programme to estimate genetic merit for feed efficiency. Since there is a routine genetic evaluation programme for Holstein cattle in South Africa, feed efficiency can simply be added to the portfolio of traits in the genetic analysis system. Estimation of the economic value of feed efficiency will be required, in order to incorporate the trait in the breeding objective thereby improving selection for the overall goal.

7.3.1.2 Selection to improve feed efficiency

Despite its outstanding importance, feed efficiency is not included in the South African dairy genetic evaluation programme. The genetic parameters estimated in this study could provide the means to estimate breeding values for predicted feed efficiency traits, thus enabling selection to improve feed efficiency in the South African Holstein cattle population. Until directly measured dry matter intake data from lactating individual animals becomes available on a large scale, selection based on these predicted traits, as proxies for feed efficiency, could be applied to improve efficiency of feed utilisation in South African Holstein cattle.

7.3.2 Challenges and limitations of the study

7.3.2.1 Developed models

Although reliable basal prediction models were developed, the amount of data used of 30 records on a group of 100 primiparous and 110 multiparous cows, was rather small. At least 1000 records on 100 cows, recorded along the whole lactation, would be desirable. Furthermore, factors such as stage of lactation and body condition score of the cow, which may explain some of the variation in individual feed intake, were not accounted for in the models.

Inclusion of milk spectral data, in addition to live weight and milk components, has been shown in recent research to improve the prediction of dry matter intake and gross feed efficiency. Unfortunately, we were unable to get milk spectral data due to unavailability of testing facilities locally.

Across-herd validation could not be carried out, to ascertain whether the prediction models can function outside of the dataset used to develop them. There was no external data available to perform such validations. Therefore, caution should be exercised if the models are to be applied on a wide scale. It is also not known if the developed models can be extrapolated to other dairy production systems, such as the pasture-based feeding system, or other dairy cattle breeds.

7.3.2.2 Genetic parameters

Due to unavailability of live weight data, the phenotypes used to estimate genetic parameters for dry matter intake and gross feed efficiency were predicted from models comprising only milk components. These were, unfortunately, not the best models developed. In addition, owing to restrictions imposed by the structure of the data, it was not possible to use random regression models to estimate genetic parameters. Random regression models are better at modelling genetic and environmental variances for test-day data along the lactation trajectory compared to repeatability models. It is, therefore, possible that the genetic parameters could have been estimated more accurately.

7.3.3 Suggested future research and development

i. **Across-herd model validation:** In order to determine the robustness of the models developed in the current study with more certainty, there is a need to carry out across-herd validation using data from other herds. It is also important to undertake further work to ascertain whether these models can be extrapolated for use in other dairy breeds or production systems.

ii. **Inclusion of milk mid-infrared spectra data in prediction models:** It will be worthwhile to establish whether inclusion of milk mid-infrared spectra data can improve the prediction ability of the developed models. The analysis can be carried out at laboratories outside the country, preferably in collaboration with international collaborators who have experience in using such data.

iii. **Accounting for other factors influencing feed intake:** A study in which comprehensive recording of data throughout the lactation is further suggested. This will help to develop comprehensive prediction models which are able to account for different stages of lactation, an important factor in explaining some of the variation in individual feed intake. Other factors influencing feed intake of lactating cows, such as body condition score at calving, could also be included in the prediction models.

iv. **Random regression modelling:** Exploring multi-trait random regression modelling is also suggested in future analyses, as this may improve the accuracy of genetic parameter estimates.

v. **Large scale recording of live weight data:** Live weight data is valuable in improving the prediction ability of the models, particularly dry matter intake. There is, therefore, a need for dairy recording schemes in South Africa to encourage, support and, where possible, provide incentives for farmers to record live weight in addition to milk production traits, for future research.

vi. **Investigating other prediction and validation methods:** It might also be worthwhile to explore other prediction and validation approaches such as artificial neural networks and partial least squares, to determine whether they can improve robustness of the prediction models.

vii. **Genome-wide association study:** A further study is warranted to establish whether there are any genes or parts of the genome that are associated with predicted feed efficiency phenotypes. Such knowledge may assist in implementing marker-assisted selection, which may enhance rates of genetic improvement in feed efficiency.