Genetic selection for improved production efficiency in the mature dairy herd

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Genetic selection for improved production efficiency in the mature dairy herd

A Thesis presented for the Degree of Doctor of Philosophy
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Table of Contents

List of Tables ........................................................................................................................................ iii
List of Figures ......................................................................................................................................... vi
List of Appendices ................................................................................................................................. x
Abbreviations ......................................................................................................................................... xi
Declaration ............................................................................................................................................... xiii
Acknowledgments ................................................................................................................................. xiv
Thesis Abstract ........................................................................................................................................ xv

Chapter 1: Introduction and Literature Review ..................................................................................... 1
  1.1 Introduction ....................................................................................................................................... 2
  1.2 Definitions of production efficiency and their limitations ......................................................... 4
  1.3 Targets for production efficiency ................................................................................................. 9
  1.4 Genetic parameters of production and feed efficiency ............................................................. 18
  1.5 Inclusion of production efficiency in breeding goals ............................................................... 26
  1.6 Production efficiency in grazing dairy cows ............................................................................. 31
  1.7 Statistical analysis and data quality ............................................................................................ 39
  1.8 Gaps in knowledge addressed in this thesis ............................................................................. 40

Chapter 2: Are subjectively scored linear type traits suitable predictors of the genetic merit for feed intake in grazing Holstein-Friesian dairy cows? ........................................................................ 43
  2.1 Preface ........................................................................................................................................... 43
  2.2 Abstract .......................................................................................................................................... 44
  2.3 Introduction .................................................................................................................................... 44
  2.4 Materials and Methods .............................................................................................................. 46
  2.5 Results ........................................................................................................................................... 51
  2.6 Discussion ..................................................................................................................................... 58
  2.7 Conclusions .................................................................................................................................. 62

Chapter 3: Genetic and non-genetic factors associated with lactation length in seasonal-calving pasture-based dairy cows .............................................................................................................. 63
  3.1 Preface ........................................................................................................................................... 63
  3.2 Abstract .......................................................................................................................................... 64
  3.3 Introduction .................................................................................................................................... 65
  3.4 Materials and Methods .............................................................................................................. 66
  3.5 Results ........................................................................................................................................... 72
3.6 Discussion ............................................................................................................ 79
3.7 Conclusions ........................................................................................................... 86

Chapter 4: Exploiting genetic variability in the trajectory of lactation yield and somatic cell score with each progressing parity ......................................................... 87
4.1 Preface .................................................................................................................. 87
4.2 Abstract .................................................................................................................. 88
4.3 Introduction ............................................................................................................ 89
4.4 Materials and Methods ......................................................................................... 90
4.5 Results ................................................................................................................... 95
4.6 Discussion ............................................................................................................ 107
4.7 Conclusions .......................................................................................................... 112

Chapter 5: Re-assessing the importance of linear type traits in prediction genetic merit for survival in an aging Holstein-Friesian dairy cow population ................. 113
5.1 Preface .................................................................................................................. 113
5.2 Abstract .................................................................................................................. 114
5.3 Introduction ............................................................................................................ 114
5.4 Materials and Methods ......................................................................................... 116
5.5 Results ................................................................................................................... 122
5.6 Discussion ............................................................................................................ 129
5.7 Conclusions .......................................................................................................... 133

Chapter 6: Thesis Summary and Conclusions ............................................................ 135
6.1 Thesis Summary .................................................................................................... 136
6.2 Thesis Conclusions and Implications ..................................................................... 142
6.3 Further Research .................................................................................................. 151

Chapter 7: References ................................................................................................ 153

Chapter 8: Publications and Contributions ................................................................. 183
8.1 Peer Reviewed Publications ................................................................................... 184
8.2 Conferences .......................................................................................................... 184
8.3 Other Publications ............................................................................................... 185
8.4 Industry Dissemination ....................................................................................... 186
8.5 Research Awards ................................................................................................. 186
8.6 Courses Attended ................................................................................................ 187

Chapter 9: Appendices ................................................................................................ 188
List of Tables

Table 1.1. Expected loss of milk yield and milk solids yield in short lactations relative to expected 305-day lactation yields in Holstein-Friesian cows of three different genotypes. ................................................................. 12
Table 1.2. Dairy cow milk yields (kg) reported in individual parities by previous studies in different countries. ................................................................. 14
Table 1.3. Genetic correlations between measures of dairy cow survival/longevity and linear type traits. ................................................................. 17
Table 1.4. Heritability ($h^2$; standard errors in parenthesis) and genetic standard deviation ($\sigma_g$) estimates for within-lactation ratio efficiency traits. ....... 20
Table 1.5. Heritability estimates ($h^2$; standard errors in parenthesis) for residual feed intake reported in different populations of dairy cows. ............. 21
Table 1.6. Heritability estimates ($h^2$; standard errors in parenthesis) for residual feed intake reported in different populations of growing dairy heifers. ...................................................................................... 22
Table 1.7. Heritability estimates (standard error in parenthesis) for lactation length from a range of studies across different breeds and countries. ................................................................. 23
Table 1.8. Economic values (€) and relative emphasis (%) of milk (lbs), fat (lbs), and protein (lbs) yields in United States dairy selection indexes. ........... 29
Table 1.9. Genetic correlations between dairy cow DMI, body weight (BW) and linear type traits previously reported in the literature. ................. 38
Table 2.1. Mean, genetic standard deviation ($\sigma_g$), heritability ($h^2$; standard error in parenthesis) and within-lactation repeatability (t; standard error in parenthesis) for dry matter intake (DMI; kg), body weight (kg), daily milk yield (kg) as well as the body-related linear type traits (scale 1 to 9). ...................................................................................... 51
Table 2.2. Phenotypic correlations (standard error in parenthesis) between dry matter intake (DMI; unadjusted and adjusted for phenotypic differences in body weight), body weight, milk yield, and linear type traits. ...................................................................................... 52
Table 2.3. Genetic correlations (standard errors in parenthesis) between dry matter intake (unadjusted, adjusted for phenotypic or genetic...
differences in body weight), body weight, milk yield, and linear type traits ................................................................. 53
Table 2.4. Genetic correlations (standard errors in parenthesis) between dry matter intake (DMI) measured in early, mid, and late lactation (unadjusted, adjusted for phenotypic or genetic differences in body weight), body weight (BW), milk yield, and linear type traits .......... 55
Table 2.5. Pearson correlations and regression coefficients (standard errors in parentheses) for yield deviation of dry matter intake (DMI) on estimated breeding value (EBV) for DMI; the EBVs were generated using combinations of DMI, body weight (BW), and/or linear type trait phenotypes ............................................................. 57
Table 3.1. Number of records, cows, and herds, as well as the mean and median lactation length, genetic standard deviation (σg), heritability (h2; standard error in parenthesis), and repeatability (t; standard error in parenthesis) of lactation length when restricted to ≤365 for cows calving in January, February, March, and April and May, as well as all five calendar months combined ........................................................................................................ 69
Table 3.2. Breed covariate solutions (standard error in parentheses) of the six dairy breeds, Jersey (JE), Ayshire (AY), Brown Swiss (BS), Montbéliarde (MO), Norwegian Red (NR), and Normande (NO) relative to Holstein-Friesian for lactation length restricted to ≤365 days (LL365) and lactation length defined as a binary trait ≥150 days (LL150), ≥200 days (LL200), ≥240 days (LL240), ≥270 days (LL270), and ≥305 days (LL305) ........................................................................ 73
Table 3.3. The percentage achieved as well as the genetic standard deviation (σg), heritability estimate (h2; standard error in parenthesis), repeatability (t; standard error in parenthesis), and heritability estimate on the underlying liability scale (h2_L) of binary lactation length traits; lactation length ≥150 days (LL150), ≥200 days (LL200), ≥240 days (LL240), ≥270 days (LL270), and ≥305 days (LL305) .................................................................................. 78
Table 4.1. Number of records (n), raw means, and standard deviations (SD) for 305-day milk protein, and fat yield, protein and fat percentage, and somatic cell score (SCS) for parities 1 to 8 .................................................................................. 96
Table 4.2. Regression coefficient (standard error in parentheses) and the root mean square error (RMSE) from the regression of milk, fat and protein yield, fat and protein percentage, and SCS in the parity of maximum production or highest average composition or SCS on their respective values in first parity; also included is the correlation between the independent and dependent variables................................. 97

Table 4.3. Genetic correlations (standard errors in parenthesis) between 305-day milk yield (kg) in different parities (above diagonal) and somatic cell score (log_{10} units) in different parities (below diagonal)..................... 101

Table 4.4. Genetic correlations (standard errors in parentheses) between 305-day fat percentage in different parities (above diagonal) and 305-day protein percentage in different parities (below diagonal). ....................... 102

Table 5.1. List of all linear type traits with explanation of measurement scale and the corresponding mean, additive genetic standard deviation (σ_g), heritability estimate (h^2; standard error in parenthesis).......................... 118

Table 5.2. Pairwise genetic correlations (above diagonal) and their respective standard errors (below diagonal) between survival in first to ninth parity............................................................... 124

Table 6.1. Previous studies that suggested linear type traits may be suitable proxy measures for feed intake or feed efficiency................................. 149
List of Figures

Figure 1.1. Lactation curves for (A) milk yield and (B) milk solids of three different genotypes of Holstein-Friesian dairy cows – high production Holstein-Friesians (green), high durability Holstein-Friesians (blue), and New Zealand Holstein-Friesians (yellow). .......... 11

Figure 1.2. For heritability values of 0.35, 0.20, 0.10, 0.05, and 0.03 (in order of increasing line darkness), (A) the number of progeny required to achieve a give accuracy of selection using traditional ancestry-based genetic evaluation and (B) the number of records of phenotyped and genotyped animals to achieve accuracy of genomic evaluations (based on 1,000 effective chromosomal segments and 80% of the genetic variance accounted for by the genotyped markers). ........................................................................... 19

Figure 1.3. Expected differences in lactation length between dairy cows when ranked on their estimated breeding values (EBV) for lactation length based on the genetic standard deviations published by (A) Ojango and Pollott (2001) and (B) Goshu et al. (2014). ......................... 24

Figure 1.4. Relative emphasis of each sub-index included in the Economic Breeding Index as it evolved since the Relative Breeding Index (RBI). ........................................................................................................... 27

Figure 1.5. Some of the factors that influence dairy cow lifetime production efficiency. ........................................................................................................... 28

Figure 1.6. Average yearly milk production (kg) per cow in the European Union (EU; Stele and Svetin, 2021), the United Kingdom (UK; Shahbandeh, 2021), the United States (US; USDA, 2020), Australia (Dairy Australia, 2020), and New Zealand (LIC and DairyNZ, 2020) in 2019. ........................................................................................................... 32

Figure 3.1. The change in lactation length (LL; standard error bar represents ± 1 SE) associated with A) calving month relative to cows calving in January; B) parity relative to first parity cows; C) age at calving relative to cows calving between 180 and 120 days earlier than the parity median; D) heterosis coefficient relative to cows with a heterosis coefficient of 0%; E) calving difficulty score relative to
cows with a calving difficulty score of 1; F) dry period length relative to cows a with dry period of between 15 and 35 days; G) herd size relative to herds with ≤50 cows.

Figure 3.2. The association between the change in the percentage that achieved lactation length ≥150 days (♦), ≥200 days (■), ≥240 days (▲), ≥270 days (∗), ≥305 days (□) and A) calving month relative to cows calving in January; B) parity relative to first parity cows; C) age at calving relative to cows calving between 180 and 120 days earlier than the parity median; D) heterosis coefficient relative to cows with a heterosis coefficient of 0%; E) recombination loss coefficient relative to cows with a recombination loss coefficient of 0%; F) calving difficulty score relative to cows with a calving difficulty score of 1; G) dry period length relative to cows a with dry period of between 15 and 35 days; H) herd size relative to herds with ≤50 cows. Standard error bar represents ± 1 SE unit.

Figure 3.3. The genetic trend by year of birth for lactation length estimated for Holstein-Friesian cows (■), and Holstein-Friesian males with ≥10 progeny with lactation length records (♦).

Figure 4.1. Heritability estimates for 305-day milk yield (kg), fat percentage (%), protein percentage (%), somatic cell score (log10 unit), 305-day fat yield (kg), and 305-day protein yield (kg). Standard error bars represent one standard error above and below the heritability estimate.

Figure 4.2. Additive genetic standard deviation estimates for 305-day (a) milk yield (kg; primary axis), somatic cell score (log10 units; secondary axis), and (b) fat yield (kg; primary axis), protein yield (kg; primary axis), fat percentage (%; secondary axis), and protein percentage (%; secondary axis).

Figure 4.3. The variance of genetic change between parities for (a) 305-day milk yield (kg²; primary axis) and somatic cell score (log10 unit²; secondary axis) and (b) 305-day fat yield (kg²; primary axis), 305-day protein yield (kg²; primary axis), fat percentage (%²; secondary axis), and protein percentage (%²; secondary axis).
Figure 4.4. Eigenfunctions associated with the largest, middle, and smallest eigenvalues for (a) 305-day milk yield, (b) somatic cell score, (c) fat percentage, (d) protein percentage, (e) 305-day fat yield, and (f) 305-day protein yield. ................................................................. 104

Figure 4.5. Estimated breeding values (EBV) for cows with the most extreme (diverse) EBV, when compared to all cows reaching ≥ 5th parity, for each parity for (a) 305-day milk yield, (b) somatic cell score, (c) fat percentage, (d) protein percentage, (e) 305-day fat yield, and (f) 305-day protein yield. ................................................................. 105

Figure 4.6. Estimated breeding values (EBV) for cows with median lifetime production values when compared to all cows reaching ≥ 5th parity, in each parity for (a) 305-day milk yield, (b) somatic cell score, (c) fat percentage, (d) protein percentage, (e) 305-day fat yield, and (f) 305-day protein yield. ................................................................. 106

Figure 5.1. Mean survival per parity (line; primary axis) and the percentage of survival records per parity included in the analysis (bar; secondary axis). ........................................................................................................ 122

Figure 5.2. Heritability estimates for survival (blue circle with solid line; primary axis), survival adjusted for 305-day yield (orange square with solid line; primary axis), and additive genetic standard deviation estimates for survival (blue circle with broken line; secondary axis), survival adjusted for 305-day milk yield (orange square with broken line; secondary axis). Standard errors bars represent one standard error above and below the heritability estimate. .................. 123

Figure 5.3. Genetic correlations between survival in each parity and (a) angularity, (b) body condition score, (c) body depth, (d) chest width, (e) rump angle, (f) rump width, and (g) stature. Standard error bars represent one standard error above and below the genetic correlation................................................................. 126

Figure 5.4. Genetic correlations between survival in each parity and (a) milking ease, (b) fore udder attachment, (c) rear udder height, (d) udder depth, and (e) udder support. Standard error bars represent one standard error above and below the genetic correlation................................. 127
Figure 5.5. Genetic correlations between survival in each parity and (a) rear teat placement, (b) teat length, (c) front teat placement (rear view), and (d) front teat placement (side view). Standard error bars represent one standard error above and below the genetic correlation. .................................................................

Figure 5.6. Genetic correlations between survival in each parity and (a) bone quality, (b) foot angle, (c) locomotion, and (d) rear legs (side view). Standard error bars represent one standard error above and below the genetic correlation. ........................................................................

Figure 6.1. Phenotypic trend for fifth parity lactation length of Holstein-Friesian dairy cows that reached at least fifth parity and were born between 2000 and 2015 (blue) and the expected phenotypic trend for fifth parity lactation length for Holstein-Friesian dairy cows born between 2016 and 2025 estimated using linear extrapolation from the previous sixteen years (purple). ..............................................................................................

Figure 6.2. Phenotypic trend for longevity of Holstein-Friesian dairy cows born between 2000 and 2008 (blue) and the expected phenotypic trend for longevity for Holstein-Friesian dairy cows born between 2009 and 2025 estimated using linear extrapolation from the previous ten years (purple)........................................................................................................

Figure 6.3. Median calving date (blue) and dry-off date (purple) for spring-calving Irish Holstein-Friesians calving between 2000 and 2020......
List of Appendices

Appendix A. Number of observations (n), mean, genetic standard deviation (σg), heritability (h²; standard error in parenthesis) for dry matter intake (kg), body weight (kg), and daily milk yield (kg) in early, mid and late lactation. ................................................................. 189

Appendix B. Phenotypic correlations (standard error in parenthesis) between DMI measured in early, mid, and late lactation (unadjusted and adjusted for phenotypic differences in body weight) body weight (BW), milk yield, and linear type traits............................................. 190

Appendix C. The genetic correlations (above diagonal; standard error in parenthesis) and phenotypic correlations (below diagonal; standard error in parenthesis) between the traditional linear type traits and novel composite traits.................................................................................................................. 191

Appendix D. The percentage achieved as well as the genetic standard deviation (σg), heritability estimate (h²; standard error in parenthesis), repeatability (t; standard error in parenthesis), and heritability estimate on the underlying liability scale (h²_L) of binary lactation length traits where all cows calved in January, February, March, and April and May combined; lactation length ≥150 days (LL150), lactation length ≥200 days (LL200), lactation length ≥240 days (LL240), lactation length ≥270 days (LL270), lactation length ≥305 days (LL305). ........................................................................................................... 192

Appendix E. The proportion of cows reaching maximum 305-day milk, fat, and protein yield, highest average fat and protein percentage and highest average somatic cell score in each parity. ............................................... 193

Appendix F. Genetic correlations and their respective standard errors between 305-day fat yield (kg) in different parities (above diagonal) and 305-day protein yield (kg) in different parities (below diagonal). .... 194

Appendix G. Pairwise genetic correlations (standard errors in parentheses) between survival adjusted for 305-day milk yield (above diagonal) and their respective standard errors (below diagonal) between survival in first to ninth parity............................................................ 195
Abbreviations

σ_g: Genetic standard deviation

BCS: Body condition score

BD: Body depth

BDSTA: Body depth*Stature

CW: Chest width

CWBD: Chest width*Body depth

CWSTA: Chest width*Stature

CWBDSTA: Chest width*Body depth*Stature

DMI: Dry matter intake

DIM: Days in milk

EBI: Economic Breeding Index

EBV: Estimated breeding value(s)

EU: European Union

FCE: Feed conversion efficiency

h^2: Heritability

ICBF: Irish Cattle Breeding Federation

kg: Kilogram

lbs: Pounds

MIRS: Mid infrared spectrometry

mL: millilitre

NIRS: Near infrared spectrometry

PTA: Predicted transmitting ability

r: correlation

RBI: Relative breeding index

RFI: Residual feed intake
RMSE: Root mean square error
RSP: Residual solids production
SCC: Somatic cell count
SCS: Somatic cell score
SE: Standard error
STA: Stature
\( t \): Repeatability
UFL: Unité fourragère du lait
UK: United Kingdom
US: United States
Declaration

_I declare that this thesis, which I submit to Munster Technological University, is my own personal effort. Where any of the content presented is the result of input or data from a related collaborative research programme, this is duly acknowledged, such that it is possible to ascertain how much of the work is my own. I have not already obtained a degree from Munster Technological University or elsewhere on the basis of this work. Furthermore, I took reasonable care to ensure that the work is original, and, to the best of my knowledge, does not breach copyright law, and has not been taken from other sources except where such work has been cited and acknowledged within the text._

Candidate: ______________________

Maeve Williams

Date: ______________________
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Thesis Abstract

Improving dairy cow production efficiency is highly desirable because of its well-documented impact on profitability and sustainability. Long-term gains in dairy cow production efficiency have already been delivered through genetic selection. Nonetheless, achieving further improvements in production efficiency could cement the economic and environmental efficiency of the dairy industry, globally. To date, several components contributing to production efficiency have been overlooked, with many studies focusing on dairy cow production efficiency over short periods rather than lifetime efficiency. Therefore, the objectives of this thesis were to quantify the genetic variance components of complementary dairy cow efficiency metrics; including dry matter intake, lactation length, lactation yields, and survival, and to quantify the usefulness of linear type traits in predicting the genetic merit for difficult to measure efficiency-related traits during different stages of lactation and across different parities. Results indicate that considerable genetic variation existed for the range of production efficiency-related traits investigated, with heritability estimates ranging from 0.02 for survival from first to second parity to 0.66 for first parity milk protein percentage. This exploitable genetic variation indicates that potential exists to breed for improved lifetime production efficiency by lengthening lactations and increasing the number of the lactations achieved while not necessarily reducing milk yield or increasing somatic cell count as cows get older. Additionally, the usefulness of some linear type traits as predictors of the genetic merit for survival, particularly in older cows, has been demonstrated and it has been determined that linear type traits have limited use as predictors of the genetic merit for dry matter intake in grazing Holstein-Friesian dairy cows.
Chapter 1: Introduction and Literature Review
1.1 Introduction

The importance of production efficiency to the profitability and sustainability of dairy production systems is unquestionable. Genetic selection has already been shown to deliver long-term gains in production efficiency that accumulate with each generation (Brito et al., 2021). In addition to genetic selection, intensification of production systems and improvements in reproductive technologies have also contributed to greater production efficiency in dairy cows (Brito et al., 2021). Nevertheless, achieving further improvements in production efficiency could contribute to cementing the economic and environmental sustainability of the dairy industry globally. For dairy production to be sustainable, it must return a profit, produce a quality product for consumers, be environmentally benign, and ensure good standards of animal welfare (von Keyserlingk et al., 2013; De Ondarza and Tricarico, 2017). At present, 80% of Irish dairy farms are economically viable (Dillon et al., 2021), and the global demand for dairy products is continuing to grow (Bach et al., 2020; Brito et al., 2021); therefore, the principles of sustainability that the dairy industry should now focus on are the environmental impact of production and ensuring a good standard of animal welfare.

The EU has set the year 2050 as the target for achieving climate-neutrality (European Commission, 2019). Given the agricultural sector represents 37.1% of the Irish greenhouse gas emissions (EPA, 2021), if climate-neutrality is to be achieved, the status quo is not sustainable. In the future, farmers will need to produce more food with fewer resources and lesser environmental impact. One option for dairy producers to reduce the environmental impact of production and improve profitability is to improve production efficiency. The simplest definition of production efficiency is the profit produced by an animal over its lifetime, although recognition of the impact on factors such as the environment and welfare should be considered. The production efficiency of dairy cows could be improved by lengthening lactations, improving longevity, increasing milk solids production per lactation, and improving feed efficiency. Improving any of these aspects of production efficiency could reduce the environmental impact of dairy production either by diluting the environmental impact over a greater volume of milk (i.e., longer lactations, improved longevity, greater milk production) or by improving the environmental efficiency of cows (i.e., improving feed efficiency). Improvements in dairy cow production efficiency have already been
reported to lead to a reduction in resource use and a reduction in the environmental impact per kilogram of milk produced (Bell et al., 2013; Capper and Bauman, 2013) and per cow (Bell et al., 2013). Improving multiple aspects of production efficiency, such as longevity, lactation length, and milk production, simultaneously has the potential to drastically improve the environmental impact of dairy production.

The potential to lengthen dairy cow lactations has long been of interest to dairy producers in confinement systems globally (Bachman and Schairer, 2003; Pezeshki et al., 2008; Atashi et al., 2013). Not only could extended lactations reduce the non-productive portion of a cow’s life, they could also reduce the number of calves born each year, potentially contributing to an overall reduction in environmental impact of the dairy herd. Nevertheless, extending the calving interval of dairy cows beyond 365 days in pasture-based production systems it not an economically viable option, as it would erode the production efficiency and profitability of the sector (Shalloo et al., 2014). An alternative method to achieve the required improvement in dairy cow production efficiency, in both confinement and pasture-based production systems, might be to improve the longevity of dairy cows. The productive lifespan of dairy cows in most developed dairy industries is limited to an average of 2.5 to 4.5 lactations per cow (Poland: Adamczyk et al., 2016; New Zealand: Kerslake et al., 2018; US: De Vries and Marcondes, 2020). More lactations per cow could improve profitability through a reduced need for replacement heifers, a greater herd average milk yield, a greater opportunity for voluntary culling, and greater selection intensity contributing to greater genetic gain (van Pelt et al., 2015). Improving the longevity of dairy cows could also reduce the environmental impact of the dairy industry by reducing the need for non-productive replacement heifers and by diluting the environmental footprint of the non-productive period of a cow’s life over more lactations and a greater volume of milk. Given that feed costs represent approximately 60% of the costs of production on Irish dairy farms (Connor, 2015), reducing the requirement for replacement heifers could reduce the total feed required on dairy farms. Although production efficiency is not synonymous with feed efficiency, improving production efficiency either by reducing inputs (i.e., feed costs) and maintaining production, or by maintaining inputs and increasing production, should improve profitability by reducing or diluting the cost of feed.
Given the array of factors that influence production efficiency (Bauman et al., 1985; De Vries and Marcondes, 2020), it is likely that an approach combining genetic selection for multiple traits associated with production efficiency, in addition to improved management, should improve the production efficiency of the dairy herd. Any improvements in the genetic merit of production efficiency-related traits could result in lasting improvements, as these gains are permanent and accumulate with each advancing generation. Additionally, since dairy cows need to go in calf to remain in the milking herd, the penetrance rate of genetic gain is high. The objectives of this literature review were:

1) To summarise current metrics of production efficiency, their limitations, and the targets for production efficiency set by the dairy industry

2) To compile and discuss the genetic parameters of production efficiency metrics and their inclusion in breeding objectives

3) To review the factors limiting production efficiency in grazing systems and the difficulties associated with measuring efficiency-related traits.

### 1.2 Definitions of production efficiency and their limitations

Although the concept of production efficiency is simple, in practice, measuring production efficiency is difficult and there is no one agreed upon definition. Production efficiency can be measured at the herd level or at the lifetime level for an individual animal (Berry and Crowley, 2013). Either way, production efficiency should ideally account for the pre-productive period (i.e., from birth to first calving), non-productive periods (i.e., dry periods), and productive periods of a cow or herd (De Ondarza and Tricarico, 2017). Although, production efficiency and feed efficiency are not interchangeable terms, studies often report measures of both production efficiency and feed efficiency; improvements in feed efficiency have the potential to improve production efficiency by reducing the costs of production.

#### 1.2.1 Within-lactation production efficiency

Given the difficulties quantifying all inputs across an animal’s lifetime, within-lactation measures of production efficiency and feed efficiency are frequently used to reflect production efficiency in dairy cows. These within-lactation measures may be
simple ratio measures, the residuals from regression models, or indeed lactation length itself.

1.2.1.1 Ratio traits

Three simple within-lactation ratio measures of production and feed efficiency in lactating dairy cows are often reported. These are 1) the ratio between feed intake and body weight (Prendiville et al., 2009; Coleman et al., 2010), 2) the ratio between milk production (either solids, corrected milk, or milk solids) and body weight (Prendiville et al., 2009; Coleman et al., 2010; Evers et al., 2021; Berry and McCarthy, 2021), and 3) the ratio between milk solids and feed/energy intake (feed conversion efficiency [FCE]; Prendiville et al., 2009; Coleman et al., 2010; Hurley et al., 2017). The main advantage of these simple ratio traits as estimates of production efficiency is their ease of calculation (and interpretation) and, if measured over the same length or at the same point in lactation, the estimates from different populations can easily be compared (Berry and Crowley, 2013). Nonetheless, each of the ratio traits has its own limitations as a measure of production efficiency based on their failure to consider some of the factors that influence efficiency. For example, the ratio between milk solids production and body weight fails to account for feed intake differences, which is the largest variable cost on dairy farms. Additionally, although easily fixed, the ratio between milk solids production and body weight, does not account for the differences in the energetic costs of producing a kg of fat versus a kg of protein (O’Mara, 1996) or the difference in the economic value of fat versus protein (Berry and McCarthy, 2021). Feed conversion efficiency fails to explicitly consider the size and, therefore, the maintenance requirement of the dairy cow.

Estimates of dry matter intake (DMI) are generally limited to research herds, particularly in pasture-based production systems; therefore, the requirement for DMI measurements limits the applicability of some ratio traits (i.e., FCE and the ratio between feed intake and body weight), particularly in commercial settings. Even when available, DMI measurements do not consider differences in the energy content of diets, although this could easily be rectified by considering the net energy for lactation available from the diet. Additionally, where ratio traits include body weight, there is a failure to account for body condition score (BCS) and the mobilisation of body tissue reserves, which could have ramifications for subsequent health and fertility (Roche et al., 2009). Other limitations of ratio traits, especially for breeding programs, include
1) the strong correlation between the ratio trait and their component traits, many of which are already included in breeding objectives and 2) the fact that the relative selection pressure on the components of the ratio trait cannot be known (Berry and Crowley, 2013; Berry and McCarthy, 2021).

1.2.1.2 Residual traits

Residual feed intake (RFI), also known as net feed efficiency, is a popular feed efficiency trait used particularly in research studies of growing cattle, although it is now also reported in lactating dairy cows (Coleman et al., 2010; Connor et al., 2015). Adapted from a model first proposed by Byerly (1941) for laying hens, Koch et al. (1963) developed RFI with a least squares regression method to determine the efficiency of feed use for weight gain in growing beef cattle. This regression approach has been adapted for use in lactating dairy cows and can generally be defined as the difference between actual feed intake and predicted feed intake, based on the energy required for maintenance and milk production (i.e., energy sinks). The complexities associated with accounting for the differences in body tissue mobilisation have resulted in the definition of RFI in lactating cows differing somewhat between studies (Coleman et al., 2010; McParland et al., 2014; Hurley et al., 2017) but most calculations of RFI may be summarised as:

\[
RFI = DMI - (Fat + Protein + Lactose + BW^{0.75} + ΔBW + BCS)
\]

where \( DMI \) is daily dry matter intake, \( Fat \) is daily fat production (kg), \( Protein \) is daily protein production (kg), \( Lactose \) is daily lactose production (kg), \( BW^{0.75} \) is metabolic body weight, \( ΔBW \) is the daily change in body weight, and \( BCS \) is body condition score. In addition to the energy sinks included in the above model to predict feed intake, Coleman et al. (2010) included year as a fixed effect to remove temporal effects. McParland et al. (2014) and Hurley et al. (2017) expanded the typical RFI model to better represent the daily fluctuations in body weight and condition score. Furthermore, McParland et al. (2014) and Hurley et al. (2017) included days in milk (DIM), the interaction between metabolic body weight and BCS, daily change in BCS, and the interaction between the daily change in body weight and the daily change in BCS when defining RFI.

Residual solids production (RSP), proposed by Coleman et al. (2010), is an alternative approach to estimate the feed efficiency of lactating dairy cows. Rather than regressing DMI on energy sinks for maintenance and milk production, as is the
case with RFI, Coleman et al. (2010) proposed regressing milk solids yield on DMI and energy sinks (i.e., maintenance and growth), or energy sources (i.e., body reserve mobilisation). Residual solids production can be defined as:

$$RSP = MS - (DMI + BW^{0.75} + ΔBW + BCS)$$

where $MS$ is daily milk solids yield, $DMI$ is dry matter intake, $BW^{0.75}$ is metabolic body weight, $ΔBW$ is the daily change in body weight, and $BCS$ is body condition score. As with RFI, Coleman et al. (2010) also included year as a fixed effect in the regression model to ensure the RSP values were independent of year effects. Hurley et al. (2017) also reported a residual production trait but defined RSP in terms of residual energy production and included parity, DIM, the interactions between body weight change and $BCS$ additional to the terms outlined by Coleman et al. (2010).

Although an estimate of feed efficiency, RFI does not reflect production efficiency, as it fails to differentiate between the partitioning of energy into the traits of different economic importance (i.e., milk solids and metabolic body weight). Coleman et al. (2010) highlighted this discrepancy between feed efficiency and production efficiency stating that lighter cows producing more milk solids from similar DMI can have poorer RFI values than their heavier herd-mates that produce less milk. Even though RSP is also a measure of feed efficiency, RSP may potentially be more reflective of production efficiency given it was positively phenotypically correlated with milk solids production (Coleman et al., 2010). When cows with similar DMI, body weight, body weight change, and $BCS$ are compared, cows with better RSP values produced more milk solids. As with some of the ratio measures, the requirement for feed intake measurements to estimate these residual traits is one of the largest limitations for the adoption of both RFI and RSP, particularly for pasture-based commercial dairy cows.

Pryce et al. (2015) proposed feed saved as an alternative to RFI for inclusion in selection indexes; feed saved combines the feed required for maintenance with RFI into one feed requirement trait (Pryce et al., 2015; Parker Gaddis et al., 2021). One of the advantages of feed saved over RFI alone is that animals with the same RFI can be distinguished from one another based on their maintenance requirements (Pryce et al., 2015); if two cows have equal values for RFI, the larger cow would be penalised for having a greater maintenance requirement. Given RFI is corrected for body weight, feed saved could be a more desirable trait for selection than RFI (Pryce et al., 2015).
In April 2021, Lactanet in Canada published genetic evaluations for a similar feed efficiency trait in Holstein animals (Jamrozik et al., 2021; Sweett and Fleming, 2022); the Canadian feed efficiency trait considers energy corrected milk to account for production, in addition to DMI, and metabolic body weight to determine maintenance requirements (Jamrozik et al., 2021; Sweett and Fleming, 2022).

1.2.1.3 Lactation length

Lactation length, in particular lactation length in primiparous cows, has been proposed as a measure of production efficiency in dairy cows (Neja et al., 2015; Van Eetvelde et al., 2017). Lactation length may be a suitable measure of production efficiency in confinement systems, but given the importance of seasonal calving in pasture-based dairy production, short lactations may not be a reflection of the animal’s genetic merit for lactation length but rather a reflection of poor management practices.

Individually, each of these within-lactation measures of production and feed efficiency fail to capture at least one aspect of production efficiency, but if several measures were combined, it could be possible to get an accurate estimate of the within-lactation efficiency of dairy cows.

1.2.2 Lifetime production efficiency

Although within-lactation measures of production efficiency are frequently reported, they all fail to fully capture production efficiency over the lifetime of a cow. This is especially true if calculated at a herd-level, since within-lactation production efficiency measures do not account for non-productive animals. Lifetime efficiency, defined as the feed energy captured in milk, conceptus, and body tissue divided by the total energy intake during a cow’s lifespan, is a more pertinent measure of a dairy cow’s lifetime production efficiency (VandeHaar and St-Pierre, 2006). Nonetheless, lifetime efficiency is (almost) impossible to calculate accurately as it would involve measuring daily feed intake during the entire lifespan of an animal; hence, lifetime efficiency has only ever been estimated based on expected values. Nevertheless, when lifetime efficiency was calculated, using expected values, a typical US dairy cow producing 9,000 kg of milk per year at maturity has a lifetime efficiency of 17% (percentage of total lifetime energy intake captured in milk, conceptus, and body tissue) after first lactation, 20.5% after third lactation, rising to 21.4% after fifth
lactation (VandeHaar and St-Pierre, 2006). The increase in lifetime production efficiency with each advancing lactation highlights the importance of longevity as a strategy to dilute the energy used during non-productive periods.

Given lifetime efficiency cannot be accurately determined for individual cows, due in part to the difficulty in measuring an individual animal’s energy intake across their entire life, studies have reported simpler traits that consider the lifetime production of dairy cows (Haworth et al., 2008; Dinesh et al., 2014; Neja et al., 2015). As with within-lactation production efficiency, simple ratios are often proposed; for example, total lifetime milk production per day of age and per day of productive life have previously been reported as measures of lifetime production efficiency in Jersey and Holstein-Friesian cows (Dinesh et al., 2014; Neja et al., 2015). Other possible metrics for lifetime production efficiency include lifespan in days, total number of days in milk, and number of lactations per lifetime (Haworth et al., 2008).

As with all of the within-lactation measures of production efficiency, limitations exist for each measure of lifetime production efficiency. All of the relatively simple measures of lifetime production efficiency fail to consider (daily) feed efficiency. Additionally, given that these traits require lifetime production to be known, they cannot be estimated before an animal is culled, which would make genetic selection for such efficiency traits slower, although genomic selection could mitigate this to some extent.

1.3 Targets for production efficiency

1.3.1 Milk solids per kg of body weight

Improving kg of milk solids produced per kg of body weight is of interest to dairy producers, particularly because the component traits are easy to measure and the metric is easy to calculate and understand (Berry and McCarthy, 2021). Though not mentioned in the literature, the target of producing one kg of milk solids for every kg of body weight is regularly purported by dairy producers. Two recent studies based on data from commercial Irish farms report that mean kg of milk solids per kg of body weight is close to one (Evers et al., 2021; Berry and McCarthy, 2021). Nonetheless, mean kg of milk solids per kg of body weight varies greatly between herds (0.73 to
1.14; Evers et al., 2021) and between animals within herds (0.42 to 1.47; Evers et al., 2021).

Although the motivation to increase milk solids per kg of body weight is to improve the production efficiency of dairy cows, genetic selection for milk solids per kg of body weight may not necessarily have the desired effect. Even though greater milk solids per kg of body weight suggests a lower proportion of energy being partitioned to maintenance, the metric does not account for feed intake; therefore, it is possible that some cows with a high ratio of milk solids to body weight may just have higher DMI in relation to their size. Additionally, though improving the ratio between milk solids and body weight may improve production efficiency within single lactations (Prendiville et al., 2009), the inverse relationship may exist between this metric of efficiency and lifetime production efficiency (Berry and McCarthy, 2021). This apparent anomaly between within-lactation efficiency and lifetime efficiency is a result of the relationship between kg milk solids per kg of body weight and BCS; the genetic correlation between kg milk solids per kg of body weight and BCS is -0.41 (Berry and McCarthy, 2021). Given there is a strong genetic relationship between BCS and fertility, health, and survival (Berry et al., 2003; Roche et al., 2009), genetic selection for increased milk solids per kg of body weight could reduce longevity, thereby, impacting lifetime production efficiency.

1.3.2 Lactation length

The profitability of the Irish dairy industry, as with all pasture-based dairy production systems, is reliant on compact seasonal calving immediately prior to the initiation of grass growth (Dillon et al., 2003). Therefore, the maintenance of a 365-day calving interval is necessary, limiting lactation length to 305 days if a 60-day dry period is maintained. Lactation yields are frequently standardised to 305 days to facilitate the comparison of milk yield between cows or management strategies (Kok et al., 2016). These standardised lactation yields are almost exclusively used in management decision support tools and dairy cow genetic evaluations (Quist et al., 2007). The use of such standardised lactation yields implies that most dairy cows are expected to achieve lactations of the standardised length, but, the average lactation length of Irish dairy cows, between 1990 and 2001, was 265 days (Evans et al., 2006). Although the average lactation length of Irish dairy cows has not been reported in the
literature since 2006, the average lactation length of dairy cows in New Zealand, which is a comparable pasture-based production system, was 271 days in 2019 (LIC and DairyNZ, 2019). Both statistics therefore imply that 305-day lactations are not being achieved, certainly in grazing production systems. To highlight the impact of lactation length on production efficiency, parameters of the Wilmink lactation function fitted to the yield of three genotypes of Irish dairy cows were used (Horan et al., 2005) to estimate the loss in production associated with shorter lactations of between 260 and 300 days (Figure 1.1).

The three genotypes defined by Horan et al. (2005) were high production Holstein-Friesian cows, high durability Holstein-Friesian cows, and New Zealand Holstein-Friesian cows. The dams of the high production Holstein-Friesian cows were Irish Holstein-Friesian cows of high genetic merit for milk production and the sires of these high production cows were North American Holstein-Friesians with superior genetic merit for milk production. The high durability cows were bred from Irish Holstein-Friesian cows with lower genetic merit for milk production and were sired by North American Holstein-Friesian sires selected for superior milk production, fertility, and linear traits. The New Zealand cows were imported to Ireland as embryos from New Zealand and were selected for the highest possible genetic merit expressed in the New Zealand genetic evaluation system (Horan et al., 2005).

![Lactation curves](image)

**Figure 1.1.** Lactation curves for (A) milk yield and (B) milk solids of three different genotypes of Holstein-Friesian dairy cows – high production Holstein-Friesians (green), high durability Holstein-Friesians (blue), and New Zealand Holstein-Friesians (yellow).

1 Lactation curve parameters were reproduced from Horan et al. (2005).
Based on the parameters from Horan et al. (2005), the expected milk solids yield from a 260-day lactation was approximately 90% of the yield of the respective 305-day lactation (Table 1.1). A cow with a lactation of 280 days was expected to produce approximately 250 fewer kg of milk and 24 fewer kg of milk solids than would be expected from a 305-day lactation (Table 1.1).

**Table 1.1.** Expected loss of milk yield and milk solids yield in short lactations relative to expected 305-day lactation yields in Holstein-Friesian cows of three different genotypes.

<table>
<thead>
<tr>
<th>Lactation length (days)</th>
<th>High production(^1)</th>
<th>High durability</th>
<th>New Zealand</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>kg loss</td>
<td>% loss</td>
<td>kg loss</td>
</tr>
<tr>
<td>Milk yield (kg)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>260</td>
<td>500</td>
<td>7.4</td>
<td>467</td>
</tr>
<tr>
<td>270</td>
<td>373</td>
<td>5.5</td>
<td>348</td>
</tr>
<tr>
<td>280</td>
<td>254</td>
<td>3.8</td>
<td>238</td>
</tr>
<tr>
<td>290</td>
<td>146</td>
<td>2.2</td>
<td>136</td>
</tr>
<tr>
<td>300</td>
<td>46</td>
<td>0.7</td>
<td>43</td>
</tr>
<tr>
<td>Milk solids yield (kg)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>260</td>
<td>43</td>
<td>8.7</td>
<td>47</td>
</tr>
<tr>
<td>270</td>
<td>33</td>
<td>6.6</td>
<td>35</td>
</tr>
<tr>
<td>280</td>
<td>23</td>
<td>4.6</td>
<td>25</td>
</tr>
<tr>
<td>290</td>
<td>13</td>
<td>2.7</td>
<td>15</td>
</tr>
<tr>
<td>300</td>
<td>4</td>
<td>0.9</td>
<td>5</td>
</tr>
</tbody>
</table>

\(^1\)High production - High production Holstein-Friesian cows; High durability - High durability Holstein-Friesian cows; New Zealand - New Zealand Holstein-Friesian cows

Considering lactation yields are standardised to 305 days in most management decision support tools and genetic evaluations, producers may be basing decisions on currently unattainable estimated yields. If 305-day lactations were achieved, not only would the standardised yields be more reflective of actual production, but the production and environmental efficiency of dairy cows may improve by diluting their feed intake and environmental impact over a greater volume of milk. Nevertheless, lactations should not be lengthened at the expense of extending calving intervals or shortening dry periods, both of which could have repercussions for lifetime production efficiency. Additionally, lactation length should not be artificially lengthened, at the expense of profitability, by introducing expensive feed sources, such as grass silage or concentrates, towards the end of lactation when yield is reducing unless the price paid.
per litre of milk outweighs the additional expense. Although some non-genetic factors such as parity (Hossein-Zadeh, 2012), age at calving (Bajwa et al., 2004), season of calving (Bajwa et al., 2004), milk yield (Weber et al., 2015), and fertility (Tiezzi et al., 2012; Weber et al., 2015) have all been associated with lactation length in dairy cows, these studies were restricted to confinement systems. Given all previous studies were restricted to confinement systems, the factors associated with dairy cow lactation length in pasture-based production systems remains unknown.

1.3.3 Dairy cow longevity

Interest in improving the longevity of dairy cows is increasing globally. This is because extending the productive life of dairy cows has been reported to both reduce environmental impact and increase profitability (Grandl et al., 2019; De Vries 2020). When the trade-offs between economically important factors (i.e., replacement costs, mature production, costs associated with aging, genetic gain, and calf value) are considered, the optimum productive lifespan of dairy cows is approximately five lactations (De Vries, 2020). Nonetheless, in developed countries, the achieved average productive lifespan of dairy cows is currently between 2.5 and 4.5 years (Adamczyk et al., 2016; Kerslake et al., 2018; De Vries and Marcondes, 2020). It has, however, been suggested that the productive lifespan of an incumbent asset (i.e., a mature dairy cow) should be shortened if the challenger asset (i.e., a replacement heifer) is more economically efficient or genetically superior (De Vries, 2020). This has often resulted in a shorter productive lifespan in dairy herds of fixed size, due to an abundance of genetically superior dairy heifers (De Vries, 2020). Although these young herds can capitalise on the genetic superiority of their herds, fewer cows reach their potential mature production, contributing to these herds having higher replacement costs.

Replacement heifer rearing is a substantial cost to dairy producers, representing 15-20% of the total cost of dairy production (Heinrichs, 1993). Although a function of milk price and input costs, it has been estimated that, on average, the cost of heifer rearing is €1,545 and this is not repaid until the cow has achieved 1.63 lactations. Increasing the number of mature cows in the herd, through greater longevity, can improve the economic sustainability of a herd by reducing the requirement for replacements. Additionally, mature cows yield up to 28% more milk than their first parity counterparts (Table 1.2; Yang et al., 2005; Lee and Kim, 2006; Torshizi et al.,
2017) and mature cows produce heavier calves for sale (De Vries, 2020; Dunne et al., 2021).

A high replacement rate was traditionally a prerequisite for genetic gain, stifling improvements in dairy cow longevity. The recent advancements of genomic evaluations and reproductive technologies (Berry et al., 2014a; García-Ruiz et al., 2016) have removed this requirement for a high replacement rate. In fact, improving dairy cow longevity would result in a need for proportionally fewer replacement heifers, which could be generated from maiden heifers only if sex-sorted semen was used. As well as the maiden heifers being the most fertile and genetically superior animals in the herd, if they were genomically tested, the accuracy of their genetic evaluations could be comparable to those of mature cows. Thus, good cow longevity has the potential to accelerate genetic gain within a herd, by removing the need to breed replacement heifers from mature cows, thereby, increasing selection intensity. Given genetic merit tends to improve with each new generation (Evans et al., 2006), improving dairy cow longevity could improve production efficiency by increasing the performance of younger cows as well as increasing the proportion of cows in the herd which achieve their expected mature yield.

Table 1.2. Dairy cow milk yields (kg) reported in individual parities by previous studies in different countries.

<table>
<thead>
<tr>
<th></th>
<th>Guo et al., 2002</th>
<th>Yang et al., 2005</th>
<th>Lee and Kim, 2006</th>
<th>Torshizi et al., 2017</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Denmark</td>
<td>China</td>
<td>Korea</td>
<td>Iran</td>
</tr>
<tr>
<td>1&lt;sup&gt;st&lt;/sup&gt; parity</td>
<td>4,209</td>
<td>3,863</td>
<td>8,431</td>
<td>6,582</td>
</tr>
<tr>
<td>2&lt;sup&gt;nd&lt;/sup&gt; parity</td>
<td>4,648</td>
<td>4,353</td>
<td>9,774</td>
<td>7,240</td>
</tr>
<tr>
<td>3&lt;sup&gt;rd&lt;/sup&gt; parity</td>
<td>4,930</td>
<td>4,688</td>
<td>10,191</td>
<td>7,636</td>
</tr>
<tr>
<td>4&lt;sup&gt;th&lt;/sup&gt; parity</td>
<td>4,992</td>
<td>4,827</td>
<td>10,812</td>
<td>7,688</td>
</tr>
<tr>
<td>5&lt;sup&gt;th&lt;/sup&gt; parity</td>
<td>5,001</td>
<td>4,692</td>
<td>10,611</td>
<td>7,647</td>
</tr>
<tr>
<td>6&lt;sup&gt;th&lt;/sup&gt; parity</td>
<td>4,948</td>
<td>4,387</td>
<td></td>
<td>7,458</td>
</tr>
<tr>
<td>7&lt;sup&gt;th&lt;/sup&gt; parity</td>
<td>4,943</td>
<td></td>
<td></td>
<td>7,167</td>
</tr>
</tbody>
</table>

<sup>1</sup>Milk yields presented were averaged across two Danish regions.

It is important to note that average productive lifespan of dairy cows globally has not increased in line with the improvements achieved in reproductive performance (Adamczyk et al., 2016; Kersale et al., 2018; De Vries and Marcondes, 2020); this suggests that factors other than fertility may now be limiting the productive lifespan of dairy cows. Poor lactation yield and high somatic cell count (SCC) are two of the primary reasons impacting voluntary culling in dairy cows (Berry et al., 2005; Kersale...
et al., 2018; De Vries and Marcondes, 2020). Yet to date, no study has investigated when dairy cows reach maximum 305-day milk yield, highest average somatic cell score (SCS) or, indeed, whether inter-animal variability exists in the rate of change in lactation yield or SCS before and after maximum yield or highest average SCS. It is possible that if inter-animal genetic variation exists for the trajectory of milk yield or SCS across parities, this genetic variation could be exploited to breed dairy cows with improved longevity by maintaining their mature milk production for longer and maintaining low SCS as they age.

Selection for dairy cow longevity is challenging, particularly as a cow’s true longevity is not known until she is culled (Veerkamp et al., 2001; van Pelt et al., 2015). Therefore, identifying suitable phenotypic (Cruickshank et al., 2002; Kern et al., 2015) and genetic (Brotherstone et al., 1998; Cruickshank et al., 2002; Kern et al., 2015) predictors of longevity that can be measured early in life is of great interest. Linear type traits are a subjective visual assessment of the biological extremes of a wide selection of physical characteristics (Berry et al., 2004; Manafiazar et al., 2016); they are heritable and are routinely recorded on breeding dairy cows during their first parity (Veerkamp and Brotherstone, 1997; Berry et al., 2004; Manafiazar et al., 2016). Linear type traits have been phenotypically and genetically correlated with measures of longevity in Holstein (Kern et al., 2015), Holstein-Friesian (Brotherstone et al., 1998) and Guernsey dairy cows (Cruickshank et al., 2002) and are currently often included as predictors of longevity in dairy cow genetic evaluations (Miglior et al., 2017). Genetic correlations between longevity and body size-related linear type traits range from -0.27 to 0.22, from -0.38 to -0.15, and from -0.26 to 0.00 for Holstein-Friesian (Brotherstone et al., 1998), Holstein (Kern et al., 2015), and Guernsey dairy cows (Table 1.3; Cruickshank et al., 2002), respectively. While the genetic correlations between longevity and udder-related linear type traits and feet and leg-related linear type traits range from -0.33 to 0.46 and from 0.05 to 0.21, respectively for Holstein-Friesian cows (Brotherstone et al., 1998); the genetic correlations between longevity and udder-related linear type traits and leg-related linear type traits were similar for Holstein (Kern et al., 2015) and Guernsey cows (Table 1.3; Cruickshank et al., 2002). Although the genetic correlations between longevity and linear type traits are widely reported in the literature, the majority of studies were restricted to relatively young cows (≤5th parity; Brotherstone et al., 1998; Cruickshank et al., 2002) or herds with short average productive lifespans (Kern et al., 2015) owing to the tendency to cull
cows for infertility prior to reaching maturity. Therefore, the relationship between linear type traits and longevity in older cows remains unknown, even though cumulative improvements have been achieved in the genetic merit for reproductive performance in dairy cow populations (Berry et al., 2014a; De Vries, 2020).
Table 1.3. Genetic correlations between measures of dairy cow survival/longevity and linear type traits.

<table>
<thead>
<tr>
<th>Linear type trait</th>
<th>Rogers et al., 1991</th>
<th>Brotherstone et al., 1998</th>
<th>Cruickshank et al., 2002</th>
<th>Kern et al., 2015</th>
<th>Novotný et al, 2017</th>
</tr>
</thead>
<tbody>
<tr>
<td>SURV₁²</td>
<td>SURV₂₀</td>
<td>PL₆₀</td>
<td>LS</td>
<td>LS_adj</td>
<td>THL</td>
</tr>
<tr>
<td>Body³</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>ANG</td>
<td>0.16</td>
<td>-0.02</td>
<td>0.19</td>
<td>0.10</td>
<td>-0.26</td>
</tr>
<tr>
<td>BD</td>
<td>0.19</td>
<td>0.10</td>
<td>0.26</td>
<td>0.29</td>
<td>0.26</td>
</tr>
<tr>
<td>CW</td>
<td>-0.40</td>
<td>-0.19</td>
<td>-0.10</td>
<td>-0.27</td>
<td>-0.29</td>
</tr>
<tr>
<td>RA</td>
<td>0.12</td>
<td>-0.13</td>
<td>0.22</td>
<td>0.14</td>
<td>-0.26</td>
</tr>
<tr>
<td>STA</td>
<td>0.23</td>
<td>-0.21</td>
<td>0.03</td>
<td>0.22</td>
<td>0.14</td>
</tr>
<tr>
<td>Udder</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>FUA</td>
<td>0.78</td>
<td>0.51</td>
<td>0.68</td>
<td>0.46</td>
<td>0.63</td>
</tr>
<tr>
<td>RPT</td>
<td>0.69</td>
<td>0.54</td>
<td>0.47</td>
<td>0.06</td>
<td>0.21</td>
</tr>
<tr>
<td>RUH</td>
<td>0.36</td>
<td>0.19</td>
<td>0.28</td>
<td>0.20</td>
<td>0.25</td>
</tr>
<tr>
<td>TEX</td>
<td>0.82</td>
<td>0.44</td>
<td>0.60</td>
<td>0.20</td>
<td>0.25</td>
</tr>
<tr>
<td>TL</td>
<td>0.20</td>
<td>-0.01</td>
<td>0.24</td>
<td>0.14</td>
<td>0.11</td>
</tr>
<tr>
<td>Feet</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>FA</td>
<td>0.15</td>
<td>0.05</td>
<td>0.36</td>
<td>0.21</td>
<td>0.22</td>
</tr>
<tr>
<td>RLS</td>
<td>-0.16</td>
<td>-0.13</td>
<td>-0.21</td>
<td>0.05</td>
<td>0.02</td>
</tr>
<tr>
<td>BONE</td>
<td>0.14</td>
<td>0.21</td>
<td>0.19</td>
<td>0.23</td>
<td></td>
</tr>
</tbody>
</table>

²SURV₁ – survival to the end of first lactation; SURV₂₀ – survival to 20 months after first calving; PL₆₀ – length of productive life up to 60 months; LS – number of lactations completed or expected to complete; LS_adj – LS adjusted for first lactation milk yield; THL – number of days between birth and culling; FHL – THL adjusted for milk yield; LACT – number of lactations initiated; LACT_d – total number of days during all lactations; LS_mo – time between birth and last milk recording in months; PL_mo – time from first calving to last milk recording in months; LACT_adj – number of lactations initiated adjusted for milk production.
1.4 Genetic parameters of production and feed efficiency

Both the heritability and genetic variation of a trait influence the potential rate of genetic gain. The breeder’s equation used to represent the annual genetic gain for any trait or breeding objective is (Rendel and Robertson, 1950a):

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

where \(\Delta G\) is annual genetic gain, \(i\) is the intensity of selection, \(r\) is the accuracy of selection, \(\sigma_g\) is the genetic standard deviation (i.e., measure of genetic variation), and \(L\) is the generation interval. The heritability of a trait, in combination with the quantity of information available, determines the accuracy of selection. Heritability influences the accuracy of selection regardless of whether traditional genetic or genomic evaluations are used (Figure 1.2); the lower the heritability of a trait, the greater the number of (progeny) records required to reach a given accuracy of selection. Nevertheless, high accuracy of selection can be achieved for a lowly heritable trait with sufficient records. Therefore, in efficient and effective breeding programmes, heritability has minimal impact on genetic gain.

The advent of dense genotyping panels has added a new dimension to the information available to derive an animal’s true genetic merit through genomic selection (Goddard and Hayes, 2007). Genomic selection has the potential to provide more accurate estimates of an animal’s genetic merit than traditional pedigree-based estimates; generating more accurate estimates of genetic merit could increase the rate of genetic gain (Rendel and Robertson, 1950a). Additionally, because animals can be genotyped as soon as they are born breeding decisions can be made more rapidly, which shortens the generation interval further increasing the rate of genetic gain.
Figure 1.2. For heritability values of 0.35, 0.20, 0.10, 0.05, and 0.03 (in order of increasing line darkness), (A) the number of progeny required to achieve a given accuracy of selection using traditional ancestry-based genetic evaluation and (B) the number of records of phenotyped and genotyped animals to achieve accuracy of genomic evaluations (based on 1,000 effective chromosomal segments and 80% of the genetic variance accounted for by the genotyped markers).

1 Figure reproduced from Berry et al. (2022).
1.4.1 Within-lactation measures of production and feed efficiency

1.4.1.1 Ratio traits

Of the various ratio production and feed efficiency traits proposed, heritability and genetic variance estimates are reported most frequently for FCE (Park et al., 1999; Vallimont et al., 2011; Hurley et al., 2017). Heritability estimates for FCE range from 0.06 to 0.20 (Table 1.4; Park et al., 1999; Vallimont et al., 2011; Hurley et al., 2017). Heritability estimates for kg of intake per kg of body weight range from 0.12 (SE = 0.04) to 0.18 (SE = 0.06; Table 1.4; Hurley et al., 2017) in Irish Holstein-Friesian cows. The heritability for kg of milk solids per kg of body weight is 0.37 (SE = 0.03; Table 1.4) in Irish dairy cows (Berry and McCarthy, 2021).

<table>
<thead>
<tr>
<th>Trait</th>
<th>( h^2 ) (SE)</th>
<th>( \sigma_g )</th>
<th>Country</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>FCE</td>
<td>0.20 (NA)</td>
<td>NA</td>
<td>Canada</td>
<td>Park et al., 1999</td>
</tr>
<tr>
<td>FCE</td>
<td>0.14 (0.06)</td>
<td>0.08</td>
<td>US</td>
<td>Vallimont et al., 2011</td>
</tr>
<tr>
<td>FCE</td>
<td>0.06 to 0.28</td>
<td>0.25 to 0.55</td>
<td>Ireland</td>
<td>Hurley et al., 2017</td>
</tr>
<tr>
<td>Intake/BW(^2)</td>
<td>0.12 to 0.18</td>
<td>0.67 to 0.82</td>
<td>Ireland</td>
<td>Hurley et al., 2017</td>
</tr>
<tr>
<td>MS/BW</td>
<td>0.37 (0.03)</td>
<td>0.08</td>
<td>Ireland</td>
<td>Berry and McCarthy, 2021</td>
</tr>
</tbody>
</table>

\(^1\)NA – not available; \(^2\)Intake/BW – kg of feed intake per kg of body weight; MS/BW – kg of milk solid per kg of body weight

While genetic parameters for the ratio production and feed efficiency traits have not been frequently reported, the genetic parameters for the components of each ratio trait are well documented (Berry et al., 2003; Manzanilla-Pech et al., 2016; Hurley et al., 2017). Heritability estimates for milk production traits range from 0.18 (SE = 0.05) to 0.44 (SE = 0.05; Evans et al., 2002; Berry et al., 2003; Manzanilla-Pech et al., 2016), while heritability estimates for dairy cow live weight range from 0.42 (SE = 0.05) to 0.60 (SE = 0.06; Berry et al., 2003; Manafiazar et al., 2016; Manzanilla-Pech et al., 2016; Berry et al., 2021). The heritability and genetic variability for DMI are well documented, albeit primarily for dairy cows in confinement systems (Veerkamp and Brotherstone, 1997; Toshniwal et al., 2008; Vallimont et al., 2011). Nonetheless, the heritability and genetic variance for DMI have also been reported in dairy cows in pasture-based production systems (Berry et al., 2007a; Hurley et al., 2017). Heritability estimates for DMI in dairy cows range from 0.07 to 0.44 (Veerkamp and Brotherstone, 1997; Berry et al., 2007a; Toshniwal et al., 2008;
Vallimont et al., 2011; Hurley et al., 2017). Where the heritability estimates for both the ratio efficiency traits and their component traits were reported from the same study, the heritability for the ratio trait tended to be lower than the average heritability of its component traits (Hurley et al., 2017; Vallimont et al., 2011; Berry and McCarthy, 2021). The lower heritability estimates for ratio traits relative to their component traits was potentially due to the increased error variance associated with ratio traits (Berry and Crowley, 2013).

### 1.4.1.2 Residual efficiency traits

Heritability estimates for RFI in lactating dairy cows have been reported in several studies (de Haas et al., 2011; Vallimont et al., 2011; Connor et al., 2013; Hurley et al., 2017), although the majority of these studies were restricted to dairy cows in confinement production systems. Residual feed intake is reported to be low to moderately heritable in lactating dairy cows in both confinement (Table 1.5; de Haas et al., 2011; Vallimont et al., 2011; Connor et al., 2013; Manafiazar et al., 2016) and pasture-based systems (Table 1.5; Lopez-Villalobos et al., 2008; Hurley et al., 2017). Residual feed intake is reported to be moderately heritable in growing heifers (Table 1.6; Williams et al., 2011; Pryce et al., 2012; Lin et al., 2013). Although reported less frequently in pasture-based systems, Hurley et al. (2017) reported the heritability for RFI to range from 0.04 (34 DIM) to 0.11 (280 DIM) but varied by stage of lactation in pasture-based dairy cows.

| Table 1.5. Heritability estimates (h²; standard errors in parenthesis) for residual feed intake reported in different populations of dairy cows. |
|-----------------|-----------------|-----------------|-----------------|
| Country         | h² (SE)          | Breed           | Reference       |
| US              | 0.02 (NA¹)       | Holstein        | Ngwerume and Mao, 1992 |
| Netherlands     | 0.38 (NA)        | Holstein        | Veerkamp et al., 1995 |
| Ireland         | 0.05 to 0.38     | Holstein-Friesian | Lopez-Villalobos et al., 2008 |
| Netherlands     | 0.40 (0.11)      | Holstein-Friesian | de Haas et al., 2011 |
| US              | 0.01 (0.05)      | NA              | Vallimont et al., 2011 |
| US              | 0.36 (0.06)      | Holstein        | Connor et al., 2013 |
| US              | 0.20 (0.03)      | Holstein        | Manafiazar et al., 2016 |
| Ireland         | 0.04 to 0.11     | Holstein-Friesian | Hurley et al., 2017 |
|                 | (0.03 to 0.06)   |                 |                 |
| Germany         | 0.12 to 0.39     | Holstein        | Becker et al., 2021 |
| Canada          | 0.13 (NA)        | NA              | Houlahan et al., 2021 |

¹NA – not available
Table 1.6. Heritability estimates ($h^2$; standard errors in parenthesis) for residual feed intake reported in different populations of growing dairy heifers.

<table>
<thead>
<tr>
<th>Country</th>
<th>$h^2$ (SE)</th>
<th>Breed</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Australia</td>
<td>0.22 (0.07)</td>
<td>Holstein</td>
<td>Pryce et al., 2012</td>
</tr>
<tr>
<td>New Zealand</td>
<td>0.38 (0.09)</td>
<td>Holstein</td>
<td>Pryce et al., 2012</td>
</tr>
<tr>
<td>Australia</td>
<td>0.40 (0.09)</td>
<td>Holstein-Friesian</td>
<td>Lin et al., 2013</td>
</tr>
<tr>
<td>Australia</td>
<td>0.27 (0.12)</td>
<td>Holstein-Friesian</td>
<td>Williams et al., 2011</td>
</tr>
</tbody>
</table>

Hurley et al. (2017) also reported that substantial genetic variation was evident for RFI across all stages of lactation. The genetic standard deviation for RFI ranges from 1.28 unité fourragère du lait (UFL)/day (34 DIM) to 1.74 UFL/day (280 DIM) where 1 UFL is the net energy requirements for lactation equivalent of 1 kg standard air-dry barley (Hurley et al., 2017). Since Coleman et al. (2010) proposed RSP, the genetic parameters for traits similar to RSP have only been estimated once for dairy cows in pasture-based production (Hurley et al., 2017). When the genetic parameters for RSP were estimated using random regression models, heritability estimates for RSP ranged from 0.15 at 50 DIM to 0.36 at 250 DIM (Hurley et al., 2017).

Berry and Crowley (2013) reported that the average heritability of RFI for mature beef and dairy cows was 0.04 (SE = 0.01) based on a meta-analysis of the literature available at the time. Several studies have reported the heritability for RFI in dairy cows since 2013. Therefore, a meta-analysis of published genetic parameters for RFI in dairy cows was conducted. The pooled heritability for RFI across the relevant studies was defined as (Koots et al., 1994):

$$h^2_{pooled} = \frac{\sum_{i=1}^{n} \frac{h^2_i}{(SE_{h^2_i})^2}}{\sum_{i=1}^{n} \frac{1}{(SE_{h^2_i})^2}}$$

and the standard error of the pooled heritability was defined as (Koots et al., 1994):

$$SE(h^2_{pooled}) = \sqrt{\frac{1}{\sum_{i=1}^{n} \frac{h^2_i}{(SE_{h^2_i})^2}}}$$

where $h^2 =$ heritability and $SE =$ standard error. The pooled heritability estimate for RFI in dairy cows was 0.19 (SE = 0.02) based on the four studies (de Haas et al.,
2011; Vallimont et al., 2011; Connor et al., 2013; Manafiazar et al., 2016) detailed in Table 1.5 that reported heritability estimates and corresponding standard errors for RFI.

### 1.4.1.3 Lactation length

Heritability estimates for lactation length have frequently been reported for young dairy cows in confinement production systems (Ojango and Pollot, 2001; Bakir et al., 2004; Hossein-Zadeh et al., 2012; Tiezzi et al., 2012; Goshu et al., 2014). Only one study reported the heritability for lactation length in pasture-based dairy cows and this study was limited to 1,679 and 1,230 Holstein-Friesian sires with daughters in first and second parity, respectively (Haile-Mariam et al., 2003). Heritability estimates for lactation length for dairy cows in confinement production systems range from 0.03 to 0.28 (Table 1.7; Ojango and Pollot, 2001; Bakir et al., 2004; Hossein-Zadeh, 2012; Tiezzi et al., 2012; Goshu et al., 2014), while Haile-Mariam et al. (2003) reported the heritability for lactation length to be 0.03 in pasture-based Holstein-Friesian cows. Repeatability estimates for lactation length were also reported for dairy cows in confinement systems and range from 0.11 to 0.65 (Ojango and Pollott, 2001; Bakir et al., 2004).

#### Table 1.7. Heritability estimates (standard error in parenthesis) for lactation length from a range of studies across different breeds and countries.

<table>
<thead>
<tr>
<th>Parity</th>
<th>h²</th>
<th>Country</th>
<th>Breed</th>
<th>Number of cows</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>0.04 (0.003)</td>
<td>Iran</td>
<td>HO</td>
<td>206,582</td>
<td>Hossein-Zadeh, 2012</td>
</tr>
<tr>
<td>2</td>
<td>0.04 (0.003)</td>
<td>Iran</td>
<td>HO</td>
<td>167,551</td>
<td>Hossein-Zadeh, 2012</td>
</tr>
<tr>
<td>3</td>
<td>0.03 (0.000)</td>
<td>Iran</td>
<td>HO</td>
<td>118,291</td>
<td>Hossein-Zadeh, 2012</td>
</tr>
<tr>
<td>1</td>
<td>0.05 (NA²)</td>
<td>Italy</td>
<td>BS</td>
<td>24,098</td>
<td>Tiezzi et al., 2012</td>
</tr>
<tr>
<td>1</td>
<td>0.03 (0.01)</td>
<td>Australia</td>
<td>HF</td>
<td>1,679 (sires)</td>
<td>Haile-Mariam et al., 2003</td>
</tr>
<tr>
<td>2</td>
<td>0.03 (0.01)</td>
<td>Australia</td>
<td>HF</td>
<td>1,230 (sires)</td>
<td></td>
</tr>
<tr>
<td>1-3</td>
<td>0.09 (0.03)</td>
<td>Kenya</td>
<td>HF</td>
<td>1,614</td>
<td>Ojango and Pollott, 2001</td>
</tr>
<tr>
<td>1</td>
<td>0.28 (0.12)</td>
<td>Ethiopia</td>
<td>HF</td>
<td>533</td>
<td>Goshu et al., 2014</td>
</tr>
<tr>
<td>NA</td>
<td>0.06 (0.04)</td>
<td>Turkey</td>
<td>HF</td>
<td>328</td>
<td>Bakir et al., 2004</td>
</tr>
<tr>
<td>NA</td>
<td>0.27 (0.03)</td>
<td>Turkey</td>
<td>BS</td>
<td>174</td>
<td>Bakir et al., 2004</td>
</tr>
</tbody>
</table>

¹HO – Holstein, BS – Brown Swiss, and HF – Holstein-Friesian. ²NA – not available.

Two studies documented substantial genetic variation in lactation length for Kenyan (Ojango and Pollott, 2001) and Ethiopian (Goshu et al., 2014) Holstein-Friesian cows in confinement systems. The genetic standard deviation for lactation...
length is reported to range from 15.8 (Ojango and Pollott, 2001) to 50.1 days (Goshu et al., 2014) in Kenyan and Ethiopian Holstein-Friesian cows, respectively.

Based on the genetic standard deviation for lactation length reported by Ojango and Pollot (2001), the top 20% of cows on genetic merit for lactation length would be expected, on average, to have a 44-day longer lactation than cows in the bottom 20% (Figure 1.3). This difference increased to 55 days when the top and bottom 10% of cows were compared (Figure 1.3). Based on the larger genetic standard deviation for lactation length reported by Goshu et al. (2014), a difference in lactation length of 140 days was expected between the top and bottom 20% of cows when ranked on their genetic merit for lactation length (Figure 1.3).

**Figure 1.3.** Expected differences in lactation length between dairy cows when ranked on their estimated breeding values (EBV) for lactation length based on the genetic standard deviations published by (A) Ojango and Pollott (2001) and (B) Goshu et al. (2014).
1.4.2 Lifetime production efficiency

No genetic parameters for either ratio lifetime efficiency traits or true lifetime production efficiency have been reported. Nevertheless, a plethora of genetic parameters for longevity and survival traits have been estimated for different populations of dairy cows (Brotherstone et al., 1997; Eaglen et al., 2013; Pritchard et al., 2013; Zhang et al., 2021). Substantial exploitable genetic variation has been documented for longevity traits (Eaglen et al., 2013; Kern et al., 2015; Zhang et al., 2021); the coefficient of genetic variation for longevity when defined as the length of time between first calving and culling/last milk recording ranges from 0.001 to 0.12 (Eaglen et al., 2013; Kern et al., 2015; Zhang et al., 2021). Heritability estimates for longevity-related traits range from 0.05 (Pritchard et al., 2013) to 0.11 (Eaglen et al., 2013) in dairy cows, although, the heritability estimates for longevity traits available in the literature vary depending on how longevity or survival was defined (Kern et al., 2015; Zhang et al., 2021). Zhang et al. (2021), for example, reported that the heritability for survival reduced when survival was measured over longer periods; the heritability of survival from first calving to the end of the first lactation was 0.09 (SE = 0.01), whereas the heritability for survival from first calving to the end of the fifth lactation was 0.05 (SE = 0.01; Zhang et al., 2021).

Two studies on dairy cows have estimated the heritability for survival in each parity by fitting a random regression model to the longitudinal data; these studies reported that the heritability for survival varies between 0.02 and 0.08 (Veerkamp et al., 2001; van Pelt et al., 2015), with van Pelt et al. (2015) reporting that the heritability for longevity was lower in young parities. Veerkamp et al. (2001) and van Pelt et al. (2015) considered data from dairy cows up to the end of fourth and sixth lactation, respectively, and reported that the genetic correlations between survival in different parities differed from unity suggesting that survival may not be the same trait in different parities. The strength of the genetic correlations between survival in different parities was inversely related to the distance between the two parities compared (van Pelt et al., 2015).
1.5 Inclusion of production efficiency in breeding goals

1.5.1 The breeding goal

A breeding goal is the genetic path that must be pursued to achieve the desired improvement within a breeding population (Rivero et al., 2013). Greater profitability often represents the breeding goal in dairy cow populations. Determining the breeding goal is the first step in designing a breeding program (Goddard, 1998). Once a breeding goal is defined, breeding objectives can be constructed to pursue the achievement of the breeding goal. The breeding objective should include both the traits that need to be improved to increase profitability along with the relative (economic) importance of each; the latter is used to determine the selection emphasis placed on each trait in the selection index (Rivero et al., 2013). For a trait to be included in a breeding objective, it must meet three criteria (Shook et al., 1989):

1) The trait must be economically, environmentally, or socially important
2) The trait must be heritable
3) The trait must be measurable or genetically correlated with other measurable traits or information

The main advantage of selecting animals based on selection indexes is that genetic pressure can be exerted on multiple traits simultaneously (Hazel, 1943); it is even possible to improve traits that are antagonistically correlated using selection indexes (Hazel, 1943). The Irish Cattle Breeding Federation (ICBF) manage the Irish national database of phenotypic and genomic dairy and beef data and routinely undertake genetic evaluations for dairy and beef cattle. The ICBF also validate national genetic evaluations for cattle and publish the results of genetic evaluations facilitating the identification of genetically superior animals.

1.5.1.1 Irish dairy breeding index

The Economic Breeding Index (EBI) is the national breeding goal for Irish dairy cows since 2000; Figure 1.4 demonstrates how the EBI has evolved since 2000. The objective of the EBI is to identify male and female cattle that are genetically superior for breeding more profitable dairy herd replacements (Berry et al., 2007a). The EBI is currently comprised of seven sub-indexes, each of which consists of multiple traits; the sub-indexes are milk production, fertility, calving, beef, maintenance, management, and health, and the relative emphasis of each sub-index is
shown in Figure 1.4. Each trait within each sub-index is displayed as a predicted transmitting ability (PTA). An overall index profit value is calculated by summing the products of the PTA for each trait times its respective economic weight.

![Graph showing relative emphasis of each sub-index included in the Economic Breeding Index as it evolved since the Relative Breeding Index (RBI).](image)

Figure 1.4. Relative emphasis of each sub-index included in the Economic Breeding Index as it evolved since the Relative Breeding Index (RBI).

Given production and feed efficiency are of economic and environmental importance, are heritable, and exhibit genetic variation between animals, it is not surprising that many researchers have suggested incorporating such traits in breeding objectives (Pryce et al., 2015; Parker Gaddis et al., 2021). Nevertheless, neither ratio nor residual efficiency traits are explicitly included in the Irish dairy breeding index or in the majority of dairy breeding indexes globally (Cole and VanRadjen, 2018). This does not negate the potential to improve production and feed efficiency using existing breeding objectives as most traits included in the ratio and residual efficiency traits are already included in dairy breeding indexes (Berry and McCarthy, 2021).
1.5.2 How traits currently in selection indexes can improve production and feed efficiency

Given the complexity of the factors that influence dairy cow lifetime production efficiency (Figure 1.5), direct selection for improved lifetime production efficiency is difficult. Nevertheless, many of the traits already included in dairy cow breeding objectives have the potential to improve the lifetime production efficiency of dairy cows; some of the improvements achieved in dairy cow production efficiency over the last five decades have been attributed to genetic selection for desirable traits, such as milk production (Brito et al., 2021). Using total merit indexes to breed for dairy heifers could greatly improve both the within-lactation and lifetime production efficiency of the dairy population by selecting for increased milk solids production, improved feed efficiency, reduced maintenance requirements, and improved fertility and health.

Figure 1.5. Some of the factors that influence dairy cow lifetime production efficiency.
1.5.2.1 Milk production

Considerable relative emphasis is generally placed on milk production in dairy cow total merit indexes globally (Cole and VanRaden, 2018) reflecting its importance to profitability and a continued desire to increase production. Nonetheless, the economic weights associated with the individual components of milk production, such as milk yield, fat yield, and protein yield vary by jurisdiction (ICBF, 2018; CDN, 2019; VanRaden et al., 2021; DairyNZ, 2022). Several countries including Ireland, New Zealand, and Australia place a negative economic weight on milk yield (Byrne et al., 2016; ICBF, 2018; DairyNZ, 2022), in an effort to improve the quality of milk being produced and reduce the cost of production. Conversely, three of the four dairy selection indexes in the United States have a positive economic weight on milk yield (Table 1.8; VanRaden et al., 2021), mainly reflecting the importance of the liquid milk market in the US.

Table 1.8. Economic values (€) and relative emphasis (%) of milk (lbs), fat (lbs), and protein (lbs) yields in United States dairy selection indexes.

<table>
<thead>
<tr>
<th>Trait</th>
<th>Economic value</th>
<th>Relative emphasis</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>NM</td>
<td>FM</td>
</tr>
<tr>
<td>Milk</td>
<td>0.002</td>
<td>0.13</td>
</tr>
<tr>
<td>Fat</td>
<td>3.91</td>
<td>3.91</td>
</tr>
<tr>
<td>Protein</td>
<td>4.37</td>
<td>0.00</td>
</tr>
</tbody>
</table>

1Economic values were converted to Euro based on current exchange rate on 8th of June 2022 $1 = €0.94; 2NM – net merit index; FM – fluid merit index; CM – cheese merit index; GM – grazing merit index. Economic values and relative emphasis sourced from VanRaden et al. (2021).

1.5.2.2 Feed intake and Maintenance

Despite the influence of feed costs on the profitability of dairy production, and the abundance of genetic variability in feed intake and efficiency, the direct inclusion of feed intake/efficiency in dairy breeding indexes is not ubiquitous. At present, Australia, the United States, and the Nordic countries (Denmark, Finland, and Sweden) and the Netherlands are the only countries that explicitly include a feed intake-related trait (feed saved) in their dairy breeding indexes (Pryce et al., 2015; Byrne et al., 2016; de Jong et al., 2019; CDCB, 2020; CDCB, 2021; NAV, 2022). Lactanet plans to include a feed efficiency trait in both Canadian Holstein selection indexes (Lifetime Performance Index and Pro$) in August 2022 (Sweett and Fleming, 2022). The genetic evaluations for feed saved in Australia, the United States, the Nordic countries and the
Netherlands are based on actual feed intake measures of limited populations of 1,193 (Pryce et al., 2015; Byrne et al., 2016), 6,200 (CDCB, 2020; CDCB, 2021), 5,383 (Stephansen et al., 2020), and 5,649 dairy cows (de Jong et al., 2019), respectively. The number of individuals with actual feed intake measurements used for the Nordic genetic evaluation was expected to increase to 12,525 by December 2021 (Stephansen et al., 2021).

At present, the majority of global dairy total merit selection indexes include cow live weight as a proxy for the feed required for maintenance (Cole and VanRaden, 2018; ICBF, 2020; VanRaden et al., 2021; DairyNZ, 2022). Although selection for lighter cows with lower feed requirements for maintenance and growth would likely reduce feed costs for producers, without including feed intake or efficiency traits it would not be possible to select for more net feed efficient dairy cows. The inclusion of a feed efficiency trait, such as feed saved, which combines the expected maintenance requirements of dairy cows with feed efficiency, has the potential to greatly improve the lifetime production efficiency of dairy cows by simultaneously selecting for more feed efficient cows with lower maintenance requirements.

1.5.2.3 Fertility and survival

Considerable relative emphasis is now placed on fertility (including survival) and functional longevity in dairy total merit indexes globally (Cole and VanRaden, 2018; ICBF, 2020; DataGene, 2020; Egger-Danner et al., 2015). Conversely, prior to the 21st century, dairy breeding objectives of most countries, particularly countries where Holstein or Holstein-Friesian was the predominant breed, rarely included fertility or longevity traits (Miglior et al., 2005; Berry et al., 2007a; Byrne et al., 2016). Given the antagonistic relationship between milk production and fertility, selection for milk production alone resulted in an erosion in genetic merit for fertility in the global dairy population (Roxström et al., 2001; Berry et al., 2003) which, in turn, reduced the number of lactations achieved per cow. Nonetheless, the inclusion of reproductive performance in dairy cow breeding programs has contributed to a cumulative improvement in the genetic merit for reproductive performance in many dairy cow populations (Berry et al., 2014a; Cole and VanRaden, 2018; De Vries, 2020) which should, over time, improve the longevity of dairy cows and, therefore, their lifetime production efficiency.
1.5.2.4 Health

Almost all global dairy total merit selection indexes now include some health or health-related traits (Miglior and Sewalem, 2009; Cole and VanRaden, 2018), such as SCC, udder health, feet and leg conformation, or other direct health traits. Selection for health traits will likely become more important as dairy cow longevity increases, since progressive age-related deterioration in health and fitness is common across most animal species (Padilla et al., 2021), including dairy cows (Costagliola et al., 2016; Jamali et al., 2018). Reduced muscle mass (i.e., sarcopenia) is a major health concern in the elderly human population (Cruz-Jentoft et al., 2010) and has also been observed in older dairy cows (≥15 years old; Costagliola et al., 2016). While many dairy cows may not survive long enough to be culled due to sarcopenia, age-related deterioration also contributes to mastitis (Jamali et al., 2018), which is commonly reported as the main reason for culling in older dairy cows (Pinedo et al., 2010; Kerslake et al., 2018; Wondatir Workie et al., 2021). The inclusion of health and health-related traits in dairy breeding objectives should contribute to a reduced requirement for culling due to lameness, SCC, and mastitis, as well as other health-related issues.

1.6 Production efficiency in grazing dairy cows

Although most global dairy breeding objectives currently select for increased milk yield or milk solids production and improved production efficiency, both dairy production and dairy production efficiency vary greatly between countries and production systems. Average milk production per cow tends to be considerably lower in countries operating pasture-based production systems, such as Ireland and New Zealand, relative to average milk production per cow in confinement systems. For example, of the 27 countries within the European Union, Ireland is ranked fifth lowest for milk production per cow per year (Figure 1.6; Stele and Svetin, 2021) and the milk production per cow is similarly low in New Zealand (Figure 1.6).
Figure 1.6. Average yearly milk production (kg) per cow in the European Union (EU; Stele and Svetin, 2021), the United Kingdom (UK; Shahbandeh, 2021), the United States (US; USDA, 2020), Australia (Dairy Australia, 2020), and New Zealand (LIC and DairyNZ, 2020) in 2019.

Dairy production and, therefore, dairy production efficiency in pasture-based production systems is limited by a number of factors including the requirement for seasonal calving and the lower nutritional value of grass and grass silage compared to the protein-rich and energy-rich diets fed in confinement systems. In relatively low-input pasture-based dairy production, the dairy cow is a feed-to-food transformer.
(Delaby et al., 2020), meaning that dairy cows, and all animals in pasture-based production systems, convert human inedible protein (i.e., grass) to human edible protein (i.e., milk, beef, lamb). In order to ensure maximum utilisation of grass, which is key to profitability, dairy cows must calve in spring immediately before the initiation of grass growth (Dillon et al., 2003). As a result, good fertility is essential to ensure profit in predominantly pasture-based production systems. Seasonal calving can limit both within-lactation production efficiency and lifetime production efficiency. This is because, firstly, pasture-based dairy cows tend to be dried off in early winter after the cessation of grass growth, regardless of when they calved; this can result in short lactations which limits the overall lactation yield for cows that fail to calve early in the calving season. Secondly, in order to achieve a 365-day calving interval and avoid potential culling, dairy cows must be pregnant by their 85th day of lactation (Delaby et al., 2020). The overlap of the breeding season with peak lactation can result in reproductive failure (Butler, 2014) as the energy demands for lactation may not be met by actual energy intake.

The increase in the intake capacity of dairy cows have not kept pace with the increases in milk production. Therefore, an increasing proportion of a dairy cow’s energetic needs must be met by mobilising body reserves (Veerkamp et al., 2003), particularly in early lactation. Given the fact that the nutritional value of grazed grass is lower than the high-protein and high-energy feed fed in confinement production system, the mobilisation of body tissue is further exacerbated in grazing dairy cows (Pedernera et al., 2008). O’Neill et al. (2011) compared the impact of a grazed grass diet to a total mixed ration diet on early lactation methane emissions, DMI, and milk production in spring-calving Holstein-Friesian cows, and found that grazing dairy cows had lower feed intake and lower methane emissions per kg of DMI than cows fed total mixed ration. Nonetheless, over the same 10-week period, grazing dairy cows mobilised, on average, 0.33 BCS units (scale 1 to 5) compared to an increase in the average BCS of 0.36 units for the cows fed the total mixed ration diet. Similarly, grazing cows lost 0.37 kg of body weight per day, on average, whereas the body weight of the confined cows increased by 0.54 kg per day (O’Neill et al., 2011). Any negative energy balance in early lactation can negatively affect the fertility of dairy cows (Butler and Smith, 1989; Wade et al., 1996) and in pasture-based systems where cows need to become pregnant early in lactation, any negative energy balance could reduce the productive lifespan of dairy cows.
1.6.1 Measuring feed intake

Most measures of production and feed efficiency require accurate estimates of DMI. Automated feeding systems are one of the simplest and most common methods of measuring feed intake internationally. These systems, such as the GrowSafe system and the Insentec feeding system, use radio frequency identification tags to identify individual animals and weight cells to continuously measure the amount of feed removed from the feeder. The main advantage of this system is its simplicity and accuracy of measurement. An added advantage of automated feeding systems is an ability to collect information in addition to feed intake, such as feeding time, meal size, and feeding order (Kelly et al., 2020). Nevertheless, these automated feeding systems are only suitable for cows housed indoors or fed on feeding pads (i.e., not grazing cows).

Given simple automated measuring of feed intake is not possible in grazing dairy cows, several marker techniques for estimating feed intake in grazing animals have been developed since the 1950s. Prior to the end of the 20th century, the most common marker method for estimating the DMI of grazing cows was the chromium oxide (Cr2O3) technique (Stevenson, 1962; Dillon, 2006). The chromium oxide method involved estimating the total faecal output of cows using chromium oxide as an external indigestible marker and estimating the digestibility of forage using in vitro techniques. Typically, cows were administered Cr2O3 via shredded paper boluses (de Oliveira et al., 2007) or gelatin capsules (Kane et al., 1953; Malossini et al., 1996) twice daily for a period of 12 days, with faecal samples collected twice daily for the last five days of bolus administration (de Oliveira et al., 2007). While no longer the most common method of estimating DMI, the chromium oxide method is still used to estimate DMI in grazing animals (de Oliveira et al., 2007; Carvalho et al. 2019).

The n-alkane technique is currently the most commonly used marker technique to estimate the herbage intake in Irish grazing animals (O’Neill et al., 2013; Coffey et al., 2017). Originally developed by Mayes et al. (1986), the technique was modified by Dillen and Stakelum (1989) for use in dairy cows. The n-alkane technique uses two indigestible markers (n-alkanes) to predict feed intake; the ratio of odd chained n-alkanes (C33) naturally occurring in cuticular wax of plants to synthetic even chained n-alkanes (C32) is used to estimate feed intake. Although the synthetic n-alkane is typically delivered via a paper bolus, administered twice daily for twelve days, some
studies have used controlled release capsules (de Oliveira et al., 2007), which can reduce the labour required. Nonetheless, the use of controlled release capsules would require additional trials to test the release rate (de Oliveira et al., 2008). From the sixth day of n-alkane administration, faecal samples are collected twice daily; these samples are bulked, dried, and analysed for the presence of both n-alkanes of interest. In order to estimate the presence of n-alkanes in the herbage cows are grazing, herbage samples are collected prior to grazing on the same day faecal samples are collected. Once the levels of n-alkanes in the herbage and faecal samples are established, DMI is calculated using the following equation:

\[
DMI = \frac{F_i F_j \times D}{H_i - (F_i/F_j) \times H_j}
\]

where \(F_i\) is the concentration of the natural occurring alkane (C\(_{33}\)) in the faeces; \(F_j\) is the concentration of the synthetic alkane (C\(_{32}\)) in the faeces; \(D\) is the daily dose of the even carbon alkane (C\(_{32}\)); \(H_i\) is concentration of the natural occurring alkane (C\(_{33}\)) in the herbage and \(H_j\) is concentration of the synthetic alkane (C\(_{32}\)) in the herbage.

Although both the chromium oxide and n-alkane techniques have been used since the 1950s and 1980s, respectively, there are several limitations to both techniques; the main limitation of marker techniques is the need to obtain accurate and representative samples of both the herbage consumed and faeces excreted by the cows of interest (Dove and Mayes, 1991; Dillon, 2006). Given the time and cost associated with using either of these marker techniques, neither are suitable for estimating the DMI of grazing dairy cows on commercial farms. The difficulties associated with deploying these techniques to measure the DMI of commercial grazing dairy cows have limited the inclusion of feed intake in breeding objectives. Therefore, in the last number of decades (Curran and Holmes, 1970; McParland et al., 2014; Halachmi et al., 2016), there has been an increasing focus on developing alternative and cheaper methods to predict the DMI of dairy cow that could be used on commercial farms.
1.6.2 Use of indicator traits to predict the genetic merit of feed intake

Regression-based prediction models comprised of known energy sinks are one of the most frequently suggested methods of predicting DMI of individual dairy cows (Curran and Holmes, 1970; National Research Council, 2001; Halachmi et al., 2004; Volden et al., 2011). The main advantage of such methods in dairy cows is that information pertaining to most energy sinks is readily available. The energy sinks used to predict DMI vary between studies but often include some combination of live weight, live weight change, milk yield, age, stage of lactation, BCS, and BCS change (Curran and Holmes, 1970; National Research Council, 2001; Halachmi et al., 2004; Volden et al., 2011). Some studies have also proposed including measures of digestibility and other feed-related characteristics to improve the accuracy of the models (Curran and Holmes, 1970; Delagarde et al., 2011).

An alternative to using known energy sinks, most of which are already included in dairy cow total merit selection indexes, to predict and select for the genetic merit of DMI would be to use easy-to-measure indicator traits that are genetically correlated to DMI (Manafiazar et al., 2016). Several proxy measures for dairy cow DMI have previously been suggested including, but not limited to, linear type traits (Veerkamp and Brotherstone, 1997; Manafiazar et al., 2016; Manzanilla-Pech et al., 2016), grazing and ruminating behaviour (Halachmi et al., 2016), faecal near-infrared spectroscopy (NIRS: Tran et al., 2010; Lahart et al., 2019), and mid-infrared spectroscopy of milk (MIRS: McParland et al., 2011; McParland et al., 2014; Lahart et al., 2019). Some of the suggested proxy traits for dairy cow DMI are already routinely recorded and, therefore, could easily be incorporated into breeding strategies if they are suitable.

Many studies have reported moderate to strong genetic correlation between some body-related linear type traits and DMI in dairy cows (Table 1.9; Veerkamp and Brotherstone, 1997; Manafiazar et al., 2016; Bilal et al., 2016; Manazanila-Pech et al., 2016), although these studies were restricted to dairy cows in confinement systems only. Nonetheless, based on the genetic correlations between DMI and linear type traits, these studies suggested that linear type traits may be suitable predictors of dairy cow DMI (Manafiazar et al., 2016; Bilal et al., 2016; Manazanila-Pech et al., 2016). With the exception of Bilal et al. (2016), no previous study reported the genetic correlations between DMI and linear type traits adjusted for differences in readily
available energy sinks. Bilal et al. (2016) reported adjusting the genetic correlations between linear type traits and DMI for differences in genetic merit for milk yield was relatively small and did not alter the conclusion that linear type traits may be suitable predictors of DMI.

Infrared spectroscopy involves measuring the energy absorbed by a milk sample after exposing the sample to electromagnetic radiation (De Marchi et al., 2014). Mid-infrared spectroscopy (MIRS) of milk is used globally to determine the fat, protein, and lactose concentration in milk (McParland et al., 2011), while near-infrared spectroscopy (NIRS) of faeces can be used to predict organic matter digestibility (Decruyenaere et al., 2009). In contrast to most of the studies suggesting linear type trait may be suitable predictors of DMI that did not account for correlated energy sinks, the usefulness of MIRS and NIRS as predictors of dairy cow DMI has been determined after known energy sinks are accounted for (Tran et al., 2010; McParland et al., 2014; Lahart et al., 2019). Both MIRS and NIRS explained a greater proportion of the variance in DMI when combined with known energy sinks than was explained by milk yield and body weight alone (McParland et al., 2014; Lahart et al., 2019). Similarly, it has been reported that including feeding behaviour of dairy cows in addition to body weight and milk yield improves the accuracy of predicting DMI compared to using energy sinks alone (Halachmi et al., 2016). Nonetheless, one issue with the many of the studies suggesting potential predictor traits for dairy cow DMI is a failure to validate genetic correlations between DMI and predictor traits; suitable predictor traits for DMI, or any other hard-to-measure traits, cannot be identified without determining whether the expected predictive ability for DMI derived from a multitrait genetic evaluation with the predictor trait materialises in a validation population.
Table 1.9. Genetic correlations between dairy cow DMI, body weight (BW) and linear type traits previously reported in the literature.

<table>
<thead>
<tr>
<th>Trait</th>
<th>Netherland DMI</th>
<th>Netherland BW</th>
<th>United States DMI</th>
<th>United States BW</th>
<th>Canada DMI</th>
<th>Canada BW</th>
<th>United Kingdom DMI</th>
<th>United Kingdom BW</th>
<th>Canada DMI</th>
<th>Canada BW</th>
</tr>
</thead>
<tbody>
<tr>
<td>Body weight</td>
<td>0.55</td>
<td>0.46</td>
<td>0.57</td>
<td>0.56</td>
<td>0.32</td>
<td>0.27</td>
<td>0.13</td>
<td>0.52</td>
<td>0.45</td>
<td>0.54</td>
</tr>
<tr>
<td>Stature</td>
<td>0.33</td>
<td>0.50</td>
<td>0.57</td>
<td>0.56</td>
<td>0.32</td>
<td>0.13</td>
<td>0.07</td>
<td>-0.43</td>
<td>0.44</td>
<td>-0.34</td>
</tr>
<tr>
<td>Chest width</td>
<td>0.45</td>
<td>0.77</td>
<td>0.61</td>
<td>0.84</td>
<td>0.32</td>
<td>0.28</td>
<td>0.34</td>
<td>0.69</td>
<td>0.44</td>
<td>0.22</td>
</tr>
<tr>
<td>Angularity</td>
<td>-0.02</td>
<td>-0.43</td>
<td>0.15</td>
<td>-0.18</td>
<td>0.60</td>
<td>0.07</td>
<td>-0.14</td>
<td>-0.15</td>
<td>0.44</td>
<td>-0.34</td>
</tr>
<tr>
<td>Body depth</td>
<td>0.26</td>
<td>0.45</td>
<td>0.49</td>
<td>0.56</td>
<td>0.37</td>
<td>0.34</td>
<td>-0.14</td>
<td>-0.15</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rump angle</td>
<td>0.10</td>
<td>0.05</td>
<td>0.21</td>
<td>0.03</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rump width</td>
<td>0.04</td>
<td>0.26</td>
<td>0.13</td>
<td>0.42</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>SE range</td>
<td>0.10-0.15</td>
<td>0.07-0.11</td>
<td>0.11-0.15</td>
<td>0.07-0.13</td>
<td>0.00-0.08</td>
<td>0.01-0.11</td>
<td>0.03-0.12</td>
<td>0.08-0.22</td>
<td>0.06-0.18</td>
<td></td>
</tr>
</tbody>
</table>

1 Bilal et al. (2016) did not report the genetic correlations between each linear type trait and body weight.
1.7 Statistical analysis and data quality

This thesis utilises both linear mixed models (Chapter 2 and 3) and random regression models (Chapter 4 and 5) to estimate genetic (co)variances of and between traits. Linear regression is a modelling technique that estimates the linear relationship between a response (dependent variable) and an explanatory (independent variable; van der Werf, 2003a). Linear mixed models are an extension of linear regression models that include both fixed and random effects, as well as two or more independent variables (van der Werf, 2003a); fixed effects are features that do not change across the population or that change at a constant rate, whereas random effects represent within-subject or with-group variation. Bivariate linear mixed models can be used to estimate the relationship between two dependent variables while accounting for independent variables that may affect one or both of the dependent variables. Random regression models are a further extension of linear regression models, which can be used to model how repeated measures change (van der Werf, 2003b); random regression models are typically used the measure how traits, such as growth and milk production, change over time (Van der Werf et al., 1998; Van der Werf, 2001; Togashi and Lin, 2006). Bivariate random regression models are an extension of random regression models that can not only estimate the relationship between one trait measured at multiple time points but also estimate the relationship between a trait measured at multiple times and another dependent variable. An alternative to using random regression models for repeated measures would be to use either a repeatability model or a multitrait model, nevertheless, both repeatability and multitrait models are associated with limitations when handling repeated records (van der Werf, 2003b). The typical feature of a repeatability model is that the repeated records are considered to be the same trait genetically, therefore, such models cannot be used to consider how traits change over time (van der Werf, 2003b). In contrast to the repeatability model, multitrait models allow for the genetic correlation to differ between repeated measures, nonetheless, the covariance matrix for repeated measures at multiple time points would be highly over-parameterised (van der Werf, 2003b).

Prior to using either linear mixed models or random regression models to estimate genetic (co)variances of traits in this thesis, data was edited in line with previous studies to remove erroneous records. All models were then constructed taking
the variables considered in previous studies, biological plausibility, and statistical significance into account.

1.8 Gaps in knowledge addressed in this thesis

Given the importance of dairy cow production efficiency to the economic viability of dairy production, the overall objective of this thesis was to determine the potential to improve the production efficiency of dairy cows through genetic selection. The review of the literature highlighted that the relationships between predictor traits and difficult-to-measure efficiency-related traits have not yet been fully explored, particularly in pasture-based production systems. Given the strong genetic correlations between the body-related linear type traits and body weight in dairy cows (Veerkamp and Brotherstone, 1997; Manafiazar et al., 2016; Manzanilla-Pech et al., 2016), it is likely that linear type traits would be less strongly genetically correlated with DMI if body weight information were also available. Yet, to date, no study has reported if linear type traits explain any genetic variation in DMI over and above that already explained by body weight. This is of particular importance as body weight is already included in most dairy cow national breeding objectives (Cole and VanRaden, 2018; ICBF, 2020; VanRaden et al., 2021; DairyNZ, 2022). Additionally, none of the studies estimating the genetic correlations between DMI and linear type traits reported whether the expected predictive ability for DMI derived from a multi-trait genetic evaluation with the linear score materialised in a validation population. Both of these gaps in knowledge are addressed in Chapter 2.

The majority of previously published studies on the potential to improve the production efficiency of the dairy herd have been restricted to cows in confinement systems (Eaglen et al., 2013; Kern et al., 2015; Zhang et al., 2021), using efficiency measured over short periods (Coleman et al., 2010; McParland et al., 2014; Hurley et al., 2017), or both (Ojango and Pollot, 2001; Bakir et al., 2004; Hossein-Zadeh, 2012). This has resulted in a limited understanding of the potential to genetically improve lifetime production efficiency in grazing dairy cows. Despite the frequent use of standardised lactation yields, the average lactation length of Irish dairy cows remains unreported since 2006 (Evans et al., 2006) and the genetic and non-genetic factors associated with lactation length in pasture-based dairy cows have yet to be explored. It cannot be assumed that the factors previously documented to associate with lactation
length in confinement systems will represent those associated with lactation length in seasonal-calving systems. Identifying the factors associated with lactation length in grazing dairy cows could provide an opportunity to increase the proportion of cows achieving 305-day lactations, which could improve their lifetime production efficiency; this gap in knowledge is addressed in Chapter 3.

The trajectory of milk production and SCC across parities in aging cows has yet to be investigated in grazing dairy cows. Given the importance of milk production and udder health in dairy cow breeding objectives (Cole and VanRaden, 2018), the lack of information on the trajectory of milk production and SCC per lactation and whether the trajectory across parities could be altered through genetic selection is surprising. This is addressed in Chapter 4. Identifying dairy cows that can maintain their mature milk production or maintain a low SCC for longer could reduce the need for voluntary culling, thereby, improving the longevity of the dairy herd. While the inclusion of functional traits like reproductive performance in dairy cow breeding programs has contributed to a cumulative improvement in the genetic merit for reproductive performance in most dairy cow populations (Berry et al., 2014a; Cole and VanRaden, 2018; De Vries, 2020), the productive lifespan of dairy cows remains limited to between 2.5 and 4.5 years (Adamczyk et al., 2016; Kerslake et al., 2018; De Vries and Marcondes, 2020). Therefore, an age-linked reduction in lactation yields or increases in SCC could potentially explain why productive life has not improved in line with the genetic gain in reproductive performance.

To date, the usefulness of linear type traits as predictors of the genetic merit for survival has not been fully explored. Owing to the tendency to cull dairy cows for infertility prior to reaching maturity, previously documented genetic correlations between longevity/survival and linear type traits were often restricted to relatively young cows (≤5th parity; Brotherstone et al., 1998; Cruickshank et al., 2002) or herds with short average productive lifespans (2.7 lactations; Kern et al., 2015). Veerkamp et al. (2001) and van Pelt et al. (2015) both reported that the genetic correlations between survival in different parities varied from unity, suggesting that survival may be related to genetically different traits at different time points across the lifespan. Given previous studies estimating the genetic correlations between linear type traits and survival did not consider survival to each parity as separate traits, it remains
unknown whether the genetic correlations between survival and linear type traits change over time; this is addressed in Chapter 5.
Chapter 2: Are subjectively scored linear type traits suitable predictors of the genetic merit for feed intake in grazing Holstein-Friesian dairy cows?

2.1 Preface

At the time of thesis submission, this chapter was published in the Journal of Dairy Science (accepted October 18th 2021). The full reference is:


Formatting and referencing style have been edited for consistency throughout the thesis. Figures and table captions have been assigned with a chapter prefix and acknowledgements have been removed. All other aspects are consistent with the published manuscript.

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2.2 Abstract

Measuring DMI in grazing dairy cows using currently available techniques is invasive, time consuming, and expensive. An alternative to directly measuring DMI for use in genetic evaluations is to identify a set of readily available animal features that can be used in a multitrait genetic evaluation for DMI. The objectives of the present study were thus to estimate the genetic correlations between readily available body-related linear type traits and DMI in grazing lactating Holstein-Friesian cows, but importantly also estimate the partial genetic correlations between these linear traits and DMI, after adjusting for differences in genetic merit for body weight. Also of interest was whether the predictive ability derived from the estimated genetic correlations materialised upon validation. After edits, a total of 8,055 test-day records of DMI, body weight, and milk yield from 1,331 Holstein-Friesian cows were available, as were chest width, body depth, and stature from 47,141 first lactation Holstein-Friesian cows. In addition to considering the routinely recorded linear type traits individually, novel composite traits were defined as the product of the linear type traits as an approximation of rumen volume. All linear type traits were moderately heritable, with heritability estimates ranging from 0.27 (standard error = 0.14) to 0.49 (standard error = 0.15); furthermore, all linear type traits were genetically correlated (0.29 to 0.63, standard error 0.14 to 0.12) with DMI. The genetic correlations between the individual linear type traits and DMI, when adjusted for genetic differences in body weight, varied from −0.51 (stature) to 0.48 (chest width). These genetic correlations between DMI and linear type traits suggest linear type traits may be useful predictors of DMI, even when body weight information is available. Nonetheless, estimated genetic merit of DMI derived from a multitrait genetic evaluation of linear type traits did not correlate strongly with actual DMI in a set of validation animals; the benefit was even less if body weight data were also available.

2.3 Introduction

Dairy breeding programs have contributed considerably to observed gains in a range of traits, including milk yield and fertility (Berry et al., 2014b; Berry et al., 2016; García-Ruiz et al., 2016). Nonetheless, interest in improving production efficiency is intensifying, with a growing emphasis on feed and environmental efficiency (Pryce et
al., 2014; Hurley et al., 2017). The heritability of feed intake in dairy cows is widely reported to be between 0.07 and 0.44, with documented exploitable genetic differences in feed intake (Veerkamp and Brotherstone, 1997; Berry et al., 2007b; Toshniwal et al., 2008). Despite this abundance of genetic variability, the direct inclusion of feed intake and efficiency into dairy breeding goals has been slow. Australia and the United States currently explicitly consider a feed intake–related measure (i.e., feed saved) in their dairy breeding objectives (Pryce et al., 2015; Byrne et al., 2016; CDCB, 2020, 2021), albeit their genetic evaluations are based on actual feed intake measured in limited populations of 2,036 and 6,200 individuals, respectively. Considering this, novel strategies to include feed intake in dairy cow breeding goals should be thoroughly investigated.

The main barrier, at present, to incorporating feed intake into a breeding program is the lack of an easy, cost-effective approach to measuring DMI, which could be used to routinely determine individual cow feed intake. This is particularly true for feed intake in grazing dairy cows, where the currently recommended marker techniques for estimating feed intake in grazing systems (e.g., the n-alkane technique; Mayes et al., 1986) have proven both complex and expensive. There is, therefore, an urgent requirement to identify indicators of feed intake, especially at a genetic level, for incorporation into dairy cow genetic evaluations. Ideally, data collection for these indicator traits would be incorporated into routine management practices, or at least be measurable at low cost in a large population of cattle. Various indicator measurements of feed intake and feed efficiency in dairy cows have been previously suggested, including milk yield, body weight, grazing and ruminating behaviour, faecal near-infrared reflectance spectroscopy, and mid-infrared reflectance spectroscopy of milk (Halachmi et al., 2004; Tran et al., 2010; McParland et al., 2014; Halachmi et al., 2016).

Linear type traits are a subjective visual assessment of the biological extremes of biometric characteristics; they are heritable and are routinely recorded on breeding dairy cows (Veerkamp and Brotherstone, 1997; Berry et al., 2004; Manafiazar et al., 2016). Although previous studies in dairy cows have reported genetic associations between linear type traits and feed intake (Veerkamp and Brotherstone, 1997; Manafiazar et al., 2016; Manzanilla-Pech et al., 2016), they have been exclusive to confined dairy cows (Veerkamp and Brotherstone, 1997; Manafiazar et al., 2016;
Manzanilla-Pech et al., 2016). To date, no study has, to the best of our knowledge, quantified the marginal information content of the linear type trait in predicting genetic merit for DMI, over and above that predictable from just body weight data. The use of body weight records as a predictor of feed intake is of particular interest given the likely uptake of automated weighing in the future (Alawneh et al., 2011; Song et al., 2018). Moreover, validation of the prediction of genetic merit from correlated linear type traits has never been undertaken using actual phenotypic data from a validation population. Furthermore, the effectiveness of linear type traits as suitable indicators of feed intake has, to the best of our knowledge, never been investigated in pasture-fed dairy cows. It cannot be assumed that the genetic correlations with feed intake will be similar to those documented from indoor systems, especially given that the genetic correlations between feed intake in grazing versus high input systems are reported to be weak to moderate (0.14 to 0.33; Berry et al., 2014b). The greater gut fill associated with grazed grass (Gill et al., 1988) may imply that rumen capacity could likely limit potential feed intake in grazing systems. Therefore, the objective of the present study was to estimate the genetic correlations between readily available body-related linear type trait information and DMI in grazing lactating dairy cows. Of particular interest was the partial genetic correlation between these linear traits and DMI after adjusting for either phenotypic or genetic differences in body weight. Also of interest was whether the expected predictive ability for DMI derived from a multitrait genetic evaluation with the linear score materialised in a validation population.

2.4 Materials and Methods

2.4.1 DMI data

Records relating to individual cow daily grass DMI estimates, concentrate DMI, body weight, and milk yield, collected between the years 1995 and 2019, inclusive, were available from the Animal and Grassland Research and Innovation Centre, Teagasc Moorepark, Co. Cork, Ireland. Feed intake data were collected as part of >25 experiments, which evaluated alternative grazing and nutritional strategies or strain of Holstein-Friesian cows on 6 Teagasc research farms. All animals were managed under a rotational grazing system and grazed predominantly on perennial ryegrass swards. All animals grazed freely with continuous access to water and each
cow received between 0 and 6.2 kg of concentrate DMI per day in the milking parlour. Grass DMI was estimated for all animals using the n-alkane technique described by Mayes et al. (1986) and modified by Dillon and Stakelum (1989). In brief, to estimate one daily grass DMI for an individual cow, each cow was dosed twice daily with dotriacontane for 12 days, whereas faecal and forage samples were collected twice daily for 6 days from the seventh day of dosing; the n-alkane technique was repeated an average of 6 times per cow (ranging from 1 to 23 times). Dry matter intake was calculated as grass DMI plus concentrate DMI. Individual cow milk yield was recorded daily using electronic milk meters (Dairymaster). Cow live weight was recorded every 1 to 3 weeks using an electronic weighing scale (Tru-Test Limited).

Before edits, 8,267 DMI records were available from 2,605 lactations on 1,384 Holstein-Friesian cows. Individual DMI and body weight records were discarded if they were greater than 3 standard deviations from the population mean. Only the body weight measurements recorded closest to each of the DMI measurements were retained for further analyses; 96% of body weight measurements were recorded within 14 days of the DMI measurement. Records from cows without a known sire were removed and parity was categorised as 1, 2, or ≥3; there were 746, 702, and 652 cows with DMI measurements in first, second, and third parity or higher, respectively. After edits, 8,055 DMI, body weight, and milk yield records remained from 2,525 lactations on 1,331 cows. Days in milk (ranging from 5 to 280 DIM) were categorised into 30-day intervals, and for use in a separate analysis, 3 stages of lactation were also defined (i.e., early, mid, and late); 2,789 records were classified as early lactation (≤90 DIM), 3,205 records were classified as mid lactation (91–180 DIM), and 2,061 records were classified as late lactation (≥181 DIM). Contemporary group for DMI, body weight, and daily milk yield was defined as experimental treatment by date of measurement; after edits, there were 854 contemporary groups for DMI and daily milk yield with 1,156 contemporary groups for body weight.

2.4.2 Linear type trait data

Linear type traits recorded by the Irish Holstein-Friesian Association were available from the ICBF national database. Records pertaining to 19 linear type traits recorded on 197,627 registered Holstein-Friesian cows during first lactation were available. Of the linear type traits records, chest width (CW), body depth (BD), and
stature (STA) were retained for analyses in the present study. Each of the retained traits were scored on a scale of 1 to 9; CW was scored from narrow (i.e., score of 1) to wide (i.e., score of 9), BD was scored from shallow to deep, and stature was scored from short to tall. Classification of cows was performed by a single professional classifier for a given herd on a given date. Differences between classifiers were accounted for by adjusting each linear type trait by the ratio of the standard deviation of each classifier in each year to the mean standard deviation of all other classifiers for each linear type trait, as described by Brotherstone (1994). For the purposes of estimating rumen volume, in the present study, 4 novel composite traits were generated as the product of the scores of 2 or 3 linear type traits, namely CW × BD (CWBD), CW × STA (CWSTA), BD × STA (BDSTA), and CW × BD × STA (CWBDSTA). Adjusting for differences between classifiers transformed the linear type trait scores from a discrete scale (1 to 9) to a continuous scale.

Contemporary group for the linear type traits was defined as herd-date of inspection. Contemporary groups with no paternal half-sibling to a cow with DMI information were removed. All linear type trait records from cows with both DMI and body weight information were also retained. Of the remaining 123,464 linear type trait records, only contemporary groups with at least 5 paternal half-siblings to cows with DMI data were retained. Subsequently, contemporary groups with <10 cows were discarded. Following edits, linear type trait data relating to 47,141 cows in 2,314 contemporary groups, sired by 3,428 bulls, were available for analyses. Of the 3,428 sires in the linear type trait data set, 129 also had progeny with DMI information. Of the 48,163 cows retained for analyses, 309 cows had both DMI information and linear type trait information.

2.4.3 Statistical analyses

2.4.3.1 Estimation of variance components

Univariate animal linear mixed models in ASReml (Gilmour et al., 2008) were used to estimate the variance components for all traits. The following model was used to estimate the variance components for DMI, body weight, and milk yield across the entire lactation, as well as within early, mid, and late lactation separately:
\[ y_{ijklmn} = CG_j + Parity_k \cdot Days\ in\ milk_l + a_i + pe\ within_m + pe\ across_n + e_{ijklmn} \]

where \( y_{ijklmn} \) was the observed value of DMI, body weight, or milk yield for cow \( i \); \( CG_j \) was the fixed effect for contemporary group \( j \); \( Parity_k \) was the fixed effect of parity \( k \) \((k=1, 2, \geq 3)\); \( Days\ in\ milk_l \) was the fixed effect for days in milk class \( l \) \((l=1\ to\ 10)\); \( a_i \) was the additive random effect of cow \( i \) where \( a \sim N(0,A\sigma_a^2) \) and \( \sigma_a^2 \) represents the direct genetic variance and \( A \) the numerator relationship matrix; the pedigree of all cow were traced back at least four generations; \( pe\ within_m \) was the random cow by lactation permanent environmental effect where \( pe\ within_m \sim N(0, I\sigma_{pe\ within}^2) \) and \( \sigma_{pe\ within}^2 \) represents the within-lactation permanent environmental variance and \( I \) the identity matrix; \( pe\ across_n \) was the random cow permanent environmental effect where \( pe\ across_n \sim N(0, I\sigma_{pe\ across}^2) \) and \( \sigma_{pe\ across}^2 \) represents the across-lactation permanent environmental variance and \( I \) the identity matrix; \( e_{ijklmn} \) was the residual term where \( e \sim N(0, I\sigma_e^2) \) and \( \sigma_e^2 \) represents the residual variance and \( I \) the identity matrix.

Variance components for DMI were also estimated having adjusted phenotypically for differences in body weight via its inclusion as a covariate in the mixed model. The variance components of linear type traits were estimated using the following model (Berry et al., 2004):

\[ y_{ijkt} = CG_j + Days\ in\ milk_k + calving\ month_l + a_i + e_{ijkt} \]

where \( y_{ijkt} \) was the adjusted value of the linear type trait for cow \( i \); \( CG_j \) was the fixed effect of contemporary group \( j \); \( Days\ in\ milk_k \) was the fixed effect for days in milk at the time of classification and was classified into 30-day intervals \((k=1\ to\ 12)\); \( calving\ month_l \) was the fixed effect for month of calving \((l=1\ to\ 12)\); \( a_i \) was the additive random effect of cow \( i \) where \( a \sim N(0, A\sigma_a^2) \) and \( \sigma_a^2 \) represents the direct genetic variance and \( A \) the numerator relationship matrix, and \( e_{ijkt} \) is the residual term where \( e \sim N(0, I\sigma_e^2) \) and \( \sigma_e^2 \) represents the residual variance and \( I \) the identity matrix.

### 2.4.3.2 Estimation of genetic phenotypic covariances

A series of bivariate sire linear mixed models were used to calculate the genetic and phenotypic covariances between both body weight and each type trait with DMI across the entire lactation, as well as within early, mid, and late lactation separately. The genetic and phenotypic covariances among the linear type traits were estimated.
using a separate series of bivariate sire linear models. The fixed and random effects included in the models were those used in the univariate analyses, with the exception of a random sire term included in place of the random cow term. The partial genetic correlation between DMI and each linear type trait, adjusted for genetic differences in body weight, was calculated as (Wherry, 1984):

\[ r_g(DMI, type_i | BW) = \frac{r_g(DMI, type_i) - r_g(DMI, BW) r_g(type_i, BW)}{\sqrt{1 - r_g^2(DMI, BW)} \sqrt{1 - r_g^2(type_i, BW)}} \]

where \( r_g(DMI, type_i) \) was the genetic correlation between DMI and type trait \( i \); \( r_g(DMI, BW) \) was the genetic correlation between the DMI and body weight; \( r_g(type_i, BW) \) was the genetic correlation between the linear type trait \( i \) and body weight.

### 2.4.3.3 Genetic evaluation

A series of multitrait animal model genetic evaluations for DMI were undertaken using the MiX99 software suite (Strandén and Lidauer, 1999) with body weight or one linear type trait (or both) to validate the usefulness of linear type traits as predictor traits of genetic merit for DMI, particularly when body weight information was also available. The data set from which the breeding values were estimated was the same as that used to estimate the phenotypic and genetic (co)variances. The cows with DMI and body weight phenotypes from one farm (1,747 records from 246 cows) were chosen as the validation population, whereas the DMI, body weight, and linear type trait records of all other cows (53,140 records from 47,917 cows) were used as the calibration data set. The fixed effects, random effects, and (co)variance components specified in the genetic evaluations were based on the results from the bivariate models used to estimate the genetic (co)variances of DMI, body weight, and the linear type traits; the sire (co)variances were multiplied by 4 to convert them to animal-level (co)variances.

Separate genetic evaluations were run with different combinations of DMI, body weight, and linear type traits, (i.e., including DMI only; DMI and body weight; DMI and a linear type trait; DMI, body weight, and a linear type trait). Each genetic evaluation was run twice, once with the DMI, body weight, and linear type trait phenotypes of validation cows masked, and once with just the DMI and linear type trait phenotypes of the validation cows masked. The accuracy of breeding values for DMI estimated using the genetic evaluations was determined by correlating the
estimated breeding values (EBV) of the validation cows with their respective DMI yield deviations, which were calculated using their DMI phenotypes. The DMI yield deviation values were regressed on the EBV for DMI using linear mixed models.

2.5 Results

2.5.1 Variance components

Descriptive statistics and heritability estimates for all traits are presented in Table 1; the heritability, genetic standard deviation, and coefficient of genetic variation of DMI itself were 0.19 (SE = 0.036), 0.82 kg, and 0.05, respectively. The heritability estimates for DMI were similar when estimated from the bivariate analyses. Adjusting DMI for phenotypic differences in body weight reduced the genetic standard deviation of DMI (Table 2.1). The heritability estimates of the linear type traits are in Table 2.1 and the heritability estimates for the novel composite traits of CWBD, CWSTA, BDSTA, and CWBDSTA were 0.30 (SE = 0.015), 0.31 (SE = 0.015), 0.39 (SE = 0.015), and 0.33 (SE = 0.015), respectively. Descriptive statistics for DMI, body weight, and daily milk yield in early mid, and late lactation are in Appendix A.

Table 2.1. Mean, genetic standard deviation (σg), heritability (h2; standard error in parenthesis) and within-lactation repeatability (t; standard error in parenthesis) for dry matter intake (DMI; kg), body weight (kg), daily milk yield (kg) as well as the body-related linear type traits (scale 1 to 9).

<table>
<thead>
<tr>
<th>Trait</th>
<th>Mean</th>
<th>σg</th>
<th>h²(se)</th>
<th>t(se)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dry matter intake (kg)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>DMI</td>
<td>16.78</td>
<td>0.82</td>
<td>0.19 (0.036)</td>
<td>0.30 (0.037)</td>
</tr>
<tr>
<td>DMI AdjBW</td>
<td>16.78</td>
<td>0.68</td>
<td>0.15 (0.030)</td>
<td>0.25 (0.032)</td>
</tr>
<tr>
<td>Body weight (kg)</td>
<td>520.89</td>
<td>32.80</td>
<td>0.56 (0.057)</td>
<td>0.69 (0.054)</td>
</tr>
<tr>
<td>Daily milk yield (kg)</td>
<td>21.82</td>
<td>1.55</td>
<td>0.25 (0.048)</td>
<td>0.43 (0.047)</td>
</tr>
<tr>
<td>Type trait (scale 1 to 9)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Chest width</td>
<td>5.3</td>
<td>0.73</td>
<td>0.27 (0.015)</td>
<td></td>
</tr>
<tr>
<td>Body depth</td>
<td>5.7</td>
<td>0.60</td>
<td>0.27 (0.014)</td>
<td></td>
</tr>
<tr>
<td>Stature</td>
<td>6.7</td>
<td>0.79</td>
<td>0.49 (0.015)</td>
<td></td>
</tr>
</tbody>
</table>

DMI – unadjusted dry matter intake; DMI AdjBW – dry matter intake adjusted for phenotypic differences in body weight
2.5.2 Phenotypic correlations

2.5.2.1 Across lactation

The phenotypic correlations between DMI measured across lactation and both the linear type traits and novel composite traits were weak (≤0.04) with standard errors ranging from 0.05 to 0.06 (Table 2.2). The phenotypic correlations between body weight and the linear type traits/novel composite traits ranged from 0.05 (BD; SE = 0.026) to 0.17 (STA; SE = 0.25; Table 2.2). After adjusting these phenotypic correlations for phenotypic differences in body weight, all linear type traits were negatively correlated with DMI (Table 2.2).

Table 2.2. Phenotypic correlations (standard error in parenthesis) between dry matter intake (DMI; unadjusted and adjusted for phenotypic differences in body weight), body weight, milk yield, and linear type traits.

<table>
<thead>
<tr>
<th>Trait</th>
<th>Dry matter intake</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>DMI</td>
<td>DMI Adj&lt;sub&gt;BW&lt;/sub&gt;</td>
<td>BW</td>
</tr>
<tr>
<td>Body weight</td>
<td>0.37 (0.020)</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Milk yield</td>
<td>0.40 (0.014)</td>
<td>0.36 (0.014)</td>
<td>0.26 (0.024)</td>
</tr>
<tr>
<td>Body depth</td>
<td>-0.03 (0.049)</td>
<td>-0.06 (0.052)</td>
<td>0.05 (0.026)</td>
</tr>
<tr>
<td>Chest width</td>
<td>0.00 (0.049)</td>
<td>-0.06 (0.052)</td>
<td>0.06 (0.026)</td>
</tr>
<tr>
<td>Stature</td>
<td>0.04 (0.047)</td>
<td>-0.03 (0.049)</td>
<td>0.17 (0.025)</td>
</tr>
<tr>
<td>Chest width x body depth</td>
<td>0.00 (0.052)</td>
<td>-0.07 (0.054)</td>
<td>0.07 (0.027)</td>
</tr>
<tr>
<td>Chest width x stature</td>
<td>0.02 (0.052)</td>
<td>-0.07 (0.055)</td>
<td>0.14 (0.026)</td>
</tr>
<tr>
<td>Body depth x stature</td>
<td>0.00 (0.054)</td>
<td>-0.07 (0.054)</td>
<td>0.15 (0.026)</td>
</tr>
<tr>
<td>Chest width x body depth x stature</td>
<td>0.01 (0.055)</td>
<td>-0.09 (0.057)</td>
<td>0.13 (0.027)</td>
</tr>
</tbody>
</table>

<sup>DMI</sup> – unadjusted dry matter intake; DMI Adj<sub>BW</sub>, dry matter intake adjusted for phenotypic differences in body weight

2.5.2.2 Within the stages of lactation

When DMI and body weight records in early, mid, and late lactation were considered, the phenotypic correlations between DMI and all linear type traits were positive and stronger than the phenotypic correlations between DMI and linear type traits estimated across lactation. The average phenotypic correlations between body weight and all linear type traits were strongest in early lactation (mean of 0.23) compared with mid lactation (mean of 0.13), late lactation (mean of 0.20; Appendix B), or across lactation (mean of 0.11; Table 2.2). The phenotypic correlations among the linear types are in Appendix C.
2.5.3 Genetic correlations

2.5.3.1 Across lactation

The genetic correlations among the linear type traits are in Supplemental Table S3. The genetic correlations between the linear type traits and DMI measured across the entire lactation ranged from 0.29 (SE = 0.144) to 0.63 (SE = 0.122; Table 2.3), with the correlations between the linear type traits and body weight measured across the entire lactation ranging from 0.47 (SE = 0.106) to 0.82 (SE = 0.056). Similarly, the genetic correlations between the novel composite traits and DMI measured across lactation, and the genetic correlations between the novel composite traits and body weight measured across lactation were moderately to strongly positive (Table 2.3).

Table 2.3. Genetic correlations (standard errors in parenthesis) between dry matter intake (unadjusted, adjusted for phenotypic or genetic differences in body weight), body weight, milk yield, and linear type traits.

<table>
<thead>
<tr>
<th>Trait</th>
<th>Dry matter intake</th>
<th>Body weight</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>DMI(^1)</td>
<td>DMI(_{Adjp})</td>
</tr>
<tr>
<td>Body weight</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>0.63</td>
<td>0.65</td>
</tr>
<tr>
<td></td>
<td>(0.107)</td>
<td>(0.170)</td>
</tr>
<tr>
<td>Milk yield</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>0.32</td>
<td>0.157</td>
</tr>
<tr>
<td></td>
<td>(0.122)</td>
<td>(0.166)</td>
</tr>
<tr>
<td>Body depth</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>0.02</td>
<td>-0.02</td>
</tr>
<tr>
<td></td>
<td>(0.126)</td>
<td>(0.162)</td>
</tr>
<tr>
<td>Chest width</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>0.65</td>
<td>0.32</td>
</tr>
<tr>
<td></td>
<td>(0.170)</td>
<td>(0.157)</td>
</tr>
<tr>
<td>Stature</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>0.29</td>
<td>0.29</td>
</tr>
<tr>
<td></td>
<td>(0.126)</td>
<td>(0.158)</td>
</tr>
<tr>
<td>Chest width*body depth</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>0.58</td>
<td>0.58</td>
</tr>
<tr>
<td></td>
<td>(0.128)</td>
<td>(0.163)</td>
</tr>
<tr>
<td>Chest width*stature</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>0.61</td>
<td>0.61</td>
</tr>
<tr>
<td></td>
<td>(0.112)</td>
<td>(0.162)</td>
</tr>
<tr>
<td>Body depth*stature</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>0.39</td>
<td>0.39</td>
</tr>
<tr>
<td></td>
<td>(0.142)</td>
<td>(0.166)</td>
</tr>
<tr>
<td>Chest width<em>body depth</em>stature</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>0.60</td>
<td>0.60</td>
</tr>
<tr>
<td></td>
<td>(0.118)</td>
<td>(0.168)</td>
</tr>
</tbody>
</table>

\(^1\)DMI – unadjusted dry matter intake; DMI\(_{Adjp}\) – dry matter intake adjusted for phenotypic differences in body weight; DMI\(_{AdjG}\) – dry matter intake adjusted for genetic differences in body weight

Adjusting the genetic correlations between DMI and the linear type traits for phenotypic differences in body weight weakened each of the genetic correlations. Adjusting for phenotypic differences in body weight had the greatest effect on the
genetic correlation between DMI and BDSTA, weakening the genetic correlation from 0.39 (SE = 0.142) to −0.14 (SE = 0.166). Similarly, adjusting the genetic correlations between DMI measured across lactation and the linear type traits for the genetic differences in body weight weakened the strength of all the genetic correlations; CW, CWBD, CWSTA, and CWBDSTA were the only linear type traits positively correlated with DMI after adjusting for the genetic differences in body weight.

2.5.3.2 Within the stages of lactation

The genetic correlations between DMI and the linear type traits ranged from 0.14 (SE = 0.199) to 0.72 (SE = 0.147) in early lactation, from 0.12 (SE = 0.179) to 0.43 (SE = 0.162) in mid lactation, and from 0.27 (SE = 0.189) to 0.68 (SE = 0.134) in late lactation (Table 2.4). The genetic correlations between body weight and the linear type traits were similar at each stage of lactation (Table 2.4). After adjusting for genetic differences in body weight, CW was the only linear type trait positively genetically correlated with DMI in all stages of lactation. After adjusting for genetic differences in body weight in early lactation, both CWSTA and CWBDSTA were the most strongly genetically correlated type traits with DMI, with respective genetic correlations of 0.90 and 0.88. The genetic correlation between DMI and body weight, and between body weight and daily milk yield, was weakest in early lactation (Table 2.4), whereas the genetic correlation between DMI and daily milk yield was strongest in early lactation (Table 2.4).
Table 2.4. Genetic correlations (standard errors in parenthesis) between dry matter intake (DMI) measured in early, mid, and late lactation (unadjusted, adjusted for phenotypic or genetic differences in body weight), body weight (BW), milk yield, and linear type traits.

<table>
<thead>
<tr>
<th>Trait</th>
<th>Early Lactation</th>
<th>Mid Lactation</th>
<th>Late Lactation</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>DMI</td>
<td>DMI AdjP</td>
<td>DMI AdjG</td>
</tr>
<tr>
<td>BW</td>
<td>0.28</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Milk yield</td>
<td>0.83</td>
<td>0.79</td>
<td>0.81</td>
</tr>
<tr>
<td>BD $^2$</td>
<td>0.36</td>
<td>0.11</td>
<td>0.25</td>
</tr>
<tr>
<td>CW</td>
<td>0.72</td>
<td>0.53</td>
<td>0.70</td>
</tr>
<tr>
<td>STA</td>
<td>0.14</td>
<td>-0.28</td>
<td>-0.21</td>
</tr>
<tr>
<td>CWBD</td>
<td>0.65</td>
<td>0.42</td>
<td>0.65</td>
</tr>
<tr>
<td>CWSTA</td>
<td>0.63</td>
<td>0.32</td>
<td>0.90</td>
</tr>
<tr>
<td>BDSTA</td>
<td>0.35</td>
<td>-0.07</td>
<td>0.25</td>
</tr>
<tr>
<td>CWBDSTA</td>
<td>0.63</td>
<td>0.30</td>
<td>0.88</td>
</tr>
</tbody>
</table>

$^1$DMI – unadjusted dry matter intake; DMI AdjP – dry matter intake adjusted for phenotypic differences in BW; DMI AdjG – dry matter intake adjusted for genetic differences in BW; $^2$BD – body depth; CW – chest width; STA – stature; CWBD – chest width x body depth; CWSTA – chest width x stature; BDSTA – body depth x stature; CWBDSTA – chest width x body depth x stature
2.5.4 Genetic evaluation

The Pearson correlation coefficients between DMI yield deviations and the EBV for DMI in the validation population are shown in Table 2.5. The correlation between DMI yield deviations and the EBV for DMI of the validation cows, estimated via their relationships with the cows with just DMI phenotypes, was 0.14 (Table 2.5). When DMI yield deviations of the validation population were regressed on their EBV for DMI, estimated with the DMI phenotypes only, a 1-unit increase in the EBV for DMI was associated with a 0.63-kg (SE = 0.103) increase in DMI (Table 2.5). With the exception of STA, EBV for DMI using one linear type trait plus DMI information of the calibration population did not strengthen the correlation between DMI yield deviations and the EBV for DMI relative to generating the EBV for DMI with DMI phenotypes only. Regressing DMI yield deviations of the validation population on their EBV for DMI, generated with DMI and STA phenotypes of the calibration population, resulted in a regression coefficient of 0.65 (SE = 0.102). The correlation between DMI yield deviations and the EBV for DMI strengthened by 30.6% (i.e., 0.14 to 0.19) when DMI and body weight phenotypes of the calibration population were used to generate EBV for DMI compared with just using DMI information.

The correlation between DMI yield deviation and breeding values for DMI estimated using both the DMI phenotypes from the calibration population and all available body weight phenotypes was 0.32 (Table 2.5). With the exception of STA, including a linear type trait, along with both DMI information from the calibration population and all available body weight phenotypes, did not strengthen the correlations with DMI. Including STA records from the calibration cows, in addition to their DMI records and all body weight data, strengthened the correlation between DMI yield deviation and EBV for DMI by just 0.01 (1.9%) over and above not considering STA (Table 2.5). When the EBVs for DMI generated without any DMI information from the calibration population were compared with their respective EBVs for DMI generated with DMI information from the calibration population (e.g., comparing the EBV for DMI generated with CWBDSTA only to the EBV for DMI generated with DMI from the calibration data and CWBDSTA), the EBVs for DMI generated without any DMI information were always more weakly correlated with phenotypic DMI (Table 2.5).
Table 2.5. Pearson correlations and regression coefficients (standard errors in parentheses) for yield deviation of dry matter intake (DMI) on estimated breeding value (EBV) for DMI; the EBVs were generated using combinations of DMI, body weight (BW), and/or linear type trait phenotypes.

<table>
<thead>
<tr>
<th>Phenotypes used to calculate DMI EBV</th>
<th>All phenotypes of 246 validation cows masked</th>
<th>DMI and linear type trait phenotypes of 246 validation cows masked</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Correlation coefficient</td>
<td>Regression Coefficient</td>
</tr>
<tr>
<td>-------------------------------------</td>
<td>----------------------------</td>
<td>------------------------</td>
</tr>
<tr>
<td>DMI¹</td>
<td>0.144</td>
<td>0.63 (0.103)</td>
</tr>
<tr>
<td>DMI and BD</td>
<td>0.140</td>
<td>0.58 (0.099)</td>
</tr>
<tr>
<td>DMI and CW</td>
<td>0.148</td>
<td>0.61 (0.097)</td>
</tr>
<tr>
<td>DMI and STA</td>
<td>0.151</td>
<td>0.65 (0.102)</td>
</tr>
<tr>
<td>DMI and CWBD</td>
<td>0.143</td>
<td>0.59 (0.097)</td>
</tr>
<tr>
<td>DMI and CWSTA</td>
<td>0.156</td>
<td>0.66 (0.099)</td>
</tr>
<tr>
<td>DMI and BDSTA</td>
<td>0.148</td>
<td>0.63 (0.101)</td>
</tr>
<tr>
<td>DMI and CWBDSTA</td>
<td>0.150</td>
<td>0.64 (0.100)</td>
</tr>
<tr>
<td>DMI and BW</td>
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<td>0.88 (0.110)</td>
</tr>
<tr>
<td>DMI, BD, and BW</td>
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<td>0.82 (0.107)</td>
</tr>
<tr>
<td>DMI, CW, and BW</td>
<td>0.182</td>
<td>0.80 (0.103)</td>
</tr>
<tr>
<td>DMI, STA, and BW</td>
<td>0.188</td>
<td>0.88 (0.109)</td>
</tr>
<tr>
<td>DMI, CWBD, and BW</td>
<td>0.175</td>
<td>0.77 (0.103)</td>
</tr>
<tr>
<td>DMI, CWSTA, and BW</td>
<td>0.179</td>
<td>0.79 (0.103)</td>
</tr>
<tr>
<td>DMI, BDSTA, and BW</td>
<td>0.172</td>
<td>0.82 (0.113)</td>
</tr>
<tr>
<td>DMI, CWBDSTA, and BW</td>
<td>0.169</td>
<td>0.73 (0.102)</td>
</tr>
<tr>
<td>BD</td>
<td>0.092</td>
<td>1.19 (0.307)</td>
</tr>
<tr>
<td>CW</td>
<td>0.116</td>
<td>0.93 (0.190)</td>
</tr>
<tr>
<td>STA</td>
<td>0.076</td>
<td>0.72 (0.224)</td>
</tr>
<tr>
<td>CWBD</td>
<td>0.126</td>
<td>1.11 (0.210)</td>
</tr>
<tr>
<td>CWSTA</td>
<td>0.127</td>
<td>0.78 (0.147)</td>
</tr>
<tr>
<td>BDSTA</td>
<td>0.088</td>
<td>0.72 (0.196)</td>
</tr>
<tr>
<td>CWBDSTA</td>
<td>0.117</td>
<td>0.78 (0.159)</td>
</tr>
<tr>
<td>BW</td>
<td>0.128</td>
<td>0.53 (0.097)</td>
</tr>
<tr>
<td>BD and BW</td>
<td>0.130</td>
<td>0.60 (0.108)</td>
</tr>
<tr>
<td>CW and BW</td>
<td>0.160</td>
<td>0.73 (0.107)</td>
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<tr>
<td>STA and BW</td>
<td>0.117</td>
<td>0.57 (0.116)</td>
</tr>
<tr>
<td>CWBD and BW</td>
<td>0.145</td>
<td>0.65 (0.106)</td>
</tr>
<tr>
<td>CWSTA and BW</td>
<td>0.146</td>
<td>0.67 (0.108)</td>
</tr>
<tr>
<td>BDSTA and BW</td>
<td>0.040&lt;sup&gt;NS&lt;/sup&gt;</td>
<td>0.13 (0.086)</td>
</tr>
<tr>
<td>CWBDSTA and BW</td>
<td>0.140</td>
<td>0.66 (0.113)</td>
</tr>
</tbody>
</table>

¹BD – body depth, CW – chest width, STA, stature, CWBD – chest width*body depth, CWSTA – chest width*stature, BDSTA – body depth*stature, CWBDSTA – chest width*body depth*stature; <sup>NS</sup> Correlation coefficient was not different (P<0.05) from zero.
2.6 Discussion

The inclusion of feed intake in dairy cow breeding goals is currently limited by the large resource requirements associated with the capture of individual cow feed intake data (Berry and Crowley, 2013), particularly in grazing cows. Various indicator measurements for feed intake have been proposed including near-infrared reflectance spectroscopy (Tran et al., 2010; Lahart et al., 2019), mid-infrared reflectance spectroscopy of milk (McParland et al., 2014; Wallén et al., 2018), and linear type traits (Bilal et al., 2016; Manafiazar et al., 2016; Manzanilla-Pech et al., 2016). Individual cow body weight is routinely recorded on some farms and therefore investigation into the utility of body weight records in addition to other proxy traits in genetic evaluations for DMI is warranted. There is a dearth of information on the marginal predictive ability of proxy traits in predicting DMI over and above that already captured from routine body weight measurements. Moreover, previous studies that proposed potential predictor traits for DMI did not actually undertake a validation of DMI EBV generated using these proxy traits. Therefore, the objectives of the present study were to estimate the genetic and phenotypic covariances between DMI and linear type traits, in particular after adjusting for differences in body weight, and to validate a series of multitrait genetic evaluation models for DMI generated using such indicator traits. Should the linear type traits have some predictive ability for DMI in the validation population, EBV for DMI could be generated for the national population of Holstein-Friesian dairy cows.

2.6.1 Genetic variance estimates

The heritability estimates of DMI, body weight, and milk yield across lactations were similar to those previously reported in dairy cows (Berry et al., 2003; Manafiazar et al., 2016; Manzanilla-Pech et al., 2016). No previous study has, to the best of our knowledge, reported variance components for DMI adjusted for phenotypic differences in body weight. The effect on heritability of DMI from adjusting for phenotypic differences in body weight was associated with a change in the coefficient of genetic variation of DMI, rather than a change in the coefficient of residual variation. The heritability estimates of the novel composite traits CWBD, CWSTA, BDSTA, and CWBDSTA, presented herein have not previously been reported, but are
broadly in line with those associated with individual linear type traits in dairy cows (Veerkamp and Brotherstone, 1997; Manzanilla-Pech et al., 2016).

The heritability estimates of DMI and daily milk yield were lowest in early lactation; relative to DMI and daily milk yield measured in mid lactation, the lower heritability estimates of DMI and milk yield were associated with a 17% and 58% reduction in genetic variance, respectively, and a 39% and 24% increase in residual variance, respectively. The greater residual variance in early lactation was likely due to the changes in metabolic or physiological insults associated with early lactation in dairy cows, which were not accounted for in the statistical model due to a lack of available data on such metabolic and physiological changes.

2.6.2 Indirect selection for feed intake across lactation

Genetic and phenotypic correlations between DMI and linear type traits have not been reported previously for grazing dairy cows. Nevertheless, they are similar to those reported by Veerkamp and Brotherstone (1997) and Manafiazar et al. (2016) in lactating Holstein and Holstein-Friesian dairy cows fed in confinement systems. While not previously reported, the phenotypic and genetic correlations between DMI and the novel composite traits were broadly in line with those of their component linear type traits in confined dairy cows (Manafiazar et al., 2016; Manzanilla-Pech et al., 2016). The genetic correlations suggest that between 8% (STA) and 39% (CW) of the genetic variance in DMI is explained by differences in genetic merit for the traditional linear type traits. Similarly, based on the genetic correlations, 15% (BDSTA) to 37% (CWSTA) of the genetic variance in DMI is explained by the difference in genetic merit for the novel composite traits. The strength of the genetic correlations between CW and DMI, and between CWSTA and DMI, suggests both traits reflect rumen volume more accurately than other linear type traits or novel composite traits. Assuming a traditional multitrait genetic evaluation with DMI as the goal trait and one linear type trait (here assumed to be CWSTA) in the selection index, a theoretical accuracy of selection for DMI of 0.60 could be achieved with 500 progeny linear score records without a requirement for DMI information on the progeny. The accuracy could never surpass 0.61 (i.e., the genetic correlation between DMI and CWSTA) in the absence of other information, either on DMI itself or other correlated traits.
While the genetic correlations between the linear type traits and DMI demonstrate their potential usefulness in predicting genetic merit for DMI within a multitrait genetic evaluation, the genetic correlations between the linear type traits, the novel composite traits, and body weight were moderate to strong (0.47 to 0.86); other studies have reported genetic correlations ranging from 0.13 to 0.84 between the linear type traits used in the present study and body weight in dairy cows (Veerkamp and Brotherstone, 1997; Berry et al., 2004; Manafiazar et al., 2016; Manzanilla-Pech et al., 2016). The strong genetic correlations between body weight and the linear type traits, and between body weight and the novel composite traits, reflect the accuracy with which linear type traits could predict genetic merit for body weight; it has previously been reported that linear type measurements could provide suitable estimates of the genetic merit of body weight (Banos and Coffey, 2012). Nonetheless, advances in automation technology imply that the routine recording of body weight may soon become a reality on many farms (Song et al., 2018). Such data, if captured, could be directly incorporated into a multitrait genetic evaluation for DMI. Given this, of particular interest in the present study was the marginal information content of linear type traits, especially the novel composite traits, over and above that already captured by body weight. While adjusting for body weight generally weakened the genetic correlations, some linear type traits were still moderately genetically correlated with DMI, even after adjusting DMI phenotypically or genetically for differences in body weight. The strong positive genetic correlation between CW and DMI after adjusting for genetic differences in body weight suggests that even when body weight records are available, the inclusion of CW could improve the accuracy of predicting DMI; the strong genetic correlation between CW and DMI suggests that CW might be a suitable estimator of rumen volume. Assuming a traditional multitrait genetic evaluation with DMI as the goal trait, including progeny CW records in the selection index, in addition to progeny body weight records, could increase the accuracy of selection for DMI by up to 17% compared with using only progeny body weight records. Nonetheless, when EBV for DMI were generated with CW, in combination with body weight phenotypes from either the calibration population or from all animals, an improvement in predictive ability of DMI never actually materialised. In fact, based on the results from the genetic evaluations, neither the traditional linear type traits nor the novel composite traits were useful predictors of DMI when body weight phenotypes were also available to predict DMI. Nevertheless, should neither body weight nor DMI phenotypes be
available, breeding values of similar accuracy to those estimated with DMI phenotypes of the calibration population could be estimated using either CWBD or CWSTA. As only 309 cows had both DMI and linear type trait phenotypes in the present study, 77 of which were in the validation population, there were insufficient records to generate accurate EBV for DMI using the linear type trait phenotypes of the validation population. Given that the genetic correlations between some of the linear type traits and DMI were similar to the genetic correlation between DMI and body weight, it could be speculated that if linear type trait information was available for the entire validation population, then more accurate EBV for DMI could be generated from linear type trait phenotypes, as was the case when body weight phenotypes of the validation population were used.

2.6.3 Indirect selection for feed intake in different stages of lactation

Both feed intake and milk production increase in early-lactating dairy cows, but the energy ingested is not sufficient to meet the total energy demands of the cow, resulting in negative energy balance (Beam and Butler, 1997; Berry et al., 2006). Therefore, the associations between the linear type traits and DMI were investigated within each stage of lactation, with the predictive ability of DMI in early lactation being of particular interest. The phenotypic and genetic correlation between body weight and DMI were weakest in early lactation; implying 1 of 2 things: (1) in early lactation, energy sinks other than body weight (e.g., milk production) are a greater drain on the energy available, or (2) other health conditions common in early lactation (Bradley and Green, 2005; LeBlanc et al., 2005; Dubuc et al., 2010) may cloud the association between body size, here represented by body weight, and DMI. Although the genetic correlation between DMI and body weight was weak in early lactation, with the exception BD, STA, and BDSTA, the genetic correlations between DMI and the linear type traits were positive and strongest in early lactation, after adjusting for genetic differences in body weight. This suggests that linear type traits may be suitable indicators of DMI in early lactation. The novel composite trait CWSTA explained 80% of the genetic variance in DMI in early lactation after differences in genetic merit for body weight were accounted for; this was much greater than the 4% of the genetic variance of DMI explained by CWSTA across the entire lactation. This increase in the proportion of the genetic variance of DMI explained by linear type traits in early
lactation, relative to in mid and late lactation, reflect the pasture-based nature of the Irish production system; because grass dry matter is lower in spring, compared with other seasons (McGilloway and Mayne, 1996), a greater rumen volume is required to ingest the same DMI and it is in early lactation where as high as possible DMI is desired by the cow to meet her energy requirements. Hence, a trait reflecting the rumen capacity of the cow could provide a useful prediction of the genetic propensity for feed intake in early lactation when feed intake is crucial.

2.7 Conclusions

The inclusion of feed intake in dairy cow breeding goals is currently restricted due to the resource requirements associated with the capture of individual cow feed intake data, particularly in a pasture-based environment. While the genetic correlations between DMI and linear type traits across lactation suggested linear type traits might be suitable proxy measures for DMI, the expected improvement in the prediction of DMI from the inclusion of information on linear type trait did not materialise. Nevertheless, a novel composite trait, representing rumen capacity, could provide a useful prediction of the genetic merit for feed intake in early lactation and therefore potentially generate breeding values for DMI in early lactation for a large population of dairy cows. As DMI in early lactation is often not sufficient to meet the total energy demands of the cow, EBV for DMI could assist producers in selecting for cows with greater DMI in early lactation potentially negating the complications associated with negative energy balance.
Chapter 3: Genetic and non-genetic factors associated with lactation length in seasonal-calving pasture-based dairy cows

3.1 Preface
At the time of thesis submission, this chapter was published in the Journal of Dairy Science (accepted August 31st 2020). The full reference is:


Formatting and referencing style have been edited for consistency throughout the thesis. Figures and table captions have been assigned with a chapter prefix and acknowledgements have been removed. All other aspects are consistent with the published manuscript.

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3.2 Abstract

Lactation yield estimates standardised to common lactation lengths of 270-day or 305-day equivalents are commonly used in management decision support tools and dairy cow genetic evaluations. The use of such measurements to quantify the (genetic) merit of individual cows fails to penalise cows that do not reach the standardised lactation length, or indeed reward cows that lactate for more than the standardised lactation length. The objective of the present study was to quantify the genetic and non-genetic factors associated with lactation length in seasonal-calving, pasture-based dairy cows. A total of 616,350 lactation length records from 285,598 Irish cows were used. Linear mixed models were used to quantify the associations between lactation length and calving month, parity, age at calving, previous dry period length, calving difficulty score, heterosis, recombination loss, breed, and herd size, as well as to estimate the genetic and residual variance components of lactation length. The median lactation length in the edited data set was 288 days, with 27% of cows achieving lactations of at least 305 days. Relative to cows calving in January, the lactation of a cow calving in February, March, or April was, on average, 4.2, 12.7, and 21.9 days shorter, respectively. The lactation length of a first parity cow was, on average, 7.8, 8.6, and 8.4 days shorter than that of second, third, and fourth parity cows, respectively. Norwegian Red and Montbéliarde cows had, on average, a 4.7- and 1.6-day shorter lactation than Holstein-Friesian cows, respectively. The heritability estimate, coefficient of genetic variation, and repeatability estimate of lactation length were 0.02, 1.2%, and 0.04, respectively. Based on the genetic standard deviation for lactation length estimated in the present study (3.3 days), cows ranked in the top 20% for genetic merit for lactation length would be expected to have lactations 9.2 days longer than cows in the bottom 20%, demonstrating exploitable genetic variability. Given the vast array of genetic and non-genetic factors associated with lactation length, an approach which combines improved management practices and selective breeding may be an efficient and effective strategy to lengthen lactations.
3.3 Introduction

Lactation yield estimates standardised to a common lactation length are almost exclusively used in both management decision support tools and dairy cow genetic evaluations (Quist et al., 2007). Commonly used standardised lactation lengths are those to 305-day equivalents (Olori et al., 1999) or 270-day equivalents (Harris and Winkelman, 2004), with the former often standardised further to a mature equivalent (Marti and Funk, 1994). The use of such standardised metrics to quantify the (genetic) merit of individual cows, however, often fails to fully penalise cows that (consistently) do not reach the standardised lactation length (i.e., cows that naturally dried off prematurely), and likewise fails to reward animals that lactate for more than 270 or 305 days. Substantial variability in lactation length has been reported in both Holstein cows (Hossein-Zadeh, 2012) and Holstein-Friesian cows (Evans et al., 2006; Van Eetvelde et al., 2017). Nonetheless, limited research exists on the factors associated with lactation length in dairy cows. Indeed, where studies have been conducted, they have generally been restricted to cows in confinement systems (Tiezzi et al., 2012; Weber et al., 2015) or tropical regions (Bajwa et al., 2004; Hossein-Zadeh, 2012).

Factors previously identified as being associated with lactation length in dairy cows include parity (Hossein-Zadeh, 2012), age at calving within parity (Bajwa et al., 2004), season of calving (Bajwa et al., 2004), inadequate milk yield in late lactation (Weber et al., 2015), and poor fertility (Tiezzi et al., 2012; Weber et al., 2015). Hossein-Zadeh (2012) reported that first parity Iranian Holstein cows had a 16-day and 23-day longer lactation compared with second and third parity cows, respectively. A strong positive genetic correlation between lactation length and interval from first service to conception has been reported by Tiezzi et al. (2012), suggesting that extended lactations may be a consequence of poor fertility in year-round calving confinement systems.

Nonetheless, factors previously documented to associate with lactation length in confinement systems may not reflect those associated with lactation length in seasonal-calving systems. Seasonal-calving systems are characterised by all cows calving in a concentrated period of the year (Macdonald et al., 2008; Berry et al., 2013) as well as being dried off in a relatively short period. In the 5-year period before 2019, inclusive, approximately 70% of Irish cows calved between January and March each year (ICBF, 2019). Hence, poor fertility (i.e., calving later in the season) in a seasonal-
calving system should negatively affect lactation length. Should cows fail to achieve a lactation length of 305 days, their actual yield may be less than their reported standardised yield. Given the reliance on standardised milk yield for management decisions and genetic evaluations, determining the factors associated with lactation length is of significant importance. Therefore, the objective of the present study was to identify the genetic and non-genetic factors associated with lactation length in a seasonal pasture-based dairy cow production system.

3.4 Materials and Methods

All Irish dairy producers are legally required to inform the Irish Department of Agriculture, Food and the Marine of certain details relating to calving events, including the date of birth and unique dam identifier. Producers must also legally record all animal deaths and inter-location movements. This information is shared with the ICBF and held in the national database. Additional information including dry-off dates, test-day milk yield and composition, as well as calving difficulty scores are recorded on a voluntary basis and provided to the ICBF. All the above information was downloaded from the pre-existing ICBF national database for the purpose of this study; therefore, it was not necessary to obtain animal ethics committee approval in advance of conducting this study.

3.4.1 Data edits

Dairy herds were defined as spring-calving if >70% of cows calved between the months of January and June, inclusive (Ring et al., 2019); only spring-calving herds, which are the predominant system in Ireland (Berry et al., 2013), were retained. Calving dates and dry-off dates were available for 3,070,479 lactations from 1,265,504 cows calving in 9,748 spring-calving herds between the years 2008 and 2017, inclusive. Lactation length was calculated as the number of days between calving and recorded dry-off; culling dates were not used in the derivation of lactation length and only 3.8% of the cows in the herds retained were culled with no recorded dry-off date. Records where the cow parity was >10 or lactation length was >730 days (or both) were discarded, as were cows without a known sire. First parity cows recorded to have calved younger than 600 days of age were also removed. Further to this, the median
age at calving was calculated for each parity; 432,949 parity records where the cows calved more than 180 days before or after the median age at calving within parity were not considered further. For all remaining records, age at calving was categorised, within parity, into 6 groups, each 60 days in duration, relative to the median age at calving within parity. Where a dry-off date in the preceding lactation was available, the dry period length before the commencement of lactation was calculated. Dry periods ≤14 days or >112 days were removed and the remaining dry periods were categorised into 5 groups: >14 to ≤35 days, >35 to ≤56 days, >56 to ≤77 days, >77 to ≤98 days, and >98 to ≤112 days; the frequency per class was 1.3%, 9.6%, 35.8%, 37.0%, and 16.3%, respectively. Missing previous dry period length records (e.g., first lactation cows) or where a dry-off date was not recorded in the previous lactation were coded separately to facilitate their inclusion in the subsequent statistical analyses. Herd size was categorised into 5 groups, in intervals of 50 cows, from ≤50 cows calving in a given year to >250 cows calving in a given year. Heterosis and recombination loss coefficients were calculated for each cow as described by Ring et al. (2018). Heterosis was divided into 12 classes (0%, >0% and ≤10%, >10% and ≤20%, >20% and ≤30%, >30% and ≤40%, >40% and ≤50%, >50% and ≤60%, >60% and ≤70%, >70% and ≤80%, >80% and ≤90%, >90% and ≤99%, and >99%). Recombination loss was divided into 7 classes (0%, >0% and ≤10%, >10% and ≤20%, >20% and ≤30%, >30% and ≤40%, >40% and ≤50%, and >50%). Calving difficulty was subjectively recorded by producers on a scale of 1 to 4, in which 1 = no assistance required during calving, 2 = assistance provided with some calving difficulty, 3 = assistance provided with considerable calving difficulty, but no veterinary intervention, and 4 = assistance provided with considerable calving difficulty resulting in veterinary intervention. Lactations with no calving difficulty score were coded separately to facilitate their inclusion in the statistical analyses.

For the purpose of subsequent analyses, the edited data set was stratified by month of calving as January, February, March, and both April and May combined (due to the fact that there were fewer calving events in these months because of the seasonal nature of calving in Ireland; Berry et al., 2013); records relating to cows calving in June were removed as, on average, <3% of Irish cows calve in June (ICBF, 2019). Within each month of calving, animals were assigned to a contemporary group, based on calving date. The algorithm used to generate contemporary groups was that used in
the Irish national genetic evaluations (Berry et al., 2013). Animals that calved in the same herd and month within 10 days of each other were initially clustered together. Where <10 animals were clustered together, these animals were grouped with an adjacent contemporary group in time within the same herd and calving month until each contemporary group contained ≥10 records. Records from contemporary groups with <10 animals were removed. Cow records from 1,078 herds with at least one contemporary group represented in each of the calendar months of January, February, and March, as well as the combined calendar months of April and May, across the period of the present study were retained. Following these edits, 109,988 records from 80,390 cows calving in January, 327,023 records from 193,402 cows calving in February, 121,358 records from 97,802 cows calving in March, and 30,554 records from 27,666 cows calving in April or May were available for analyses.

For the identification of the phenotypic factors associated with lactation length, all data from the 1,078 herds were retained but an alternative contemporary group was regenerated. Using the contemporary group algorithm already defined (Berry et al., 2013), contemporary groups were assigned within herd, across calving months, with a maximum distance between the calving dates of 60 days. Following the removal of contemporary groups with <10 records, 616,350 records from 285,598 cows in 1,078 herds remained.

To estimate the variance components of lactation length within individual calving months, a random sample of 50% of the 1,078 herds represented in all calving month subsets, with assigned contemporary groups, were retained for January, February, and March; given the limited number of calving events available for April and May, all records were retained for these months. Following all edits, 56,858 records from 41,479 cows calving in January, 169,603 records from 99,878 cows calving in February, 61,889 records from 49,813 cows calving in March, and 30,554 records from 27,666 cows calving in April or May were retained for genetic analyses (Table 3.1). For a separate analysis to estimate variance components of lactation length across calving months, the records retained from each calving month were combined. A random sample of 20% of the herds represented in all calving months was retained; 58,565 records for 27,955 cows in 108 herds remained. Pedigree information for all animals was traced back to the founder animals and founders were assigned to 11 genetic groups based on breed.
Table 3.1. Number of records, cows, and herds, as well as the mean and median lactation length, genetic standard deviation ($\sigma_g$), heritability ($h^2$; standard error in parenthesis), and repeatability ($t$; standard error in parenthesis) of lactation length when restricted to ≤365 for cows calving in January, February, March, and April and May, as well as all five calendar months combined.

<table>
<thead>
<tr>
<th></th>
<th>Records</th>
<th>Cows</th>
<th>Herds</th>
<th>Mean</th>
<th>Median</th>
<th>$\sigma_g$</th>
<th>$h^2$ (standard error)</th>
<th>$t$ (standard error)</th>
</tr>
</thead>
<tbody>
<tr>
<td>All months</td>
<td>58,565</td>
<td>27,955</td>
<td>108</td>
<td>286.1</td>
<td>288.0</td>
<td>3.29</td>
<td>0.022 (0.004)</td>
<td>0.039 (0.005)</td>
</tr>
<tr>
<td>January</td>
<td>55,164</td>
<td>40,188</td>
<td>539</td>
<td>303.5</td>
<td>305.0</td>
<td>3.43</td>
<td>0.025 (0.005)</td>
<td>0.053 (0.009)</td>
</tr>
<tr>
<td>February</td>
<td>166,454</td>
<td>97,773</td>
<td>539</td>
<td>289.4</td>
<td>290.0</td>
<td>3.24</td>
<td>0.024 (0.003)</td>
<td>0.061 (0.004)</td>
</tr>
<tr>
<td>March</td>
<td>60,217</td>
<td>48,437</td>
<td>539</td>
<td>269.0</td>
<td>268.0</td>
<td>3.14</td>
<td>0.018 (0.004)</td>
<td>0.018 (0.004)</td>
</tr>
<tr>
<td>April/May</td>
<td>27,850</td>
<td>25,289</td>
<td>1,078</td>
<td>251.7</td>
<td>250.0</td>
<td>3.21</td>
<td>0.013 (0.006)</td>
<td>0.013 (0.006)</td>
</tr>
</tbody>
</table>
3.4.2 Lactation length phenotypes

Six different phenotypes representing alternative measures of lactation length were defined. One continuous trait was defined as lactation length where the lactation length was restricted to be ≤365 days. Preliminary analyses revealed minimal differences in model solutions or variance components when lactations ≤365 days in length were considered, lactations between 100 and 365 days in length were considered, or indeed when lactations of all lengths were considered. Five binary lactation length variables were also defined based on whether (i.e., coded as one) or not (i.e., coded as zero) the lactation length reached a given length, which, in the present study, was set at 150 days (LL150), 200 days (LL200), 240 days (LL240), 270 days (LL270), or 305 days (LL305); that is, if a cow had a code of 1 for LL305, it also had a code of 1 for LL150, LL200, LL240, and LL270.

3.4.3 Statistical analyses

3.4.3.1 Phenotypic analyses

The associations between lactation length variables and fixed effects were quantified using linear mixed models in ASReml (Gilmour et al., 2009). Both cow and contemporary group were fitted as random effects.

$$\text{LL}_{ijklmnopqrst} = \text{Het}_j + \text{Rec}_k + \text{Herd Size}_l + \text{Dry period length}_m + \text{Calving difficulty score}_n$$

$$+ \text{Age}_o | \text{Parity}_p + \text{Calving month}_q | \sum_{u=1}^{2} \text{Calving day}^u + \sum_{r=1}^{6} \text{Breed}_r + \text{CG}_s + \text{Cow}_t + \varepsilon_{ijklmnopqrst}$$

where \(\text{LL}_{ijklmnopqrst}\) was the lactation length phenotype for animal \(i\); \(\text{Het}_j\) was the fixed effect for heterosis class \(j\) \((j=0\) to \(11)\); \(\text{Rec}_k\) was the fixed effect for recombination loss class \(k\) \((k=0\) to \(6)\); \(\text{Herd size}_l\) was the fixed effect for herd size class \(l\) \((l=1\) to \(5)\); \(\text{Dry period length}_m\) was the fixed effect of the previous dry period length class \(m\) \((m=1\) to \(6)\); \(\text{Calving difficulty score}_n\) was the fixed effect of calving difficulty score \(n\) \((n=1\) to \(4)\); \(\text{Age}_o | \text{Parity}_p\) was the fixed effect of the interaction between age at calving \(o\) and parity \(p\) \((o=1\) to \(6), p=1\) to \(10)\); \(\text{Calving month}_q | \sum_{u=1}^{2} \text{Calving day}^u\) was the fixed effect of the interaction between calving month \(q\) and calving day relative to the contemporary group median; \(\sum_{r=1}^{6} \text{Breed}_r\) was the breed proportion \(r\) of the animal \(i\) fitted as a linear covariate representing for all of the main dairy breeds separately (i.e.,
Jersey, Ayshire, Brown Swiss, Montbéliarde, Norwegian Red, and Normande) except Holstein-Friesian; $CG_s$ was the random effect of contemporary group $s$ where $CG_s \sim N(0, I \sigma_{CG}^2)$ and $\sigma_{CG}^2$ represents the contemporary group variance and $I$ the identity matrix; $Cow_i$ was the random cow effect across lactations where $Cow_i \sim N(0, I \sigma_{cow}^2)$ and $\sigma_{cow}^2$ represents the cow variance and $I$ the identity matrix, and $e_{ijklmnoqpqrst}$ was the residual term where $e \sim N(0, I \sigma_{e}^2)$ and $\sigma_{e}^2$ represents the residual variance and $I$ the identity matrix.

### 3.4.3.2 Estimation of variance components

The genetic and residual variance components for all lactation length phenotypes were estimated using linear mixed models in ASReml (Gilmour et al., 2009) for each month of calving individually as well as for all months of calving combined. The linear model fitted to each month separately was:

$$LL_{ijklmnoq} = CG_j + Het_k + Rec_l + Age_m + Parity_n + Dry \text{ period length}_o + \sum_{p=1}^{2} Calving \ text{ day}^p + a_i + pe_q + e_{ijklmnoq}$$

where $LL_{ijklmnoq}$ was the observed lactation length phenotype for animal $i$; $CG_j$ was the fixed effect for contemporary group $j$; $Het_k$ was the fixed effect for heterosis class $k$ ($k=0$ to $11$); $Rec_l$ was the fixed effect for recombination loss class $l$ ($l=0$ to $6$); $Age_m$ was the fixed effect for age at calving class $m$ ($m=1$ to $6$); $Parity_n$ was the fixed effect for parity $n$ ($n=1$ to $10$); $\sum_{q=1}^{2} Calving \ text{ day}^q$ was the linear and quadratic fixed effect for calving day relative to the contemporary group median calving day; $Dry \ text{ period length}_o$ was the fixed effect for previous dry period length class $o$ ($o=1$ to $6$); $a_i$ was the additive random effect of animal $i$ where $a \sim N(0, A \sigma_{a}^2)$ and $\sigma_{a}^2$ represents the genetic variance and $A$ the numerator relationship matrix; the pedigree of all animals was traced back to their founder animals and allocated to genetic groups based on breed to construct the numerator relationship matrix; $pe_q$ was the random animal permanent environmental effect across lactations where $pe_q \sim N(0, I \sigma_{pe}^2)$ and $\sigma_{pe}^2$ represents the permanent environmental variance and $I$ the identity matrix and $e_{ijklmnoq}$ was the residual term where $e \sim N(0, I \sigma_{e}^2)$ and $\sigma_{e}^2$ represents the residual variance and $I$ the identity matrix. The heritability estimates for the binary lactation length phenotypes were transformed from the observed scale to the underlying liability scale.
using the percentage of cows achieving each trait enabling the comparison of heritability estimates between traits (Robertson and Lerner, 1949).

### 3.4.3.3 Genetic evaluation

To estimate the genetic trend for lactation length in Irish seasonal-calving, pasture-based dairy cows, additional lactation records from cows born since 2000 and calving before the end of 2017 were obtained from the ICBF national database. All edits applied previously were imposed as was the statistical model developed and the variance components estimated in the present study. Contemporary group was defined within calving month, with records from April and May combined. A total of 1,678,070 lactation records from 817,625 cows remained. Pedigree information for all animals was traced back to the founder animals and founders were assigned to genetic groups based on breed. Individual animal EBV for lactation length were calculated using the MIX99 software suite (Strandén and Lidauer, 1999). The genetic trend by year of birth for lactation length was estimated for all Holstein-Friesian females (572,981 cows) with lactation length records as well as separately for 6,327 Holstein-Friesian male animals born since 2000 with ≥10 (grand)progeny with lactation length records.

### 3.5 Results

Of the 616,350 records from milk recorded herds used in the phenotypic analyses, 20.1%, 53.6%, 20.5%, 4.9%, and 0.9% of the cows calved in January, February, March, April, and May, respectively. The median lactation length in the edited data set was 288 days; before edits, the median lactation length was 280 when lactation length was restricted to ≤365 days. Whereas 27% of cows achieved a target lactation length of 305 days, 76% of cows achieved a lactation length of 270 days. February 14 was the median calving day of the year in the edited data set, with 41% of the cows in the data set calving between February 4 and 24. Before edits, the median calving date was February 23. The median dry-off date was November 26, with 37% of cows being dried off between November 16 and December 6. Before edits, the median dry-off date was November 25.
3.5.1 Phenotypic risk factors

Except for recombination loss and some breed covariates, all the fixed effects included in the phenotypic model were associated (P < 0.05) with the continuous dependent variable of lactation length. When lactation length was defined as a binary trait, all fixed effects included in the phenotypic models were associated with lactation length with the exception of the interaction between calving day and calving month when lactation length was defined as LL150, heterosis coefficient when lactation length was defined as LL200, and recombination loss coefficient when lactation length was defined as LL270. The model solutions for each breed covariate associated with each binary lactation length trait are detailed in Table 3.2.

### Table 3.2. Breed covariate solutions (standard error in parentheses) of the six dairy breeds, Jersey (JE), Ayshire (AY), Brown Swiss (BS), Montbéliarde (MO), Norwegian Red (NR), and Normande (NO) relative to Holstein-Friesian for lactation length restricted to ≤365 days (LL365) and lactation length defined as a binary trait ≥150 days (LL150), ≥200 days (LL200), ≥240 days (LL240), ≥270 days (LL270), and ≥305 days (LL305).

<table>
<thead>
<tr>
<th></th>
<th>JE</th>
<th>AY</th>
<th>BS</th>
<th>MO</th>
<th>NR</th>
<th>NO</th>
</tr>
</thead>
<tbody>
<tr>
<td>LL365</td>
<td>-0.07</td>
<td>0.31</td>
<td>-2.62</td>
<td>-1.56**</td>
<td>-4.73***</td>
<td>-2.51</td>
</tr>
<tr>
<td></td>
<td>(0.37)</td>
<td>(1.69)</td>
<td>(2.03)</td>
<td>(0.59)</td>
<td>(0.51)</td>
<td>(4.54)</td>
</tr>
<tr>
<td>LL150</td>
<td>0.003**</td>
<td>0.001</td>
<td>-0.009</td>
<td>-0.001</td>
<td>0.001</td>
<td>-0.007</td>
</tr>
<tr>
<td></td>
<td>(0.001)</td>
<td>(0.004)</td>
<td>(0.005)</td>
<td>(0.001)</td>
<td>(0.001)</td>
<td>(0.012)</td>
</tr>
<tr>
<td>LL200</td>
<td>0.004**</td>
<td>0.001</td>
<td>-0.022**</td>
<td>0.001</td>
<td>0.003</td>
<td>-0.014</td>
</tr>
<tr>
<td></td>
<td>(0.001)</td>
<td>(0.007)</td>
<td>(0.008)</td>
<td>(0.002)</td>
<td>(0.002)</td>
<td>(0.019)</td>
</tr>
<tr>
<td>LL240</td>
<td>0.000</td>
<td>-0.011</td>
<td>-0.005</td>
<td>0.001</td>
<td>-0.020***</td>
<td>0.000</td>
</tr>
<tr>
<td></td>
<td>(0.003)</td>
<td>(0.013)</td>
<td>(0.016)</td>
<td>(0.005)</td>
<td>(0.004)</td>
<td>(0.036)</td>
</tr>
<tr>
<td>LL270</td>
<td>-0.008*</td>
<td>0.005</td>
<td>-0.025</td>
<td>-0.027***</td>
<td>-0.043***</td>
<td>-0.068</td>
</tr>
<tr>
<td></td>
<td>(0.005)</td>
<td>(0.023)</td>
<td>(0.027)</td>
<td>(0.008)</td>
<td>(0.006)</td>
<td>(0.007)</td>
</tr>
<tr>
<td>LL305</td>
<td>0.009</td>
<td>0.043</td>
<td>0.043</td>
<td>-0.029*</td>
<td>-0.060***</td>
<td>-0.019</td>
</tr>
<tr>
<td></td>
<td>(0.025)</td>
<td>(0.030)</td>
<td>(0.030)</td>
<td>(0.009)</td>
<td>(0.008)</td>
<td>(0.007)</td>
</tr>
</tbody>
</table>

Significance of the difference from Holstein-Friesian (i.e., zero); *P < 0.05, ** P < 0.01, ***P < 0.001.

3.5.1.1 Month of calving, parity, age at calving

Relative to cows calving in January, the lactation of a cow calving in February, March, April, or May was 4.2, 12.7, 21.9, and 33.7 days shorter, respectively (Figure 3.1). For cows calving in January, the likelihood of achieving LL150, LL200, LL240, LL270, and LL305 was 0.5%, 8.1%, 26.2%, 42.4%, and 63.1% higher, respectively, than for cows calving in May (Figure 3.2); the percentage change in likelihood of
achieving each binary trait was calculated by dividing the model solution for the class of interest (calving in May) by the model solution for the population mean.

A first parity cow had a 7.8, 8.6, and 8.4 days shorter lactation than a second, third, and fourth parity cow, respectively (Figure 3.1). Ninth parity cows were the least likely to achieve LL150 and first parity cows were the least likely to have lactations of ≥305 days relative to cows in second, third, fourth, or fifth parity (Figure 3.2). Cows calving 121 to 180 days beyond the parity median lactated for 5.3 additional days (Figure 3.1) and were more likely to lactate ≥305 days compared with cows calving 120 to 180 days earlier than their parity median (Figure 3.2). Relative to cows calving 120 to 180 days older than the parity median age at calving, cows calving 120 to 180 days younger than the parity median were the least likely to lactate for at least 305 days.

3.5.1.2 Breed, heterosis, and recombination loss coefficient

Norwegian Red and Montbéliarde cows had, on average, a 4.7 and 1.6 days shorter lactation, respectively, than Holstein-Friesian cows (Table 3.2). The likelihood of achieving LL150 was 0.26% greater in Jersey cows relative to Holstein-Friesian cows. The likelihood of achieving LL200 was 0.45% greater and 2.2% less in Jersey cows and Brown Swiss cows, respectively, than their Holstein-Friesian contemporaries. A Norwegian Red cow had a lower likelihood of achieving LL240 than a Holstein-Friesian cow. Relative to Holstein-Friesian cows, Jersey cows, Montbéliarde cows, and Norwegian Red cows were less likely to achieve LL270, respectively (Table 3.2). Norwegian Red cows and Montbéliarde cows were also less likely to achieve LL305 relative to Holstein-Friesians (Table 3.2).

Cows with a heterosis coefficient of 0% had a 0.95 day longer lactation, a lower likelihood of achieving LL150 and LL200, and a higher likelihood of achieving LL270 and LL305 relative to cows with a heterosis coefficient of between 91% and 99% (Figures 3.1 and 3.2). Cows with a heterosis coefficient of >99% had the highest likelihood of achieving LL240 relative to cows with a heterosis coefficient of 0% (Figure 3.2). Cows with a recombination loss coefficient of between 41% and 50% had a higher likelihood of achieving LL150 and LL200 relative to cows with a recombination loss coefficient of between 1% and 10%.
Figure 3.1. The change in lactation length (LL; standard error bar represents ± 1 SE) associated with A) calving month relative to cows calving in January; B) parity relative to first parity cows; C) age at calving relative to cows calving between 180 and 120 days earlier than the parity median; D) heterosis coefficient relative to cows with a heterosis coefficient of 0%; E) calving difficulty score relative to cows with a calving difficulty score of 1; F) dry period length relative to cows with a dry period of between 15 and 35 days; G) herd size relative to herds with ≤50 cows.
Figure 3.2. The association between the change in the percentage that achieved lactation length ≥150 days (♦), ≥200 days (■), ≥240 days (▲), ≥270 days (×), ≥305 days (□) and A) calving month relative to cows calving in January; B) parity relative to first parity cows; C) age at calving relative to cows calving between 180 and 120 days earlier than the parity median; D) heterosis coefficient relative to cows with a heterosis coefficient of 0%; E) recombination loss coefficient relative to cows with a recombination loss coefficient of 0%; F) calving difficulty score relative to cows with a calving difficulty score of 1; G) dry period length relative to cows with a dry period of between 15 and 35 days; H) herd size relative to herds with ≤50 cows. Standard error bar represents ± 1 SE unit.
Cows with a recombination loss coefficient of >50% were more likely to achieve LL240 relative to cows with a recombination loss coefficient of 1% to 20%. Having a recombination loss coefficient of 1% to 10% was associated with an improvement in achieving LL305 relative to cows with a recombination loss coefficient of 0% (Figure 3.2).

3.5.1.3 Calving difficulty, dry period length, and herd size

Cows that received veterinary assistance at calving lactated, on average, for an additional 0.9 days (Figure 3.1) relative to a cow calving with a score of 2 (assistance provided with some calving difficulty). Cows that received veterinary assistance at calving were more likely to lactate for at least 270 or 305 days, respectively, relative to a cow calving without any recorded difficulty (Figure 3.2). Conversely, cows calving without any recorded calving difficulty were more likely to reach 150 and 200 days in lactation relative to cows calving with difficulty (Figure 3.2).

Relative to cows with a dry period of between 15 and 35 days, cows with a dry period of between 36 and 56 days had a 3.3 days longer lactation and were more likely to have lactations at least 150, 200, or 240 days (Figures 3.1 and 3.2). Cows with a dry period of between 99 and 112 days were less likely to lactate for at least 270 or 305 days, respectively, relative to cows with dry period of >36 to ≤56 days.

Lactation length was, on average, 6 days (SE = 0.8 d) shorter in herds with >200 cows relative to herds with ≤50 cows calving a year (Figure 3.1). Similarly, the largest herds had a lower likelihood of lactating for at least 150, 200, 240, 270, and 305 days compared with herds with ≤50 cows (Figure 3.2).

3.5.2 Genetic parameters

The genetic standard deviation, heritability, and repeatability estimates of lactation length were 3.29 days, 0.022, and 0.039, respectively, when data from all calving months were analysed together (Table 3.1) and the lactation length was defined as a continuous trait. When calving months were analysed separately, the genetic standard deviation, heritability, and repeatability estimates of lactation length ranged from 3.1 to 3.4 days, from 0.013 to 0.025, and from 0.013 to 0.061, respectively (Table 3.1). The coefficient of genetic variation for lactation length was 1.2% and did not vary by more than 0.16 percentage units across the different calving months. The
coefficient of genetic variation, calculated as described by Burdon (2008), for the binary traits ranged from 4.9% and 8.7%. When binary lactation length traits were analysed by calving month, the heritability estimates for all traits on the underlying liability scale were lowest for cows calving in April and May except for LL270. LL270 was the most repeatable trait apart from cows calving in April and May when LL150 was the most repeatable trait (Table 3.3; Appendix D). In addition to frequently being the most repeatable trait, LL270 had the greatest coefficient of genetic variation relative to all other binary lactation length traits.

Table 3.3. The percentage achieved as well as the genetic standard deviation ($\sigma_g$), heritability estimate ($h^2$; standard error in parenthesis), repeatability ($t$; standard error in parenthesis), and heritability estimate on the underlying liability scale ($h^2_L$) of binary lactation length traits; lactation length $\geq$150 days (LL150), $\geq$200 days (LL200), $\geq$240 days (LL240), $\geq$270 days (LL270), and $\geq$305 days (LL305).

<table>
<thead>
<tr>
<th>Trait</th>
<th>Percentage achieved, %</th>
<th>$\sigma_g$</th>
<th>$h^2$ (standard error)</th>
<th>t (standard error)</th>
<th>$h^2_L$</th>
</tr>
</thead>
<tbody>
<tr>
<td>LL150</td>
<td>99.61</td>
<td>0.003</td>
<td>0.0021 (0.0014)</td>
<td>0.0021 (0.0014)</td>
<td>0.061</td>
</tr>
<tr>
<td>LL200</td>
<td>98.95</td>
<td>0.004</td>
<td>0.0023 (0.0017)</td>
<td>0.0062 (0.0053)</td>
<td>0.031</td>
</tr>
<tr>
<td>LL240</td>
<td>94.64</td>
<td>0.018</td>
<td>0.0097 (0.0032)</td>
<td>0.0146 (0.0051)</td>
<td>0.044</td>
</tr>
<tr>
<td>LL270</td>
<td>75.96</td>
<td>0.037</td>
<td>0.0138 (0.0035)</td>
<td>0.0418 (0.0049)</td>
<td>0.026</td>
</tr>
<tr>
<td>LL305</td>
<td>27.24</td>
<td>0.029</td>
<td>0.0073 (0.0023)</td>
<td>0.0073 (0.0023)</td>
<td>0.013</td>
</tr>
</tbody>
</table>

3.5.3 Genetic evaluation

With the exception of a small reduction in the mean EBV for lactation length in cows born in 2009 relative to cows born in 2008, the mean EBV for lactation length of Holstein-Friesian cows increased year on year (Figure 3.3). The EBV for lactation length of a Holstein-Friesian cow born in 2015 was, on average, 3.75 days higher than the EBV of a cow born in 2000. The average increase in the EBV for lactation length, estimated from a linear regression model fitted through the mean annual EBV, was 0.25 days/year for Holstein-Friesian cows. The trend in the EBV for lactation length of Holstein-Friesian males born after 2000 increased, on average, by 0.09 days/year.
Figure 3.3. The genetic trend by year of birth for lactation length estimated for Holstein-Friesian cows (■), and Holstein-Friesian males with ≥10 progeny with lactation length records (♦).

3.6 Discussion

The profitability of the Irish dairy industry, as with any in situ grazing-based production system, is fundamentally reliant on compact seasonal calving just before the initiation of grass growth (Dillon et al., 2003). This is reflected in the median calving date and dry-off date of cows in the edited data set being February 14 and November 26, respectively. Although achieving lactations of 305 days ensures the recommended 60-day dry period (Capuco et al., 1997), it also enables the maintenance of the crucial 365-day calving interval. Additionally, if lactations of 305 days were achieved, the standardised yields currently used in dairy cow genetic evaluations and management decision support tools would be more reflective of actual milk yield. Nevertheless, the median lactation length of Irish dairy cows in the edited data set used in the present study was 288 days, which is low relative to most international estimates (Hossein-Zadeh, 2012; M’hamdi et al., 2012), particularly in first lactation cows (Van Eetvelde et al., 2017). This shortened lactation length is likely due to differences in the constraints imposed in seasonal pasture-based production systems versus confinement systems. In line with this, mean lactation length calculated from tanker collection information in New Zealand, which also operates a seasonal-calving, pasture-based dairy production system, was 271 days (LIC and DairyNZ, 2019). The fact that only
27% of cows in the present study achieved lactations of 305 days implies that there is significant scope to improve the average lactation length of pasture-based dairy cows, but also that the often quoted standardised 305-day yield may be an overestimate for many. Using the parameters of a lactation function fitted to the yield of 3 genotypes of Irish dairy cows as presented by Horan et al. (2005), it was possible to calculate daily yield and deduce the loss in yield with a 288-day lactation versus a 305-day lactation. For the 3 genotypes, the yield in the first 288 days of lactation was 97.1% to 97.5% that of the respective 305-day yield. Whereas limited research has been undertaken to quantify the associations between both genetic and non-genetic factors with lactation length in confinement systems (Tiezzi et al., 2012), no equivalent studies exist for pasture-based, seasonal-calving temperate dairy production systems. The motivation for the present study was to fill this void.

3.6.1 Management factors

The plethora of management factors associated with lactation length in the present study represents opportunities to lengthen lactations, but also a checklist for extension officers when exploring why a given herd has relatively short lactations. Given the large differences in lactation length associated with calving month, increasing the proportion of the herd calving in earlier months would be advantageous to lengthen lactations. This large impact is a function of seasonal-calving systems where all cows tend to be dried off in early winter, regardless of the previous or the subsequent predicted calving date. Increasing the proportion of the herd calving earlier in the year could be achieved through optimised reproductive management together with astute breeding decisions. Excellent reproductive performance is therefore key; considerable gains in performance have been achieved in most global dairy cow populations owing to genetic gain achieved following the consideration of reproductive performance in dairy cow breeding goals (Berry et al., 2014a; Ma et al., 2019). In Ireland, for example, between the years 2010 and 2018, inclusive, there was an 8.2 percentage unit increase in the proportion of Irish dairy cows calving in January and February (ICBF, 2019). The emphasis on compact seasonal calving, corresponding to the commencement of grass growth, is replicated in other pasture-based systems (Macdonald et al., 2008) but not in confinement systems where year-round calving is more the norm. Therefore, since previous studies were based on
tropical and confinement systems, before the present study, calving month had not been considered as a factor associated with lactation length. The closest comparable trait to calving month in a confinement system is season of calving and this indeed has been documented to be associated with lactation length in dairy herds (Bajwa et al., 2004; M’hamdi et al., 2012; Hossein-Zadeh, 2013). Nonetheless, the association between season of calving and lactation length in confinement systems may reflect more seasonal feeding regimens, changes in ambient temperatures, or other seasonal factors rather than management practices per se.

In contrast to calving month, the association between parity and lactation length has been reported extensively (Hossein-Zadeh, 2012; M’hamdi et al., 2012; Hossein-Zadeh, 2013). Although frequently associated with shorter lactations in confinement systems (M’hamdi et al., 2012; Hossein-Zadeh, 2013), older cows, on average, had longer lactations in the present study. The difference in the association between increasing parity and lactation length in the present study relative to previous studies (M’hamdi et al., 2012; Hossein-Zadeh, 2013) may be dependent on diet, location, or production system. Cows are often dried off early due to low milk yield or poor BCS (Melendez et al., 2007; Weber et al., 2015) rather than estimated calving dates. This is particularly true for primiparous who have yet to reach their mature size (Berry et al., 2006; Coffey et al., 2006) and have a lower intake capacity as evidenced by their lower feed intake (Azizi et al., 2009). High concentrate diets may help primiparous cows to reach their potential lactation length easier than pasture alone, demonstrated by their longer lactations in confinement systems relative to older cows (M’hamdi et al., 2012; Hossein-Zadeh, 2013). Conversely, multiparous cows may be able to achieve their potential lactation length based on almost exclusively pasture. Additionally, without the emphasis on achieving a 365-day calving interval in confinement systems, primiparous cows are associated with an extended calving interval, across multiple dairy breeds (391 to 407 days; Hare et al., 2006). Conversely, in pasture-based systems, primiparous Holstein-Friesian cows were associated with shorter calving intervals (367 days; Evans et al., 2006) and, therefore, shorter lactations.

Reducing the proportion of primiparous cows in the herd could be achieved through improving the health and fertility status of the herd, which, in turn, could contribute to longer lactations being achieved in pasture-based production systems. In
addition to increased milk production from longer lactations, multiparous cows have been associated with higher standardised 305-day milk yield relative to primiparae (Horan et al., 2005; Lee and Kim, 2006). Nevertheless, reducing the proportion of primiparous cows may not be feasible in expanding herds where additional heifers are bred to fulfill expansion requirements.

The effect of shortening the dry period on lactation yield has been extensively studied (Bachman and Schairer, 2003; Rastani et al., 2005; Pezeshki et al., 2008; Atashi et al., 2013), with many suggesting shortening dry periods would improve energy balance and metabolic status in early lactation, without affecting lactation production (Rastani et al., 2005; Pezeshki et al., 2008). The traditional dry period of approximately 60 days enables the involution and regeneration of the mammary gland (Capuco et al., 1997). The results of the effect of dry period on milk production are, however, inconsistent (Rastani et al., 2005; Pezeshki et al., 2008; Atashi et al., 2013), with many reporting that shorter dry periods were associated with shorter lactations (present study) or actually lower yields in the subsequent lactation, particularly in early lactation (Pezeshki et al., 2008; Atashi et al., 2013). Conversely, Rastani et al. (2005) reported no effect on solid-corrected milk yield in 65 primiparous and multiparous US Holstein cows following dry periods of <28 days relative to a traditional-length dry period. While longer lactations before dry-off may compensate for lower yields (Pezeshki et al., 2008; Atashi et al., 2013), no study, to our knowledge, has looked at the effect of repeated short dry periods on production. Nonetheless, corroborating most previous studies in dairy cows, where dry periods of traditional lengths were associated with the highest production levels (Pezeshki et al., 2008; Atashi et al., 2013), dry periods of between 36 and 77 days were associated with the longest lactations in the present study.

Although not considered as a factor associated with lactation length in previous studies, the longer lactation and higher likelihood of achieving LL270 and LL305 associated with requiring veterinary assistance at calving in the present study were likely due to delayed submission and conception in cows that experienced a very difficult calving. Haile-Mariam et al. (2003) reported a phenotypic correlation of 0.47 between calving interval and lactation length in Australian dairy cows. Using data available from the Irish national database, Berry et al. (2019) reported that multiparous cows that required veterinary assistance at calving had a 15.1-day longer calving
interval than those that required no assistance at calving. Greater calving difficulty may lengthen lactations, as some producers dry off cows based on expected calving dates, yet the delayed calving in the subsequent lactation would likely lead to a shorter subsequent lactation or even culling.

3.6.2 Breed effects

The longer average lactations in Holstein-Friesian cows relative to Montbéliarde and Norwegian Red cows detected in the present study has not been previously reported. An Irish study comparing the production efficiency of imported French dual-purpose breeds (35 Montbéliarde cows and 33 Normande cows) and 64 Holstein-Friesian cows (31 imported from Holland and 33 upgraded Irish Holstein-Friesians) reported no significant difference in lactation length between breeds in a spring-calving, pasture-based system (Dillon et al., 2003). Dillon et al. (2003) did, however, report a 5-day longer lactation in Dutch imported Holstein-Friesian relative to Montbéliarde cows, although it was not significant.

Interbreed differences in lactation persistency have been reported since the 1980s (Wood, 1980; Grossman et al., 1986). Neither lactation length nor lactation persistency are included in the genetic evaluations of the Economic Breeding Index (the Irish dairy breeding index spanning all dairy breeds; Berry et al., 2007a). While Norman et al. (1985) recommended extending lactation yields of all cows dried off early to the standardised length for genetic evaluations, this could contribute to a bias in yield estimates for cows that, in particular, were dried off early (which could include cows that dried themselves off naturally). Hence, to fairly compare breeds of different persistency, consideration should be given to including lactation length in genetic evaluations or breeding objectives where cows naturally cease lactation before the standardised lactation length. Recording the reason for dry-off (e.g., natural or injury) may be useful in ensuring a differentiation is made between animals with a genetic predisposition to shorter lactations versus those that had a short lactation for some random reason not captured in a contemporary group effect (e.g., injury). How best to handle short lactations in either genetic evaluation models or breeding objectives warrants further investigation while continuing to conform to ICAR guidelines. This could involve the status quo test-day model genetic evaluation procedure and some post-hoc adjustment or scaling of yield for differences in genetic merit for lactation.
length. Consideration should also be given to the use of lactation length in the generation of cow-specific phenotypic yields, thus achieving closer concordance between the sum of the lactation yields per cow and the total herd milk supplied to the processor.

3.6.3 **Intrabreed effects**

To our knowledge, no study has reported heritability estimates for lactation length in seasonal-calving, pasture-based dairy herds with multiple European dairy breeds. The heritability estimate of lactation length in the present study was lower than previously reported in pasture-based Holstein-Friesian cows in Australia (0.03; Haile-Mariam et al., 2003) and in confinement-based cows of multiple dairy breeds (0.06 to 0.37; Ojango and Pollott, 2001; Bakir et al., 2004; Goshu et al., 2014). The repeatability estimates for lactation length reported in confined cows (0.11 to 0.65; Ojango and Pollott, 2001; Bakir et al., 2004) was higher than that reported in the present study (0.04). The coefficient of genetic variation, though not previously reported, was calculated from the documented statistics provided in other studies for Holstein-Friesian cows (Ojango and Pollott, 2001; Goshu et al., 2014). The coefficient of genetic variation for lactation length in the present study (i.e., 1.2%) was lower than that previously reported in Holstein-Friesian cows (5.3% to 15.3%; Ojango and Pollott, 2001; Goshu et al., 2014). The complexity of factors associated with lactation length in pasture-based systems, particularly the reliance on the calving pattern to coincide with commencement of grass growth (Berry et al., 2013) and maintenance of a 365-day calving interval, are reflected in the lower heritability estimate and coefficient of genetic variation of lactation length relative to those reported from confinement systems. In an analysis of 2,060,784 lactation records from 1,022,329 cows, Berry et al. (2013) reported a heritability of fertility traits varying from 0.01 to 0.07, which is consistent with the heritability of 0.01 to 0.03 for lactation length in the present study. This was also reflected in the lower heritability estimates for lactation length in cows calving in March (0.018) or April and May (0.013) relative to cows calving in January (0.025) or February (0.024), echoing the seasonal nature of Irish dairy production. As cows are generally dried off over a strict period in early winter, cows calving in January or February have the necessary time to reach their potential lactation length and will likely only be dried off early when milk yield is low. Although
the heritability estimates of lactation length in January and February are likely to somewhat reflect the heritability of yield in late lactation (0.16 to 0.27; Bastin et al., 2011; McCarthy and Veerkamp, 2012), the lower heritability estimate of lactation length relative to late lactation milk yield is likely due to the influence of other management factors or decisions. Conversely, the length of lactation of March-, April-, or May-calving cows is more reflective of the low heritability of fertility traits (Berry et al., 2014a). The greater influence of management factors in later-calving cows is reflected in the higher coefficient of residual variation in April- and May-calving cows (0.11) relative to those calving in January (0.07).

Genetic gain is a function of selection intensity, accuracy of selection, genetic standard deviation, and generation interval (Rendel and Robertson, 1950a). Selection accuracy is the only component directly influenced by heritability. Nonetheless, the same selection accuracy can be achieved irrespective of heritability once sufficient data are available (Berry et al., 2011). Hence, if dry-off dates and reason for drying off were frequently recorded, as could be the case if recording was mandatory, high selection accuracy for lactation length could be achieved. Of importance then would be the extent of the genetic variability. Based on the genetic standard deviation estimated in the present study (3.3 d), the top 20% of cows on genetic merit for lactation length would be expected, on average, to have a 9.2-day longer lactation than cows in the bottom 20%. This difference increased to 11.6 days when the top and bottom 10% of cows were compared. Similarly, when based on the estimated genetic variability for LL305, the top 20% of cows genetically would be, on average, 8.1 percentage units more likely to achieve lactations of 305 days or longer than the bottom 20% of cows. This difference increases to 10 percentage units when the top and bottom 10% are compared.

Poor fertility often results in longer calving intervals and therefore longer lactations in year-round calving systems (Tiezzi et al., 2012). In seasonal-calving, pasture-based systems, however, where cows tend to be dried off on a given date, poor fertility leading to delayed calving dates actually results in shorter lactations. Increasing the proportion of cows that calve early in the calving season, achieved through improved fertility, should result in longer lactations. Hence, the improvements in the genetic merit for lactation length of Holstein-Friesian cows and sires achieved to date are likely due to the year-on-year improvement in genetic merit for
reproductive performance in Irish dairy cows (Berry et al., 2014a). Both the genetic variation in lactation length and the improvements in genetic merit for lactation length already achieved highlight the considerable progress achievable through breeding.

3.7 Conclusions

With only 27% of the cows in the present study achieving lactations of 305 days or greater, the suitability of yields standardised to a 305-day lactation, without the consideration of lactation length or persistency for genetic evaluations and decision support tools, is questionable. While the heritability estimates for lactation length in the present study were lower than previously reported (for cows in confinement production systems), genetic variation exists for lactation length in pasture-based dairy cows. Given the array of genetic and non-genetic factors associated with lactation length, an approach combining selective breeding and improvements in management practices may prove an efficient and effective strategy to lengthen lactations.
Chapter 4: Exploiting genetic variability in the trajectory of lactation yield and somatic cell score with each progressing parity

4.1 Preface

At the time of thesis submission, this chapter was published in the Journal of Dairy Science (accepted December 9th 2021). The full reference is:


Formatting and referencing style have been edited for consistency throughout the thesis. Figures and table captions have been assigned with a chapter prefix and acknowledgements have been removed. All other aspects are consistent with the published manuscript.

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4.2 Abstract

The inclusion of reproductive performance in dairy cow breeding schemes has resulted in a cumulative improvement in genetic merit for reproductive performance; this improvement should manifest in longer productive lives through a reduced requirement for involuntary culling. Nonetheless, the average length of dairy cow productive life has not changed in most populations, suggesting that risk factors for culling, especially in older cows, are possibly more associated with lower yield or high SCS than compromised reproductive performance. The objective of the present study was to understand the dynamics of lactation yields and SCS in dairy cows across parities and, in doing so, quantify the potential to alter this trajectory through breeding. After edits, 3,470,520 305-day milk, fat, and protein yields, as well as milk fat and protein percentage and somatic cell count records from 1,162,473 dairy cows were available for analysis. Random regression animal models were used to identify the parity in which individual cows reached their maximum lactation yields, and highest average milk composition and SCS; also estimated from these models were the (co)variance components for yield, composition, and SCS per parity across parities. Estimated breeding values for all traits per parity were calculated for cows reaching ≥fifth parity. Of the cows included in the analyses, 91.0%, 92.2%, and 83.4% reached maximum milk, fat, and protein yield in fifth parity, respectively. Conversely, 95.9% of cows reached their highest average fat percentage in first parity and 62.9% of cows reached their highest average protein percentage in third parity. In contrast to both milk yield and composition traits, 98.4% of cows reached their highest average SCS in eighth parity. Individual parity estimates of heritability for milk yield traits, milk composition, and SCS ranged from 0.28 to 0.44, 0.47 to 0.69, and 0.13 to 0.23, respectively. The strength of the genetic correlations per trait among parities was inversely related to the interval between the parities compared; the weakest genetic correlation was 0.67 (SE = 0.02) between milk yield in parities 1 and 8. Eigenvalues and eigenfunctions of the additive genetic covariance matrices for all investigated traits revealed potential to alter the trajectory of parity profiles for milk yield, milk composition, and SCS. This was further demonstrated when evaluating the trajectories of animal estimated breeding values per parity.
4.3 Introduction

The inclusion of functional traits, like reproductive performance, in dairy cow breeding programs has contributed to a cumulative improvement in the genetic merit for reproductive performance in most dairy cow populations (Berry et al., 2014a; Cole and VanRaden, 2018; De Vries, 2020). The improvement achieved in genetic merit for reproductive performance should have manifested itself in a longer dairy cow productive life via reduced involuntary culling for reproductive failure. Yet, the expected improvements in productive life have not been realised in many populations with the average productive lifespan of a dairy cow remaining between 2.5 and 4.5 year (Adamczyk et al., 2016; Kerslake et al., 2018; De Vries and Marcondes, 2020). As the improvement in reproductive performance leads to a reduced need for involuntary culling due to reproductive failure, risk factors for culling are therefore likely transitioning from involuntary to voluntary causes. Poor lactation yield and high SCC are already two of the primary reasons reported for voluntary culling in dairy cows (Berry et al., 2005; Kerslake et al., 2018; De Vries and Marcondes, 2020) and the rate of culling due to high SCC will likely increase as European dairy producers are required to implement selective dry cow therapy from 2022 (Animal Health Ireland; 2020). Therefore, age-linked reductions in lactation yield or increases in SCC could potentially explain why productive life has not improved in line with the genetic gain in reproductive performance.

No study has, to date, specifically investigated the parity at which individual dairy cows reach maximum 305-day milk yield, highest average SCS, or indeed, whether inter-animal variability exists in the rate of change in lactation yield or SCS before and after maximum yield or highest average SCS. Nonetheless, based on the documented 305-day milk yield per parity reported by Guo et al. (2002) and Yang et al. (2005), it can be assumed that dairy cows, on average, reach maximum lactation yield in the fourth or fifth parity. Using such mean values to assume the parity at which maximum yield occurs ignores the potential inter-animal variability in when maximum lactation yield is achieved.

Although previous studies on dairy cows have reported heritability estimates and genetic (co)variances of 305-day milk yield (Carlén et al., 2004; Yang et al., 2005; Frioni et al., 2017) and SCS per parity (Carlén et al., 2004), no study has estimated the genetic (co)variances among milk yield traits, milk composition, or SCS in dairy cows.
across a wide range of parities (i.e., first to eighth parity). Estimated 305-day milk yields up to sixth parity have been reported as moderately heritable (0.23 to 0.34; Carlén et al., 2004; Yang et al., 2005; Frioni et al., 2017), and the heritability of SCS has been reported as between 0.10 in third parity and 0.14 in first parity (Carlén et al., 2004). Whereas one study reported a relatively large reduction in heritability estimates of milk yield between parities, from 0.34 in first parity to 0.25 and 0.23 in second and third parities, respectively (Carlén et al., 2004), others have reported the heritability estimates of milk yield (Yang et al., 2005; Frioni et al., 2017) and SCS (Carlén et al., 2004) as being similar (i.e., within 0.04) across parities. The strength of the reported genetic and phenotypic correlations between milk yield (Zarnecki et al., 1991; Carlén et al., 2004; Frioni et al., 2017) and SCS (Carlén et al., 2004) across different parities were generally inversely related to the interval between the parities compared. The genetic correlation between 305-day milk yield in first and second parity, first and third parity, and second and third parity in pasture-based Uruguayan dairy cows was 0.93, 0.91, and 0.97, respectively (Frioni et al., 2017). The genetic correlations between SCS in first and second parity, first and third parity, and second and third parity in Swedish Holstein dairy cows were 0.76, 0.70, and 0.92, respectively (Carlén et al., 2004). The strong genetic correlations between milk yield and SCS in consecutive parities previously reported suggests increasing or decreasing milk yield or SCS in an individual parity would result in a similar increase or decrease in other adjacent parities. Therefore, the objective of the present study was to understand the phenotypic and genetic dynamics of lactation yields and SCS across parities in dairy cows and, in doing so, quantify the potential to alter the trajectory through breeding.

4.4 Materials and Methods

Estimated 305-day lactation yields, average milk composition, average SCC, ancestry, and calving date information were extracted from the national database managed by the ICBF; the 305-day lactation yields, average milk composition, and average SCC were estimated using the standard lactation curve method (Olori and Galesloot, 1999). Since all information was downloaded from a pre-existing national database, it was not necessary to obtain animal ethics committee approval prior to conducting this study.
4.4.1 Data edits

Estimated 305-day lactation yields, average fat and protein percentage, and average SCC were available for 1,890,902 cows (5,960,955 lactations), born between 2000 and 2015, inclusive, calving in 15,317 spring-calving herds; all cows calved between 2002 and 2019. Dairy herds were defined as spring-calving if >70% of cows calved between the months of January and June, inclusive (Ring et al., 2019). Records where cow parity was >10 were discarded, as were the records from cows without a known sire. First-parity cows recorded to have calved younger than 600 days of age were removed.

Furthermore, the median age at calving was calculated for each parity; 897,930 lactation records were discarded where cows calved more than 180 days before or after the parity median. For all remaining records, age at calving was categorised, within parity, into 6 groups, each 60 days in duration relative to the parity median age at calving. Lactation average SCC was normalised to SCS by calculating the logarithm, to base 10, of SCC. Individual 305-day milk, fat, and protein yield, fat and protein percentage, and SCS observations more than 3 standard deviations from the parity mean were removed. All data from an entire parity were discarded if one or more traits were missing; 88,960 lactation records were removed. Heterosis and recombination loss coefficients per cow were calculated as described previously by Ring et al. (2018). Heterosis was divided into 12 classes (0%, >0% and ≤10%, >10% and ≤20%, >20% and ≤30%, >30% and ≤40%, >40% and ≤50%, >50% and ≤60%, >60% and ≤70%, >70% and ≤80%, >80% and ≤90%, >90% and ≤99%, and >99%). Recombination loss was divided into 7 classes (0%, >0% and ≤10%, >10% and ≤20%, >20% and ≤30%, >30% and ≤40%, >40% and ≤50%, and >50%).

Cows were assigned to contemporary groups within herd based on calving dates using the algorithm currently used to generate contemporary groups for the Irish national genetic evaluations (Berry et al., 2013). Cows that calved within 10 days of each other were initially clustered together within each herd. Where <10 cows were clustered together, these cows were joined to an adjacent contemporary group within the same herd until each contemporary group had ≥10 records, with a maximum distance of 60 days between calving events in the same contemporary group. Records from contemporary groups with <10 records were removed. Records were not required in all preceding parities for a lactation record to be retained. Estimated 305-day yields,
average fat and protein percentage, and average SCS for 3,470,474 lactations from 1,162,469 dairy cows calving in 8,566 herds spring-calving herds remained. A random subset of 500 herds was chosen for analyses; 196,775 lactation yield records from 68,323 cows remained. After all edits, the average breed composition of all animals was 90.0% Holstein-Friesian, 3.2% Jersey, 0.7% Montbéliarde, 0.5% Norwegian Red, 0.1% Ayrshire, and 0.1% Brown Swiss. Pedigree information for all animals was traced back to the founder animals, and founders were assigned to 1 of 11 genetic groups, based on breed; there were 208,439 animals in pedigree.

4.4.2 Statistical analyses

Parity mean 305-day milk, fat, and protein yield, as well as fat and protein percentage and SCS were modelled using random regression animal models fitted across parities in ASReml (Gilmour et al., 2009). These random regression models were used to determine the parity in which a cow reached maximum milk, fat, and protein yield, highest average fat and protein percentage, and highest average SCS; they were also used to estimate the (co)variance components for each trait across parities. The random regression model fitted to all data was

\[ Y_{ijklmnopq} = CG_j + Het_k + Rec_l + Age_m + \sum_{n=1}^{3} b_n Parity^n + a_i \sum_{o=1}^{3} b_o Parity^o + PE_p \sum_{q=1}^{3} b_q Parity^q + e_{ijklmnopq} \]

where \( Y_{ijklmnopq} \) was the estimated 305-day milk, fat, or protein yield, fat or protein percentage, or SCS for cow \( i \); \( CG_j \) was the fixed effect of contemporary group \( j \); \( Het_k \) was the fixed effect for heterosis class \( k \) \((k=0 \text{ to } 11)\); \( Rec_l \) was the fixed effect for recombination loss class \( l \) \((l=0 \text{ to } 6)\); \( Age_m \) was the fixed effect for age class relative to the parity median \( m \) \((m=1 \text{ to } 6)\); \( \sum_{n=1}^{3} b_n Parity^n \) was the fixed effect \( n \)th order Legendre polynomial regression on parity number; \( a_i \sum_{o=1}^{3} b_o Parity^o \) was the random regression coefficient on parity number for the animal additive genetic effect where \( a_i \sim N(\mathbf{Qg}, \mathbf{A} \otimes \mathbf{G}) \), \( \mathbf{Q} \) was a matrix relating to animal with genetic groups, \( \mathbf{g} \) was a vector of genetic group means, \( \mathbf{A} \) was the additive animal genetic numerator relationship matrix, and \( \mathbf{G} \) was the covariance matrix of the additive animal regression
coefficients with order equal to the polynomial modelled. \( PE_p \sum_{q=1}^{3} b_q Parity^q \) was the random regression coefficient on parity number for the permanent environmental (cow) effect where \( PE_p \sim N(0, I \otimes C) \), \( I \) was the identity matrix and \( C \) was the covariance matrix of the cow random regression coefficients, and \( e_{ijklmnopq} \) was the residual term where \( e \sim N(0, I \sigma_e^2(parity)) \) and \( \sigma_e^2(parity) \) represents the residual variance and \( I \) the identity matrix. Residual variances were estimated separately for each parity. Residual variances were assumed homogenous within each parity but heterogeneous between parities.

The most parsimonious order for the fixed effect Legendre polynomial regression was determined by visually comparing the fit of a linear, quadratic, and cubic trend line to the mean lactation yield, milk composition and SCS per parity. A cubic polynomial was the most appropriate for all traits. The most parsimonious order of the random regression was determined using the Akaike Information Criterion, by comparing the estimated variance components for each order, and by investigating the eigenvalues of the genetic covariance matrix.

4.4.2.1 Phenotypic analyses

The parity and production level at which individual cows reached maximum 305-day milk, fat, and protein yield as well as the highest SCS were determined using the sum of each cow’s additive genetic and permanent environmental solutions from the random regression models. Linear regression models were used to estimate the relationship between first parity yields, composition or SCS, estimated from the animal solutions of the random regression models, and the yields, composition, or SCS in the parity of maximum yield, composition or SCS, also estimated from the random regression model.

4.4.2.2 Estimation of the genetic (co)variances and genetic correlations

The animal covariance functions were estimated as:

\[
\delta^2 = \Phi' K \Phi
\]

where \( \delta^2 \) was the animal covariance matrix for parity; \( \Phi \) was the matrix of Legendre polynomial regression coefficients, and \( K \) was the animal additive genetic covariance matrix estimated from the random regression model. The genetic
correlations between different parities for each trait and their respective standard errors were calculated as:

\[ r_{gi} = \frac{covar_{ij}}{\sqrt{var_i \times var_j}} \]

\[ SE_{ij} = \frac{1 - r_{gi}^2}{\sqrt{2}} \times \sqrt{\frac{SE_i \times SE_j}{h_i^2 \times h_j^2}} \]

where \( r_{gi} \) was the genetic correlation for a trait in parities \( i \) and \( j \); \( covar_{ij} \) was the genetic covariance between the trait in parities \( i \) and \( j \); \( var_i \) and \( var_j \) were the genetic variances for the trait in parities \( i \) and \( j \), respectively; \( SE_{ij} \) was the standard error associated with the genetic correlation of the trait between parities \( i \) and \( j \); \( h_i^2 \) and \( h_j^2 \) were the heritability estimates for the milk trait in parity \( i \) and \( j \), respectively; \( SE_i \) and \( SE_j \) were the standard errors associated with the heritability estimates of the trait in parity \( i \) and \( j \), respectively. The variance of genetic change between 305-day milk, fat and protein yield, fat and protein percentage, and SCS in consecutive parities was estimated from the respective genetic covariance matrices as:

\[ Var_{cij} = var_i + var_j - 2(covar_{ij}) \]

where \( var_{cij} \) was the genetic variance of change between lactations \( i \) and \( j \); \( var_i \) and \( var_j \) were the genetic variance associated with the trait under investigation in lactations \( i \) and \( j \), respectively; and \( covar_{ij} \) was the estimated genetic covariance for that trait between lactations \( i \) and \( j \).

Animal random regression solutions from the random regression models and the matrix of Legendre polynomial regression coefficients were used to calculate an EBV per animal for each parity; only cows reaching at least fifth parity were considered further. The fixed regression solutions were used to translate the EBV to predicted performance. The lifetime production of a cow for each trait was calculated by summing the EBV for each parity, up to and including the sixth parity.
4.5 Results

Summary performance statistics per parity are presented in Table 4.1; as 5% of records in the present study relate to cows in ninth and tenth parity, only the results relating to eighth parity and younger are presented. Of the cows retained after all edits, 81% of cows reached at least second parity and 65% of cows reached at least third parity. On average, 305-day milk, fat, and protein yield increased with increasing parity up to fifth parity. After a small reduction in the mean SCS between first and second parity, SCS consistently increased thereafter; median SCC per parity ranged from 65,000 cells/mL in second parity to 122,000 cells/mL in eighth parity. Mean fat and protein percentage varied by no more than 0.11 percentage units and 0.07 percentage units, respectively, between parities (Table 4.1).

The Akaike information criterion improved with each increasing polynomial order for the additive genetic term in the model; nonetheless, the fourth eigenvalue of cubic animal random regression explained less than 1.4% of the genetic variance for all traits. Hence, the quadratic regression was chosen as the most parsimonious for both the additive genetic and permanent environmental component for all traits.
Table 4.1. Number of records (n), raw means, and standard deviations (SD) for 305-day milk protein, and fat yield, protein and fat percentage, and somatic cell score (SCS) for parities 1 to 8.

<table>
<thead>
<tr>
<th>Parity</th>
<th>n</th>
<th>Milk yield (kg)</th>
<th>Mean</th>
<th>SD</th>
<th>Protein yield (kg)</th>
<th>Mean</th>
<th>SD</th>
<th>Fat yield (kg)</th>
<th>Mean</th>
<th>SD</th>
<th>Protein %</th>
<th>Mean</th>
<th>SD</th>
<th>Fat %</th>
<th>Mean</th>
<th>SD</th>
<th>SCS (log\text{_{10}} unit)</th>
<th>Mean</th>
<th>SD</th>
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<td>5.14</td>
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4.5.1 Phenotypic analyses

Of the cows in the present study, 91% of cows reached maximum 305-day milk yield in fifth parity (Appendix E). Of the remaining 9.0% of cows, 5.8% reached maximum milk yield in either fourth (3.7%) or sixth parity (2.0%). Similarly, 98.5% and 98.6% of cows reached maximum 305-day fat and protein yield in fourth, fifth, or sixth parity, respectively (Appendix E). Although 62.9% of cows reached their highest average protein percentage in third parity, 95.9% of cows reached their highest average fat percentage in first parity (Appendix E). In contrast to all yield and composition traits, 98.4% of cows reached their highest average SCS in eighth parity (Appendix E). When milk, fat, and protein yield in the parity of maximum yield were regressed on their respective first parity yields, each additional kilogram of milk, fat, and protein produced in first parity was associated with an additional 1.22, 1.20, and 1.22 kg of milk, fat, and protein, respectively, at maximum yield (Table 4.2). A 1 percentage unit increase in protein percentage in first parity was associated with a 1.1 percentage unit increase in protein percentage in the parity with the highest average protein percentage; the corresponding value for fat percentage was 1.0 units. A 1-unit increase in SCS in first parity was associated with a 1.2 unit increase in SCS in the parity with highest average SCS (Table 4.2). The correlation between maximum milk, fat, and protein yield, protein percentage, and SCS and their respective first-parity values were 0.89, 0.87, 0.87, 0.99, and 0.66, respectively.

Table 4.2. Regression coefficient (standard error in parentheses) and the root mean square error (RMSE) from the regression of milk, fat and protein yield, fat and protein percentage, and SCS in the parity of maximum production or highest average composition or SCS on their respective values in first parity; also included is the correlation between the independent and dependent variables.

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<tr>
<th></th>
<th>Regression coefficient (SE)</th>
<th>RMSE</th>
<th>Correlation</th>
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<tr>
<td>Milk yield (kg)</td>
<td>1.219 (0.0024)</td>
<td>292.411</td>
<td>0.89</td>
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<tr>
<td>Fat yield (kg)</td>
<td>1.197 (0.0026)</td>
<td>12.076</td>
<td>0.87</td>
</tr>
<tr>
<td>Protein yield (kg)</td>
<td>1.219 (0.0026)</td>
<td>9.872</td>
<td>0.87</td>
</tr>
<tr>
<td>Fat percentage (%)</td>
<td>0.998 (0.0001)</td>
<td>0.012</td>
<td>1.00</td>
</tr>
<tr>
<td>Protein percentage (%)</td>
<td>1.069 (0.0005)</td>
<td>0.022</td>
<td>0.99</td>
</tr>
<tr>
<td>SCS (log$_{10}$ unit)</td>
<td>1.231 (0.0054)</td>
<td>0.131</td>
<td>0.66</td>
</tr>
</tbody>
</table>
4.5.2 Variance components

The genetic variance explained by the first eigenvalue of the fitted random regression model was 83.9%, 81.4%, 74.8%, 98.5%, 96.4%, and 87.3% for 305-day milk, fat, and protein yield, fat and protein percentage, and SCS, respectively. Heritability estimates for 305-day milk, fat, and protein yield ranged from 0.31 (eighth parity) to 0.44 (fourth parity), from 0.28 (eighth parity) to 0.37 (fifth parity), and from 0.30 (eighth parity) to 0.37 (fourth parity), respectively (Figure 4.1). The heritability estimates for fat and protein percentage and SCS ranged from 0.47 (eighth parity) to 0.63 (first parity), from 0.62 (eighth parity) to 0.69 (sixth parity), and from 0.13 (second parity) to 0.23 (eighth parity), respectively (Figure 4.1). The genetic standard deviation for 305-day milk, fat, and protein yield was greatest in fifth parity (Figure 4.2). The genetic standard deviation for fat percentage, protein percentage and SCS was greatest in third, fifth, and eighth parity, respectively (Figure 4.2).

Figure 4.1. Heritability estimates for 305-day milk yield (kg), fat percentage (%), protein percentage (%), somatic cell score (log10 unit), 305-day fat yield (kg), and 305-day protein yield (kg). Standard error bars represent one standard error above and below the heritability estimate.
Figure 4.2. Additive genetic standard deviation estimates for 305-day (a) milk yield (kg; primary axis), somatic cell score (log_{10} units; secondary axis), and (b) fat yield (kg; primary axis), protein yield (kg; primary axis), fat percentage (%; secondary axis), and protein percentage (%; secondary axis).

The variance of genetic change in milk, fat and protein yield, protein percentage, and SCS between consecutive parities reduced with increasing parity up to between fourth and fifth parity and increased with each parity thereafter for all traits, whereas the variance of genetic change in fat percentage reduced with increasing parity up to between fifth and sixth parity (Figure 4.3). The variance of genetic change between parities was greatest between the first and second parity for all traits. Pairwise genetic correlations between 305-day milk yield among the different parities varied from 0.67 to 1.00 (Table 4.3), the strength of the genetic correlations being inversely related to the interval between the compared parities; this trend of weakening correlations as the parities compared diverged was also true for fat and protein percentage (Table 4.4), SCS (Table 4.3), and 305-day fat and protein yield (Appendix F).
Figure 4.3. The variance of genetic change between parities for (a) 305-day milk yield (kg^2; primary axis) and somatic cell score (log_{10} unit^2; secondary axis) and (b) 305-day fat yield (kg^2; primary axis), 305-day protein yield (kg^2; primary axis), fat percentage (%^2; secondary axis), and protein percentage (%^2; secondary axis).
Table 4.3. Genetic correlations (standard errors in parenthesis) between 305-day milk yield (kg) in different parities (above diagonal) and somatic cell score (log\(_{10}\) units) in different parities (below diagonal).

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Table 4.4. Genetic correlations (standard errors in parentheses) between 305-day fat percentage in different parities (above diagonal) and 305-day protein percentage in different parities (below diagonal).

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4.5.3 Eigenfunctions

The sign of the eigenfunction of the genetic covariance matrix associated with the largest eigenvalue (i.e., the intercept term) did not change across parities for any of the traits investigated (Figure 4.4). The eigenfunction associated with the second eigenvalue accounting for 13%, 15%, and 23% of the genetic variance for 305-day milk, fat, and protein yield was moderately curvilinear, with the sign changing in the second and again in the seventh parity for milk and fat yield, whereas the sign changed only once, in seventh parity, for protein yield (Figure 4.4). The second eigenvalue accounted for 1.0% and 2.7% of the genetic variance in fat percentage and protein percentage (Figure 4.4); whereas the sign of the second eigenfunction changed once for fat percentage in seventh parity, the sign of the second eigenfunction changed twice for protein percentage (i.e., in second parity and again in eighth parity). The second eigenvalue accounted for 9.1% of the genetic variance in SCS and the sign of the associated eigenfunction changed in eighth parity for SCS (Figure 4.4).

4.5.4 Estimated breeding values

Differences existed between cows in the height and shape of the EBV profiles across parities for all traits investigated (Figure 4.5). Differences in the shape of the EBV profiles per cow for milk, fat, and protein yield were minimal prior to third parity; after third parity, the steepness of the decline or incline in EBV for the yield traits varied greatly among individual cows (Figure 4.5). The shape of the EBV profile for SCS and the steepness of the decline or incline in EBV for the SCS varied greatly among individual cows.

The lifetime yield of a cow for each trait was calculated by summing the yield EBV for each parity up to and including the sixth parity. To determine if differences in the trajectory of each trait across parities exist between cows with similar expected lifetime yield, the 11 cows with expected lifetime yield closest to the median lifetime yield for each trait were compared. The shape of the EBV profiles was generally consistent between cows up to fifth parity for all traits with differences among cows evident thereafter (Figure 4.6).
Figure 4.4. Eigenfunctions associated with the largest, middle, and smallest eigenvalues for (a) 305-day milk yield, (b) somatic cell score, (c) fat percentage, (d) protein percentage, (e) 305-day fat yield, and (f) 305-day protein yield.
Figure 4.5. Estimated breeding values (EBV) for cows with the most extreme (diverse) EBV, when compared to all cows reaching ≥ 5th parity, for each parity for (a) 305-day milk yield, (b) somatic cell score, (c) fat percentage, (d) protein percentage, (e) 305-day fat yield, and (f) 305-day protein yield.
Figure 4.6. Estimated breeding values (EBV) for cows with median lifetime production values when compared to all cows reaching $\geq 5$th parity, in each parity for (a) 305-day milk yield, (b) somatic cell score, (c) fat percentage, (d) protein percentage, (e) 305-day fat yield, and (f) 305-day protein yield.
4.6 Discussion

Low milk yield and high SCS are frequently reported as primary reasons for dairy cow culling (Pinedo et al., 2010; Kerslake et al., 2018; De Vries and Marcondes, 2020). Identifying and selecting cows that maintain their maximum milk production as they age or cows that maintain low SCS with age could therefore reduce the pressure to cull prematurely, thus improving dairy cow longevity. Achieving these improvements in dairy cow longevity will result in a higher proportion of cows surviving to older parities (>sixth parity); hence, understanding the dynamics and trajectories of milk yield and SCS will become more important. Although previous studies have investigated the trajectory and persistency of yield within a lactation (Jakobsen et al., 2002; Togashi et al., 2008; Cole and Null, 2009), no study has yet specifically investigated the dynamics of milk production or SCS across parities. The objective of the present study was thus to understand the phenotypic and genetic dynamics of lactation yields and SCS across parities in dairy cows and, by doing so, quantify the potential to alter the trajectory through breeding.

Heifer rearing is a substantial cost to dairy producers representing 15 to 20% of total production costs on a dairy farm (Heinrichs, 1993). It has been estimated that the heifer rearing cost is not repaid until the heifer completes 1.63 lactations, although this is a function of milk price and input costs (Berry et al., 2015). Hence, extending cow productive life can have a favourable impact on reducing farm costs through a lesser requirement for replacement heifers. A more mature cow herd can also improve herd revenue; more mature cows yield more milk per lactation (Berry and Ring, 2020) and produce heavier male calves for sale (Dunne et al., 2021). Traditionally high replacement rate was a prerequisite for achieving rapid genetic gain. This no longer needs to necessarily be true in light of the advancements in both genomic evaluations and reproductive technologies as well as improvements in dairy cow reproductive performance (Berry et al., 2014a; García-Ruiz et al., 2016). If cow longevity increases, owing to improvements in female reproductive performance, then proportionally fewer replacements are needed in the first place. Next, with sexed semen (assuming good conception rates) and low heifer mortality, most, if not all, replacements could be generated just from maiden heifers. These heifers should not only be the genetically most elite in the herd but also the most fertile; if genomically tested, then the accuracy of their genetic evaluations would not be that much inferior to their mature
counterparts. Hence, with good cow longevity, genetic gain in a herd could be accelerated; whether this materialises can be deterministically quantified based on the dam-to-dam selection pathway outlined by Robertson and Rendel (1950a) populated with respective statistics (i.e., selection intensity, accuracy of selection, and generation interval). Having said this, replacement rate is a function of both involuntary (e.g., reproductive failure) and voluntary (e.g., low milk yield, high SCC) culling, and therefore, the latter needs to be afforded the same research effort as has been expended on improving (genetic merit for) dairy cow reproductive performance in the past few decades.

4.6.1 Improving longevity through maintaining high milk production

The mean milk, fat, and protein yield, as well as the fat and protein percentage per parity reported in the present study were similar to average yields reported elsewhere for Irish pasture-based dairy cows (Cobuci et al., 2011; Coffey et al., 2016; O’Sullivan et al., 2019). No previous studies have investigated whether inter-animal variation exists for the parity in which maximum milk yield or highest average composition is achieved. Whereas the majority of cows in the present study reached their maximum milk, fat, and protein yield in fifth parity, consistent with the mean parity yields previously reported for dairy cows (Guo et al., 2002; Yang et al., 2005; Lee and Kim, 2006; Torshizi et al., 2017), between 7% and 17% of cows reached their maximum yields in other parities. The proportion of cows that reached their maximum yields in parities other than fifth parity highlights the extent of the inter-animal variation that currently exists for the parity in which individual cows reach maximum yield.

The heritability estimates of milk, fat, and protein yields in each parity were similar to those previously reported for individual parities in Swedish Holstein cows (Carlén et al., 2004) and Uruguayan dairy cows (Frioni et al., 2017), and across parities in Irish dairy cows (Cromie et al., 1998; McParland et al., 2015). In the present study, the eigenfunctions (continuous functions formed by decomposing variance or covariance matrices; Kirkpatrick and Heckman, 1989) provided information on how milk production and SCS trajectories across parities could change in response to selection. Such eigenfunctions for milk yield, composition, and SCS across lactations have not been previously reported, although eigenvalues and eigenfunctions of
lactation yields within individual parities have been investigated previously (Togashi et al., 2008). The majority of the genetic variance in milk, fat, and protein yield across parities in the present study was attributable to the model intercept terms, suggesting that the greatest opportunity exists to alter the height of the profiles, which could increase yields in all parities equally. The strong genetic correlations observed between milk, fat, and protein yield in consecutive parities substantiate the high proportion of the genetic variance of all yield traits explained by the model intercept term. These strong genetic correlations are consistent with the moderate repeatability of yield traits across parities in dairy cows (Berry and McCarthy, 2012; Visentin et al., 2017; Costa et al., 2019). Additionally, the inverse relationship between the strength of the genetic correlations and the interval between parities compared agrees with previous studies using random regression models on milk yield (Zarnecki et al., 1991; Carlén et al., 2004; Frioni et al., 2017). The sometimes moderate genetic correlations between the same trait in different parities imply that the appropriate statistical modelling is necessary to generate accurate genetic evaluations, especially when older parity data are included in the evaluation.

Nevertheless, the EBV profiles of cows highlight the extent of inter-animal differences that exist for the rate of decline in genetic merit for milk yield and composition after maximum yield and highest average composition has been reached. Although it was necessary for cows to have achieved ≥5 lactations to identify these differences, it may be possible to estimate breeding values for milk yields for cows in earlier parities without the need for phenotypic records. Such estimated breeding values could enable producers to make breeding decisions for young cows based on predicted yields, therefore retaining genetically superior cows without slowing down genetic improvement. Given the sign of both the second and third eigenfunctions for all yield (and composition) traits changed across parities, there is potential to alter the shape of the yield profile, and therefore the persistency of yield with advancing parity number. If selection pressure was exerted on the second eigenfunctions for any of the yield traits, the persistency of production could be improved by increasing production in parities typically associated with lower yields and decreasing production in other parities. Togashi and Lin (2006) also suggested persistency of milk production, albeit within lactation, could be improved by exerting selection pressure on the second eigenfunction of milk production. Nonetheless, in the present study, the genetic
variation associated with the second eigenfunction of milk, fat, and protein yield accounted for just 13%, 15%, and 23% of the genetic variance, respectively. Therefore, in order to alter the shape of the milk, fat, and protein yield profiles a greater weight would need to be imposed on the second eigenfunctions.

4.6.2 Improving longevity through retaining low SCS in older cows

Mastitis is the most frequent and costly disease affecting dairy cows globally (Caraviello et al., 2005; Abebe et al., 2016) with the genetic correlations between clinical mastitis and SCS ranging from 0.37 to 0.70 (Pösö and Mäntysaari, 1996; Kadarmideen and Pryce, 2001); the large range in the genetic correlations between clinical mastitis and SCS may be a result of differences in the accuracy of the diagnosis of the mastitis phenotype. It is not surprising then that both mastitis and high SCS are frequently cited as independent reasons for dairy cow culling (Pinedo et al., 2010; Kerslake et al., 2018; De Vries and Marcondes, 2020); the contribution to culling policies is expected to grow in the future given the pressures being imposed on the more prudent use of antimicrobials in dairy cow production system (Crispie et al., 2004). The risk of culling due to high SCS or mastitis is reported to increase as dairy cows age (Pinedo et al., 2010; Kerslake et al., 2018), with the risk of culling due to high SCS or mastitis doubling between first and fifth parity (Kerslake et al., 2018). This increased risk of culling corresponds with a trend of increased SCS with each progressing parity reported in the present study and previously reported trends of increased SCS and rate of clinical mastitis in aging cows (Berry et al., 2007c; Walsh et al., 2007).

The heritability of SCS in younger parities (≤seventh parity) were similar to those reported for individual parities in Swedish Holstein cows (Carlén et al., 2004) and across parities in both Irish (Berry and McCarthy, 2012) and Italian dairy cows (Costa et al., 2019). The increased heritability of SCS in older parities has not been reported previously in dairy cows, as no study has reported the heritability of SCS in individual parities above parity 3. Furthermore, the eigenfunctions associated with the additive genetic covariance matrix of SCS across parities have not previously been reported. Similar to all milk yield and composition traits, the majority of the genetic variance of SCS (87%) was attributable to the model intercept term suggesting the greatest opportunity exists to alter (i.e., lower) the overall height of the SCS profile.
The strong genetic correlations between SCS in consecutive parities substantiate the high proportion of the genetic variance of SCS explained by the model intercept term and are in agreement with the moderate repeatability of SCS between parities (0.33 to 0.53; Berry and McCarthy, 2012; Costa et al., 2019). The inverse relationship between the strength of the genetic correlations and the interval between parities compared is also in agreement with Carlén et al. (2004), who used random regression models on SCS, albeit limited to Swedish Holstein cows in first to third parity.

As the risk of culling due to high SCS increases with age, the identification of cows with a genetic predisposition for higher SCS in later lactations could be useful for enacting bespoke management strategies, such as targeted dry cow therapy for cows with a known predisposition for high SCS. Such cows, with a genetic predisposition for higher SCS as they age, could be identified from their EBV profiles for SCS. Alternatively, dairy cow longevity could be improved by maintaining low SCS in older cows, which could be achieved by selecting cows that have a genetic predisposition to maintain low SCS even in older parities or by altering the height and shape of SCS profile; the advantage of this strategy rather than selection directly on cow longevity is the greater heritability of SCS implying a more accurate genetic evaluation for individual cows. The change in the sign of both the second and third eigenfunctions for SCS provides evidence that there is indeed potential to alter the shape of the SCS profile. If selection pressure was exerted on the third eigenfunction for SCS, SCS could be decreased between fifth and eighth parity; selecting for SCS using this eigenfunction could increase dairy cow longevity by reducing SCS in all older cows (up to eighth parity) when the risk of culling due to high SCS is increased. Nevertheless, given that the genetic variation associated with the third eigenfunction for SCS was limited (4%), in order to alter the shape of the SCS through selection, a greater weight would have to be imposed on this eigenfunction.
4.7 Conclusions

By estimating the trajectories of genetic merit for daughter milk yield and SCS of individual cows, the present study highlighted the extent of inter-animal variability that currently exists for the height and shape of the EBV profiles across parities. These EBV profiles of individual cows have the potential to assist dairy producers with management decisions, such as culling based on expected trajectory of future milk yields (Kelleher et al., 2015) or selective dry cow therapy for cows expected to have high SCS in the future. Additionally, the eigenfunctions of the covariance matrices of milk yield and SCS presented provide a strategy on how the trajectory of both milk yield and SCS could be altered to improve dairy cow longevity by reducing the requirement for culling due to low milk yield and high SCS, particularly in older parities.
Chapter 5: Re-assessing the importance of linear type traits in prediction genetic merit for survival in an aging Holstein-Friesian dairy cow population

5.1 Preface

At the time of thesis submission, this chapter was published in the Journal of Dairy Science (accepted May 1st 2022). The full reference is:


Formatting and referencing style has been edited for consistency throughout the thesis. Figures and table captions have been assigned with a chapter prefix and acknowledgements have been removed. All other aspects are consistent with the published manuscript.

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5.2 Abstract

The cumulative improvement achieved in the genetic merit for reproductive performance in dairy populations will likely improve dairy cow longevity; therefore, it is time to reassess whether linear type traits are still suitable predictors of survival in an aging dairy cow population. The objective of the present study was therefore to estimate the genetic correlations between linear type traits and survival from one parity to the next and, in doing so, evaluate if those genetic correlations change with advancing parity. After edits, 152,894 lactation survival records (first to ninth parity) were available from 52,447 Holstein-Friesian cows, along with linear type trait records from 52,121 Holstein-Friesian cows. A series of bivariate random regression models were used to estimate the genetic covariances between survival in different parities and each linear type trait. Heritability estimates for survival per parity ranged from 0.02 (SE = 0.004; first parity) to 0.05 (SE = 0.01; ninth parity). Pairwise genetic correlations between survival among different parities varied from 0.42 (first and ninth parity) to 1.00 (eighth to ninth parity), with the strength of these genetic correlations being inversely related to the interval between the compared parities. The genetic correlations between survival and the individual linear type traits varied across parities for 9 of the 20 linear type traits examined, but the correlations with only 3 of these linear type traits strengthened as the cows aged; these 3 traits were rear udder height, teat length, and udder depth. Given that linear type traits are frequently scored in first parity and are genetically correlated with survival in older parities, they may be suitable early predictors of survival, especially for later parity cows. Additionally, the direction of the genetic correlations between survival and rear udder height, teat length, and udder depth did not change between parities; hence, selection for survival in older parities using these linear type traits should not hinder genetic improvement for survival in younger parities.

5.3 Introduction

Longevity has been a focus of dairy cow research since the 1950s (Rendel and Robertson, 1950b) with longevity traits now included in most dairy cow breeding objectives (Cole and VanRaden, 2018; Egger-Danner et al., 2015). Improved dairy cow longevity is associated with increased profitability through a reduced need for
replacement heifers to maintain herd size, a greater average herd yield (Williams et al., 2022a), and a greater opportunity for voluntary culling (van Pelt et al., 2015); improved longevity is also likely to reduce the carbon footprint of milk production (Lahart et al., 2021). Although greater longevity was often associated with slowing down genetic gain, developments in reproductive (Holden and Butler, 2018) and genomic (Meuwissen et al., 2001; VanRaden, 2008) technologies enable the next generation to be derived from just the younger (genetically elite) females in the herd (Williams et al., 2022a). Nonetheless, selection for dairy cow longevity remains challenging as a cow’s true longevity is not known until she is culled (Veerkamp et al., 2001; van Pelt et al., 2015). Therefore, early predictors of phenotypic (Cruickshank et al., 2002; Kern et al., 2015) and genetic (Brotherstone et al., 1998; Cruickshank et al., 2002; Kern et al., 2015) merit for survival are useful.

Linear type traits, which are frequently measured during first lactation, visually assess a wide selection of physical characteristics within the expected biological extremes of a given breed (Berry et al., 2004; Manafiazar et al., 2016). Linear type traits are heritable and have been phenotypically and genetically correlated with measures of longevity in Holstein (Kern et al., 2015), Holstein-Friesian (Brotherstone et al., 1998), and Guernsey dairy cows (Cruickshank et al., 2002). Previous genetic correlations between Holstein-Friesian cow longevity and body size-related linear type traits, udder-related linear type traits, and feet and leg-related linear type traits ranged from −0.27 to 0.22, from −0.33 to 0.46, and from 0.05 to 0.21, respectively (Brotherstone et al., 1998). The genetic correlations between cow longevity and body size-related linear type traits, udder-related linear type traits, and feet and leg-related linear type traits ranged from −0.15 to −0.38, from 0.12 to −0.30, and from −0.02 to 0.21, respectively for Holstein dairy cows (Kern et al., 2015) and from −0.26 to 0.00, from −0.25 to 0.20, and from −0.10 to 0.06, respectively for Guernsey dairy cows (Cruickshank et al., 2002).

Owing to the tendency to cull dairy cows for infertility before reaching maturity, previously documented genetic correlations between longevity or survival and linear type traits were often restricted to relatively young cows (fifth or lower parity; Brotherstone et al., 1998; Cruickshank et al., 2002) or herds with short average productive lifespans (2.7 lactations; Kern et al., 2015). The cumulative improvement achieved in the genetic merit for reproductive performance in dairy cow populations
(Berry et al., 2014a; Cole and VanRaden, 2018; De Vries, 2020) will contribute to an aging herd; therefore, the suitability of linear type traits as predictors of the genetic merit for survival should be reassessed.

To date, no study has examined whether linear type traits are good predictors of genetic merit for survival in older cows. Therefore, the objective of the present study was to estimate the genetic correlations between linear type traits and survival from one parity to the next for Holstein-Friesian cows and, in doing so, to determine if those genetic correlations change with advancing parity. It was expected that some linear type traits could be more important genetic determinants of survival as cows age.

5.4 Materials and Methods

Calving date, pedigree information, and estimated 305-day milk yields, as well as linear type trait data, were obtained from the national database managed by the ICBF. As all information was acquired from a pre-existing national database, it was not necessary to obtain animal ethics committee approval before commencing this study.

5.4.1 Survival traits

Calving information was available for 1,959,423 Holstein-Friesian dairy cows calving in 40,437 herds; all cows were born between 1999 and 2008, inclusive, and calved for the first time in or before 2010. Only records from herds where ≤50% of the cows were registered with the breed society were retained; all calving records from the herdbook-registered cows in these herds were discarded. Records of cows without a known sire or where cow parity was >10 were discarded. Cows that calved for the first time younger than 600 days of age were removed. The median age at calving was calculated for each parity; where a cow calved more than 180 days from the parity median, the record was discarded. For all remaining records, age at calving was categorised, within parity, into 6 groups of 60 days in duration relative to the parity median. The entire records of an individual cow were discarded if any calving event before culling (i.e., last recorded calving) was missing after previous edits. Survival was defined for each parity (first to ninth parity) based on whether or not a cow calved in the next lactation. Estimated 305-day milk yield was available for approximately
70% of cows with survival records; 305-day milk yield records were removed if they were more than 3 standard deviations from the parity mean yield. After edits, survival records for 1,433,609 lactations (first to ninth parity) from 348,385 Holstein-Friesian cows were available. Heterosis and recombination loss coefficients per animal were calculated as described by Ring et al. (2018). Heterosis was divided into 12 classes (0%, >0 and ≤10%, >10 and ≤20%, >20 and ≤30%, >30 and ≤40%, >40 and ≤50%, >50 and ≤60%, >60 and ≤70%, >70 and ≤80%, >80 and ≤90%, >90 and ≤99%, and >99%). Recombination loss was divided into 7 classes (0%, >0 and ≤10%, >10 and ≤20%, >20 and ≤30%, >30 and ≤40%, >40 and ≤50%, and >50%).

5.4.2 Linear type trait edits

Linear type traits recorded by the Irish Holstein-Friesian Association were available from the ICBF national database. Records pertaining to 20 linear type traits recorded on 203,136 Holstein-Friesian cows were available. Each linear type trait was scored on a scale of 1 to 9 (Table 5.1) and classification was performed by a single professional classifier for a given herd on a given date. Differences between classifiers were accounted for by adjusting each linear type trait by the ratio of the standard deviation of each classifier in each year to the mean standard deviation of all other classifiers for each linear type trait, as described by Brotherstone (1994). Adjusting for differences between classifiers transformed the linear type trait scores from a discrete scale (1 to 9) to a continuous scale. Contemporary group for the linear type traits was defined as herd-date of inspection and contemporary groups with <10 cows were discarded.
<table>
<thead>
<tr>
<th>Linear type trait</th>
<th>Score</th>
<th>Mean</th>
<th>$\sigma_g$</th>
<th>$h^2$ (SE)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Body</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Angularity</td>
<td>Coarse</td>
<td>5.79</td>
<td>0.64</td>
<td>0.34 (0.01)</td>
</tr>
<tr>
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<td>Thin</td>
<td>4.78</td>
<td>0.72</td>
<td>0.22 (0.02)</td>
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<tr>
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<td>Shallow</td>
<td>5.62</td>
<td>0.55</td>
<td>0.24 (0.01)</td>
</tr>
<tr>
<td>Chest width</td>
<td>Narrow</td>
<td>5.15</td>
<td>0.68</td>
<td>0.24 (0.01)</td>
</tr>
<tr>
<td>Rump angle</td>
<td>High</td>
<td>4.12</td>
<td>0.68</td>
<td>0.34 (0.01)</td>
</tr>
<tr>
<td>Rump width</td>
<td>Narrow</td>
<td>5.44</td>
<td>0.55</td>
<td>0.22 (0.01)</td>
</tr>
<tr>
<td>Stature</td>
<td>Short</td>
<td>6.11</td>
<td>0.67</td>
<td>0.40 (0.01)</td>
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<tr>
<td>Udder</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Milking ease</td>
<td>Slow</td>
<td>5.80</td>
<td>0.14</td>
<td>0.02 (0.05)</td>
</tr>
<tr>
<td>Fore udder attachment</td>
<td>Loose</td>
<td>5.52</td>
<td>0.59</td>
<td>0.19 (0.01)</td>
</tr>
<tr>
<td>Rear teat placement</td>
<td>On outside</td>
<td>5.68</td>
<td>0.65</td>
<td>0.23 (0.01)</td>
</tr>
<tr>
<td>Rear udder height</td>
<td>Low</td>
<td>5.93</td>
<td>0.69</td>
<td>0.26 (0.01)</td>
</tr>
<tr>
<td>Teat length</td>
<td>Short</td>
<td>4.59</td>
<td>0.75</td>
<td>0.36 (0.01)</td>
</tr>
<tr>
<td>Teat placement (rear view)</td>
<td>Wide</td>
<td>4.21</td>
<td>0.49</td>
<td>0.19 (0.01)</td>
</tr>
<tr>
<td>Teat placement (side view)</td>
<td>Close</td>
<td>5.71</td>
<td>0.71</td>
<td>0.25 (0.01)</td>
</tr>
<tr>
<td>Udder depth</td>
<td>Below hocks</td>
<td>5.63</td>
<td>0.62</td>
<td>0.29 (0.01)</td>
</tr>
<tr>
<td>Udder support</td>
<td>Broken</td>
<td>5.90</td>
<td>0.44</td>
<td>0.14 (0.01)</td>
</tr>
<tr>
<td>Feet and leg</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bone quality</td>
<td>Thick</td>
<td>6.50</td>
<td>0.53</td>
<td>0.26 (0.01)</td>
</tr>
<tr>
<td>Foot angle</td>
<td>Shallow</td>
<td>5.04</td>
<td>0.35</td>
<td>0.09 (0.01)</td>
</tr>
<tr>
<td>Locomotion</td>
<td>Lame</td>
<td>5.72</td>
<td>0.29</td>
<td>0.08 (0.01)</td>
</tr>
<tr>
<td>Rear leg (side view)</td>
<td>Straight</td>
<td>5.39</td>
<td>0.35</td>
<td>0.11 (0.01)</td>
</tr>
</tbody>
</table>

**Table 5.1.** List of all linear type traits with explanation of measurement scale and the corresponding mean, additive genetic standard deviation ($\sigma_g$), heritability estimate ($h^2$; standard error in parenthesis).
5.4.3 Subset selection for statistical analyses

Only survival records from cows with at least one paternal half-sib linear classified were retained. The retained survival records were assigned to contemporary groups based on proximity in calving dates within herd using the algorithm currently used to generate contemporary groups for the Irish national genetic evaluations (Berry et al., 2013). Cows that calved within 10 days of each other were initially clustered together within each herd. Where <10 cows were clustered together, these cows were joined to an adjacent contemporary group within the same herd until each contemporary group had ≥10 records; a maximum duration of 60 days between calving events in the same contemporary group was allowed. Only contemporary groups with ≥10 records were retained. First, all survival data from herds where at least one cow had a linear type trait phenotype were retained. Individual cow survival information from an additional 852 herds were randomly selected. Similarly, all linear type trait information from herds where at least one cow had a survival phenotype were initially retained. Linear type trait data of cows in the linear type contemporary groups where at least one sire also had progeny with survival records were also retained; all additionally retained linear scores, however, had to have been undertaken in or before 2010.

After all edits, survival records were available for 152,894 lactations (first to ninth parity) from 52,447 Holstein-Friesian cows. Linear type trait records were available from 52,121 Holstein-Friesian cows, of which 1,394 also had a phenotype for survival in the data for analysis. Estimated 305-day milk yields were available for 105,742 lactations from 38,302 Holstein-Friesian cows, all with survival information.

5.4.4 Statistical analyses

The (co)variance components of survival were quantified using random regression animal models fitted in ASReml (Gilmour et al., 2009):

\[
Surv_{ijklmno} = CG_j + Het_k + Rec_l + AGE_m + \sum_{n=1}^{3} b_n Parity^n + a_i \\
* \sum_{o=1}^{3} b_o Parity^o + e_{ijklmno}
\]
where $Surv_{ijklmno}$ was the survival observation; $CG_j$ was the fixed effect of contemporary group $j$; $Het_k$ was the fixed effect for heterosis class $k$ ($k=0$ to 11); $Recl$ was the fixed effect for recombination loss class $l$ ($l=0$ to 6); $Age_m$ was the fixed effect for age class relative to the parity median $m$ ($m=1$ to 6); $\sum_{n=1}^{3} b_nParity^n$ was the fixed effect $n$th order Legendre polynomial regression on parity number; $\sum_{o=1}^{3} a_oParity^o$ was the random Legendre polynomial regression on parity number for animal, where $a_i \sim N(0,A \otimes G)$, $A$ was the additive animal genetic numerator relationship matrix, and $G$ was the covariance matrix of the additive animal regression coefficients with order equal to the polynomial modelled; the pedigree of all cows was traced back at least four generations, and $e_{ijklmno}$ was the residual term where $e \sim N(0,I \sigma^2_{e(\text{parity})})$ and $\sigma^2_{e(\text{parity})}$ represents the residual variance per parity and $I$ the identity matrix. No significant permanent environmental variance across lactation existed. Residual variances were estimated separately for each parity with no covariance assumed among parities. The (co)variance components of survival were also estimated having adjusted for differences in 305-day milk yield by including individual 305-day milk yield as a covariate in the random regression model.

The variance components for each linear type trait were estimating using the following model (Berry et al., 2004; Williams et al., 2022b):

$$y_{ijkl} = CG_j + Days\ in\ milk_k + calving\ month_l + a_i + e_{ijkl}$$

where $y_{ijkl}$ was the value of the linear type trait adjusted for differences between classifiers for cow $i$; $CG_j$ was the fixed effect of contemporary group $j$; $Days\ in\ milk_k$ was the fixed effect for days in milk at the time of classification and was classified into 30-day intervals ($k=1$ to 12); $calving\ month_l$ was the fixed effect for month of calving ($l=1$ to 12); $a_i$ was the additive random effect of cow $i$ where $a \sim N(0,A \sigma^2_a)$ and $\sigma^2_a$ represents the direct genetic variance and $A$ the numerator relationship matrix; the pedigree of all cows was traced back at least four generations, and $e_{ijkl}$ is the residual term where $e \sim N(0,I \sigma^2_e)$ and $\sigma^2_e$ represents the residual variance and $I$ the identity matrix.

The most parsimonious order for the fixed effect Legendre polynomial regression on parity for the survival analysis was determined by visually comparing the fit of a linear, quadratic, and cubic trend line to the mean survival per parity. The most parsimonious order of the random regression was determined using the Akaike
information criterion, by comparing the estimated variance components for each order, and by investigating the eigenvalues of the genetic covariance matrix.

The animal covariance function of survival was estimated as

$$\delta^2 = \Phi' K \Phi$$

where $\delta^2$ was the animal covariance matrix for parity; $\Phi$ was the matrix of Legendre polynomial regression coefficients, and $K$ was the animal additive genetic covariance matrix estimated from the random regression model.

A series of bivariate random regression models were used to estimate the genetic covariances between survival in different parities and each linear type trait; the fixed and random effects included in the bivariate models were those used in the univariate analyses. The covariance matrix between survival and each linear type trait were estimated as $M' K M$ where:

$$M = \begin{bmatrix} 1 & 0 & 0 \\ 0 & \Phi_1(1) & \Phi_n(1) \\ 0 & \Phi_1(...) & \Phi_n(...) \\ 0 & \Phi_1(9) & \Phi_n(9) \end{bmatrix}$$

$$K = \begin{bmatrix} \sigma^2_{\text{linear}} & \sigma^2_{\text{linear, surv}_1} & \sigma^2_{\text{surv}_1} \\ \sigma^2_{\text{linear, surv}_n} & \sigma^2_{\text{surv}_1} & \sigma^2_{\text{surv}_n} \end{bmatrix}$$

The genetic correlations, and their respective standard errors, between survival in different parities and between survival in different parities and each linear type trait were calculated as:

$$r_{gij} = \frac{\text{covar}_{ij}}{\sqrt{\text{var}_i \ast \text{var}_j}}$$

$$SE_{ij} = \frac{1 - r_{gij}^2}{\sqrt{2}} \ast \sqrt{\frac{SE_i * SE_j}{h_i^2 \ast h_j^2}}$$

where $r_{gij}$ was the genetic correlation between linear type trait $i$ scored in first parity and survival in parity $j$; $\text{covar}_{ij}$ was the genetic covariance between linear type trait $i$ and survival in parity $j$; $\text{var}_i$ and $\text{var}_j$ were the genetic variances for linear type trait $i$ and survival in parity $j$, respectively; $SE_{ij}$ was the standard error associated with the genetic correlation of the trait between linear type trait $i$ and survival in parity $j$; $h_i^2$ and $h_j^2$ were the heritability estimates for linear type trait $i$ and survival in parity $j$, respectively; $SE_i$ and $SE_j$ were the standard errors associated with the heritability estimates of linear type trait $i$ and survival in parity $j$, respectively.
5.5 Results

Mean survival per parity and the frequency distribution of survival records is shown in Figure 5.1 with the summary statistics for each linear type trait in Table 5.1; on average, mean survival between consecutive parities reduced by 0.03 with each increase in parity number. A cubic polynomial was the most appropriate order for the fixed regression to model survival per parity. Although the Log-likelihood was best for the quadratic polynomial for the random regression on the additive genetic component, the Akaike information criterion was lowest for the linear polynomial. Additionally, the third eigenvalue of the quadratic polynomial explained <0.01% of the genetic variance of survival; hence, a linear regression was chosen as the most parsimonious order to model the additive genetic component.

![Figure 5.1](image.png)

**Figure 5.1.** Mean survival per parity (line; primary axis) and the percentage of survival records per parity included in the analysis (bar; secondary axis).

5.5.1 Variance components

Heritability estimates of survival ranged from 0.02 (first parity) to 0.05 (ninth parity; Figure 5.2) and when adjusted for 305-day milk yield, the heritability estimates of survival ranged from 0.03 (first parity) to 0.06 (ninth parity; Figure 5.2). The genetic standard deviation for survival and survival adjusted for 305-day milk yield increased with each progressive parity (Figure 5.2). The first and second eigenvalues of the fitted
A random regression model explained 93 and 7% of the genetic variance of survival, respectively. The sign of the eigenfunction of the genetic covariance matrix of survival associated with the largest eigenvalue (i.e., the intercept term) did not change across parities, but the sign of eigenfunction associated with the linear term changed once, occurring in sixth parity.

![Figure 5.2](image)

**Figure 5.2.** Heritability estimates for survival (blue circle with solid line; primary axis), survival adjusted for 305-day yield (orange square with solid line; primary axis), and additive genetic standard deviation estimates for survival (blue circle with broken line; secondary axis), survival adjusted for 305-day milk yield (orange square with broken line; secondary axis). Standard errors bars represent one standard error above and below the heritability estimate.

The heritability estimates for the body, udder, and feet and leg-related linear type traits ranged from 0.22 to 0.40, from 0.02 to 0.36, and from 0.08 to 0.26, respectively (Table 5.1). The genetic standard deviation for body, udder, and feet and leg-related linear type traits ranged from 0.55 to 0.72, from 0.14 to 0.75, and from 0.29 to 0.53, respectively (Table 5.1).

Pairwise genetic correlations between survival at each parity varied from 0.42 to 1.00 (Table 5.2), with the strength of the genetic correlations being inversely related to the interval between the parities compared; this trend of weakening correlations as the distance between parities increased was also true when survival was adjusted for 305-day milk yield (Appendix G).
Table 5.2. Pairwise genetic correlations (above diagonal) and their respective standard errors (below diagonal) between survival in first to ninth parity.

<table>
<thead>
<tr>
<th></th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
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<th>7</th>
<th>8</th>
<th>9</th>
</tr>
</thead>
<tbody>
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<td>0.89</td>
<td>0.79</td>
<td>0.69</td>
<td>0.61</td>
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<td>2</td>
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<td>0.92</td>
<td>0.85</td>
<td>0.78</td>
<td>0.72</td>
<td>0.67</td>
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<tr>
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</tr>
<tr>
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5.5.2 Genetic correlations between survival and linear type traits

5.5.2.1 Body-related linear type traits

Of the 7 body-related linear type traits investigated, the genetic correlations between survival and 4 of the linear type traits changed with advancing parity; these traits were angularity, body depth, rump width, and stature with the genetic correlations between survival and these traits weakening as the cow aged (Figure 5.3). Nevertheless, angularity, body depth, and stature were all moderately negatively genetically correlated with survival across all parities (Figure 5.3), suggesting shorter cows with shallower bodies and less angular ribs were more likely to survival in all parities. Good BCS was positively genetically correlated with survival across all parities (Figure 5.3; 0.32 in first parity to 0.43 in fifth parity).

5.5.2.2 Udder-related linear type traits

The genetic correlations between survival and 4 of the 10 udder-related linear type traits investigated changed with advancing parity; these traits were rear udder height, teat length, udder depth, and udder support. Udder support was the only udder-related linear type trait that became less correlated with survival as cows aged (Figure 5.4); having poorer udder support in young parities was favourably associated with survival, whereas udder support was not correlated with survival in older cows (Figure 5.4). Having a greater distance between the bottom of the vulva and the top of the rear udder relative to the height of the cow (i.e., lower rear udder height scores) was favourably associated with survival in each parity with the strength of the association increasing with progressive parities (Figure 5.4). Similarly having shorter teats and shallower udders were favourably associated with survival in all parities after first parity; the strength of the correlations between survival and both teat length and udder depth were weakest in first parity (i.e., −0.06 and 0.07, respectively) and strongest in eighth (−0.24) and ninth (0.29) parities (Figures 5.4 and 5.5). Of the remaining udder-related linear type traits, teat placement (side view) and rear teat placement were consistently moderately genetically correlated with survival across parities (Figures 5.4 and 5.5); front teats that were relatively close to the rear teats (teat placement side view) and rear teats that were relatively further apart (rear teat placement) were all favourably associated with survival.
Figure 5.3. Genetic correlations between survival in each parity and (a) angularity, (b) body condition score, (c) body depth, (d) chest width, (e) rump angle, (f) rump width, and (g) stature. Standard error bars represent one standard error above and below the genetic correlation.
Figure 5.4. Genetic correlations between survival in each parity and (a) milking ease, (b) fore udder attachment, (c) rear udder height, (d) udder depth, and (e) udder support. Standard error bars represent one standard error above and below the genetic correlation.
Figure 5.5. Genetic correlations between survival in each parity and (a) rear teat placement, (b) teat length, (c) front teat placement (rear view), and (d) front teat placement (side view). Standard error bars represent one standard error above and below the genetic correlation.

5.5.2.3 Feet and leg-related linear type traits.

Of the 4 feet and leg-related linear type traits, only the genetic correlations between locomotion and survival changed as cows aged. The genetic correlations between locomotion and survival ranged from −0.19 in first parity to 0.10 in ninth parity (Figure 5.6). The genetic correlations between foot angle and survival and between rear legs and survival were very weak, irrespective of parity (Figure 5.6).
5.6 Discussion

Progressive age-related deterioration in health and fitness is common across most animal species (Padilla et al., 2021), including dairy cows (Costagliola et al., 2016; Jamali et al., 2018). Reduced muscle mass (i.e., sarcopenia) is a major health concern in the elderly human population (Cruz-Jentoft et al., 2010) and has also been observed in older dairy cows (≥15 years old; Costagliola et al., 2016). Although many dairy cows may not survive long enough to be culled due to sarcopenia, age-related deterioration also contributes to mastitis (Jamali et al., 2018), which is commonly reported as the main reason for culling in older dairy cows (Pinedo et al., 2010; Kerslake et al., 2018; Wondatir Workie et al., 2021). Given the age-related anatomical changes previously reported in dairy cows (Costagliola et al., 2016), it is not surprising that the results of several studies, including the present study, suggest survival may not be the same trait across the entire lifetime of a dairy cow (Veerkamp et al., 2001; van Pelt et al., 2015). Irrespective of this, many studies still suggest linear type traits

Figure 5.6. Genetic correlations between survival in each parity and (a) bone quality, (b) foot angle, (c) locomotion, and (d) rear legs (side view). Standard error bars represent one standard error above and below the genetic correlation.
may be useful predictors of the genetic merit of survival across the lifetime of dairy cows due, in part, to the difficulties of actually measuring true longevity (Kern et al., 2015; Novotný et al. 2017; Khansefid et al., 2021). The motivation for the present study was to determine whether the genetic correlations between linear type traits and survival from one parity to the next change with advancing parity, as no previous study had assessed whether the relationships between linear type traits and survival change as dairy cows age. As expected, in the present study as dairy cows aged, some linear type traits associated with the genetic merit for mastitis and SCC (Seykora and McDaniel, 1986; Němcová et al., 2007; Bobbo et al., 2019) become more important genetic determinants of survival. Nonetheless, the genetic correlations between feet and leg-related linear type traits and survival that were expected to strengthen as cows aged were, in fact, not good determinants of the genetic merit of survival in older dairy cows.

5.6.1 Genetic merit for dairy cow survival in individual parities

Although most dairy cow breeding objectives already include some measures of longevity or survival, many only consider survival and longevity data from relatively young parities (Interbull, 2021), and therefore may not consider whether survival in older cows is the same trait as survival in young dairy cows. In the present study, the moderate genetic correlations between survival in parities distant from one another suggests that, indeed, survival is not genetically the same trait across the entire lifespan of dairy cows. Additionally, the large range in the genetic correlations between survival in different parities suggests that different factors, such as linear type traits, may govern the genetic merit of survival as the dairy cow ages. Although the genetic correlations between survival in parities distant from one another were only moderate, most of the genetic variance in survival across parities was attributable to the model intercept term (93%). The proportion of the genetic variance of survival explained by the intercept term suggests that the greatest opportunity exists to alter the height of the survival profile, which could increase the genetic merit for survival in all parities equally.
5.6.2 Linear type traits that become more important to the genetic merit for survival as cows age

Mastitis disproportionately affects older dairy cows, with the risk of culling due to high SCC or mastitis doubling between first and fifth or greater parity (Kerslake et al., 2018). The increased risk of culling due to mastitis and SCC corresponds with a trend of increased estimated breeding values for somatic cell score with each progressive parity (up to eighth parity; Williams et al., 2022a). Given the increased risk of culling due to mastitis in older cows, and the only moderate genetic correlations between survival in different parities, it was expected that some of the linear type traits previously associated with genetic merit for mastitis resistance or low SCS would strengthen in association with survival in older dairy cows. The linear type traits (udder depth, teat length, and rear udder height) that strengthened in genetic correlation with survival as cows aged in the present study have all previously been associated with genetic merit for mastitis or SCC in dairy cows (Seykora and McDaniel, 1986; Němcová et al., 2007; Bobbo et al., 2019). The combination of a deterioration in the intramammary and anatomical defence mechanisms in aging cows (Jamali et al., 2018) along with poor udder characteristics may put older cows at a greater risk of developing intramammary infections, and therefore, being culled. Deeper udders and longer teats are closer to the ground contributing to an increased tendency for the udder and teats to become contaminated with mastitis-inducing environmental pathogens (Bharti et al. 2015; Bobbo et al., 2019). As with shallower udders and shorter teats, the association between having a smaller distance between the vulva and the top of the rear udder may result in an increased risk of mastitis, due to the udder becoming more susceptible to coming in contact with, and thus contaminated with, pathogens from faeces. Although age-related deterioration in the intramammary and anatomical defence mechanisms of cows is difficult to prevent or reduce, there may be potential to improve the genetic merit for survival, particularly in older cows, by improving the genetic merit for udder-related linear type traits. Given udder depth, teat length, and rear udder height were moderately heritable, moderately genetically correlated with survival, and can be scored in first parity, they may be suitable early predictors of genetic merit for survival in older cows. Additionally, the direction of the genetic correlations between survival and rear udder height, teat length, and udder depth did not change between parities; hence, selection for survival in older parities using these linear type traits should not hinder survival in younger parities.
5.6.3 Linear type traits that become less important to the genetic merit for survival as cows age

There are two potential reasons why the genetic correlations between survival and some linear type traits weakened as dairy cows aged, either the linear type trait actually became less important to the genetic merit for survival in older cows, or the linear type trait which was scored in first parity no longer accurately reflected the characteristic it measured in older cows. In the present study, the latter is likely true for locomotion, which was expected to become more strongly genetically correlated with survival over time, as detected for the three udder-related linear type traits in the present study. Good locomotion (i.e., no signs of compromised locomotive ability) is important to dairy cow survival particularly in older cows, as evidenced by the increase in culling due to feet and leg issues, including poor locomotion, reported in older dairy cows (Pinedo et al., 2010; Kerslake et al., 2018). The emphasis on good locomotion is even greater in pasture-based systems, as cows must be able walk to and from a milking parlour twice daily to avoid culling. The disparity between the expected and the actual genetic correlations between survival and locomotion in the present study is likely due to changes in locomotion associated with aging and wear in older dairy cows. Aging and wear can impair the shape and cause softening of the horn and internal structures of the feet of dairy cows (Rowlands et al., 1985; Weber et al., 2013); as a result, locomotion scored in first parity may be irrelevant to actual locomotion and lameness in older dairy cows. Nonetheless, if locomotion was scored in individual parities rather than in only the first parity, as in the present study, the suitability of locomotion as a predictor of the genetic merit for survival may be improve.

5.6.4 Linear type traits equally important to the genetic merit for survival as cows age

Although the genetic correlations between survival and some of the linear type traits changed as cows aged, the majority of the linear type traits remained equally important to survival regardless of cow parity. The consistent genetic correlations between these linear type traits (i.e., BCS, chest width, rump angle, milking ease, fore udder placement, front and rear teat placement, bone quality, foot angle, and rear leg side view) and survival suggests that these traits might be the least affected by progressive age-related deterioration. Of all the traits equally genetically correlated
with survival over time, good BCS was the most favourably genetically correlated with survival in all parities, suggesting that BCS, scored in first parity, may be a suitable early predictor of the genetic merit for survival in all parities. Body condition score visually assessed, as part of linear type trait assessment, in first parity dairy cows was reported be to strongly genetically correlated with body condition scored by producers using both tactile and visual cues even when the records of cows up to parity 15 were included (0.90; Berry et al., 2021). The association between BCS and the genetic merit for survival in the present study is likely a reflection of the positive phenotypic and genetic associations between good BCS and fertility previously reported in dairy cows (Pryce et al., 2001; Roche et al., 2007).

Although traits associated with age-related deterioration may account for a high proportion of the voluntary culling reported in older dairy cows, poor fertility has been reported as a reason for culling in all parities (Pinedo et al., 2010; Kerslake et al., 2018; Wondatir Workie et al., 2021). Therefore, any genetic evaluation for survival using proxy measurements should include a balance of traits, which could improve the genetic merit for survival at all ages by negating culling for both voluntary and involuntary reasons. Alternatively, given the differences in the genetic correlations between some linear type traits and survival in different parities in the present study, it may be appropriate to implement separate genetic evaluations for survival in young and older dairy cows.

5.7 Conclusions

By estimating the genetic correlations between linear type traits and survival in individual parities, the present study has identified several linear type traits that strengthen in importance as contributors to genetic merit for survival as dairy cows aged. The cumulative improvement achieved in the genetic merit for reproductive performance is contributing to improving dairy cow longevity; therefore, culling due to age-related deterioration in the intramammary and anatomical defence mechanisms of cows will likely become more common. Incorporating linear type traits that are more strongly genetically correlated with survival in older cows or using multitrait random regression models, which account for the variation in the relationship between
survival over time, could improve the accuracy of predictions of the genetic merit of survival in older dairy cows.
Chapter 6: Thesis Summary and Conclusions
6.1 Thesis Summary

The overall objective of this thesis was to determine the potential to improve the production efficiency of dairy cows through genetic selection. This thesis objective was achieved by:

1) determining the suitability of body-related linear type traits as predictors of the genetic merit for feed intake in grazing Holstein-Friesian cows (Chapter 2)
2) quantifying the genetic variation that exists in lactation length and the potential to increase the proportion of dairy cows that lactate for 305 days (Chapter 3)
3) identifying differences in the genetic trajectory of milk yield and somatic cell score (SCS) across parities and determining the potential to alter the shape of these trajectories especially minimising the reduction in yield and increase in SCS with age (Chapter 4)
4) determining that survival throughout the lifetime of dairy cows is not the same genetic trait and, therefore, indicators traits that could be used to predict survival in young parities may differ from those suitable for older parities (Chapter 5)

Cows that achieve 305-day lactations and/or have longer productive lives are more efficient and, therefore, are expected to be less economically and environmentally expensive. The potential to improve the production efficiency of grazing dairy cows, by genetically selecting for longer and more lactations with minimal reduction in performance with age has not been quantified previously. This thesis demonstrated that exploitable genetic variation indeed exists for several efficiency-related traits suggesting there is potential to breed for improved lifetime production efficiency by lengthening lactations (Chapter 3) and achieving more lactations per cow (Chapter 5) while, at the same time, not necessarily reducing milk yield or increasing SCS as cows get older (Chapter 4). Additionally, this thesis demonstrated the usefulness of some linear type traits as predictors of the genetic merit for survival (Chapter 5), particularly in older cows, but concluded that linear type traits have limited use as predictors of the genetic merit for DMI in grazing Holstein-Friesian dairy cows (Chapter 2).

The following summarises the objectives, primary materials and methods, results and conclusions of each chapter:
Chapter 1: Literature review

- There is no one agreed definition of dairy cow production efficiency; individual dairy cow production efficiency can be estimated at the level of the lactation (i.e., residual feed intake and lactation length) or a lifetime (i.e., milk production per day of age and longevity).

- No production efficiency metric is without disadvantages, with many metrics being difficult to measure or not suitable for inclusion in selection indexes.

- Most production efficiency metrics are reported to be lowly to moderately heritable and exhibit exploitable genetic variation.

- Few national dairy cow selection indexes explicitly include efficiency traits.

- Relative to confined dairy cows, pasture-based dairy cows tend to be less production efficient due to lower quality feed and the restrictions associated with seasonal calving systems; additionally, measuring some components of production efficiency traits can be more difficult in grazing dairy cows.

- Linear type traits are genetically correlated with both dairy cow DMI in confinement systems and several measures of survival/longevity in young dairy cows.

- Gaps in knowledge include:
  - Whether linear type traits explain any of the genetic variation in DMI over and above that already explained by body weight, or whether the expected predictive ability for DMI derived from a multi-trait genetic evaluation with linear type traits materialise in a validation population.
  - The average lactation length of Irish dairy cows and the genetic and non-genetic factors associated with lactation length in pasture-based dairy cows.
  - The trajectories of milk production and SCS across parities, and the potential to alter these trajectories genetically.
  - Whether the genetic correlations between linear type traits and survival change as dairy cows age.
Chapter 2: Are subjectively scored linear type traits suitable predictors of the genetic merit for feed intake in grazing Holstein-Friesian dairy cows?

Objective: To estimate the genetic correlations between readily available body-related linear type traits and DMI in grazing lactating Holstein-Friesian cows, and to estimate the partial genetic correlations between these linear traits and DMI, after adjusting for differences in genetic merit for body weight.

- A total of 8,055 test-day records of DMI and body weight from 1,331 Holstein-Friesian cows were available, along with chest width, body depth, and stature assessments on 47,141 first lactation Holstein-Friesian cows.
- Four novel composite traits were defined as the product of the linear type traits as an approximation of rumen volume.
- Genetic and phenotypic covariances between both body weight and each type trait with DMI were calculated using bivariate sire linear mixed models.
- The partial genetic correlation between DMI and each linear type trait, adjusted for genetic differences in body weight, were calculated.
- A series of multi-trait animal genetic evaluations for DMI were undertaken with body weight and/or one linear type trait to validate the usefulness of linear type traits as predictor traits of genetic merit for DMI.
- All linear type traits were moderately heritable, with heritability estimates ranging from 0.27 to 0.49.
- All linear type traits were genetically correlated (0.29 to 0.63) with DMI but, when adjusted for genetic differences in body weight, the genetic correlations between the individual linear type traits and DMI varied from -0.51 (stature) to 0.48 (chest width).
- In a validation population of 1,747 records from 246 cows, estimated genetic merit of DMI derived from a multi-trait genetic evaluation of linear type traits did not correlate strongly with actual DMI; the benefit was even less if body weight data were also available.
- In conclusion, although the genetic correlations between DMI and linear type traits across lactation suggested linear type traits might be suitable proxy measures for DMI, the expected improvement in the prediction of DMI from the inclusion of information on linear type trait did not materialise.
Chapter 3: Genetic and non-genetic factors associated with lactation length in seasonal-calving pasture-based dairy cows.

Objective: To identify the genetic and non-genetic factors associated with lactation length in a seasonal pasture-based dairy cow production system.

- A total of 616,350 lactation length records from 285,598 Irish dairy cows were available.
- Linear mixed models were used to quantify the associations between lactation length and both cow and herd level factors, as well as to estimate the genetic variance components for lactation length.
- Animal estimated breeding values (EBV) for lactation length were averaged per year to generate genetic trends.
- The median lactation length was 288 days, with only 27% of cows achieving lactations of at least 305 days.
- Relative to cows calving in January, the lactation of a cow calving in February, March, or April was, on average, 4.2, 12.7, and 21.9 days shorter, respectively.
- The lactation length of a first parity cow was, on average, 7.8, 8.6, and 8.4 days shorter than that of second, third, and fourth parity cows, respectively.
- Norwegian Red and Montbéliarde cows had, on average, a 4.7 and 1.6-day shorter lactation than Holstein-Friesian cows, respectively.
- The heritability estimate, genetic standard deviation, and repeatability estimate of lactation length were 0.02, 3.3 days, and 0.04, respectively.
- The EBV for lactation length of a Holstein-Friesian cow born in 2015 was, on average, 3.75 days higher than cows born in 2000. The average increase in the EBV for lactation length was 0.25 days/year for Holstein-Friesian cows.
- Based on the estimated genetic standard deviation of lactation length, the top 20% of cows ranked on genetic merit for lactation length would be expected, on average, to have a 9.2-day longer lactation than cows in the bottom 20%.
- In conclusion, given the vast array of genetic and non-genetic factors associated with lactation length, an approach that combines improved management practices and selective breeding may be an efficient and effective strategy to lengthen lactation periods.
Chapter 4: Exploiting genetic variability in the trajectory of lactation yield and somatic cell score with each progressing parity.

Objective: To understand the phenotypic and genetic dynamics of lactation yields and SCS across parities in dairy cows and, in doing so, quantify the potential to alter the trajectory through genetic selection.

- A total of 3,470,520 305-day milk, fat, and protein yields, as well as milk fat and protein percentage and SCS records from 1,162,473 dairy cows were available.
- Random regression models were used to identify the parity in which individual cows reached their maximum lactation yields and highest average milk composition and SCS; also estimated from these models were the (co)variance components for yield, composition, and SCS per parity.
- On average, 91%, 92%, and 83% of cows reached maximum milk, fat, and protein yield in fifth parity, respectively; 98% of cows reached their highest average SCS in eighth parity (the oldest parity considered).
- Individual parity estimates of heritability for milk yield traits, milk composition, and SCS ranged from 0.28 to 0.44, from 0.47 to 0.69, and from 0.13 to 0.23, respectively.
- The strength of the within-trait genetic correlations among parities was inversely related to the interval between the parities compared.
- Differences existed between cows in the height and shape of the EBV profiles across parities for all milk production and SCS traits.
- Eigenvalues and eigenfunctions of the additive genetic covariance matrices for all investigated traits revealed potential to alter the trajectory of parity profiles for milk yield, milk composition, and SCS.
- The EBV profiles of individual cows have the potential to assist dairy producers with management decisions, such as culling based on expected trajectory of future milk yields or selective dry cow therapy.
- To conclude, potential exists to improve the longevity of dairy cows by altering the trajectory of milk production and SCS using eigenvalues and eigenfunctions, and by exploiting the existing inter-animal differences in EBV profiles of milk production.
Chapter 5: Re-assessing the importance of linear type traits in predicting genetic merit for survival in an aging Holstein-Friesian dairy cow population.

Objective: To estimate the genetic correlations between linear type traits and survival from one parity to the next for Holstein-Friesian cows and, in doing so, determine if those genetic correlations change with advancing parity.

- A total of 152,894 lactation survival records (1st to 9th parity) were available from 52,447 Holstein-Friesian cows, along with linear type trait records from 52,121 Holstein-Friesian cows.
- A series of bivariate random regression models were used to estimate the genetic covariances between survival in different parities and linear type traits.
- Pairwise genetic correlations between survival in different parities varied from 0.42 (1st and 9th parity) to 1.00 (8th to 9th parity), with the strength of these genetic correlations being inversely related to the interval between the compared parities.
- The less than unity genetic correlations between survival in different parities suggests that different factors, such as linear type traits, may govern the genetic merit of survival as the dairy cow ages.
- The genetic correlations between survival and the individual linear type traits varied across parities for nine of the 20 linear type traits examined, but only the genetic correlations with rear udder height, udder depth, and teat length strengthened as the cows aged.
- The linear type traits that become more strongly genetically correlated with survival as cows aged in the present study have all previously been associated with genetic merit for mastitis and/or somatic cell count in dairy cows.
- Given linear type traits are frequently scored in first parity and are genetically correlated with survival in older parities, they may be suitable early predictors of survival, especially for older cows.
- In conclusion, incorporating linear type traits that are more strongly genetically correlated with survival in older cows and/or using multi-trait random regression models, which account for the variation in the relationship between survival over time, could improve the accuracy of prediction of the genetic merit of survival in older dairy cows.
6.2 Thesis Conclusions and Implications

The main objectives of this thesis were to quantify the genetic variance components of dairy cow efficiency metrics; including DMI, lactation length, lactation yields, and survival, and to quantify, in particular, the usefulness of linear type traits in predicting genetic merit for many of these efficiency traits. Results from this thesis have demonstrated that potential exists to improve the production efficiency of lactating dairy cows by several complementary additive and even multiplicative strategies, including the lengthening of lactations (Chapter 3) and improved longevity (Chapter 5), without necessarily reducing productivity (Chapter 4). Additionally, this thesis highlights that while some linear type traits may be suitable early predictors for survival in older parities (Chapter 4), their usefulness as predictors of the genetic merit for feed intake in grazing dairy cows is limited (Chapter 2). Therefore, the primary implication of this work is that it provides potential strategies to aid in the genetic selection for more production-efficient dairy cows. The practical implications of increasing the proportion of dairy cows achieving the desired production efficiency targets, via the breeding strategies proposed in this thesis, include helping to ensure dairy producers remain economically sustainable, while continuously reducing the environmental footprint of dairy production by diluting the footprint over a greater volume of higher quality milk.

6.2.1 Current and future trajectories for production efficiency traits

Previous studies in dairy cows have demonstrated that the phenotypic and genetic trends for dairy production efficiency-related traits are already favourable (Lopez-Villalobos et al., 2021; Strapáková et al., 2019). The positive trend for the genetic merit for lactation length in Irish Holstein-Friesian dairy cows reported in Chapter 3 and the positive phenotypic trends for lactation length and overall longevity presented in Figures 6.1 and 6.2 further demonstrate that the trends for genetic and phenotypic merit for production efficiency-related traits are improving. When the phenotypic trends for lactation length and longevity (i.e., productive lifespan) were estimated for Irish Holstein-Friesian dairy cows, using similar data to those in Chapter 3 and 5, an Irish Holstein-Friesian cow born in 2015 was expected to have an 19-day longer lactation than a cow born in 2000 (Figure 6.1), and over the ten year period
between 1999 and 2008, the longevity of Holstein-Friesian dairy cows increased annually by, on average, 0.05 years (Figure 6.2).

![Figure 6.1. Phenotypic trend for fifth parity lactation length of Holstein-Friesian dairy cows that reached at least fifth parity and were born between 2000 and 2015 (blue) and the expected phenotypic trend for fifth parity lactation length for Holstein-Friesian dairy cows born between 2016 and 2025 estimated using linear extrapolation from the previous sixteen years (purple).](image)

Despite these year-on-year improvements in dairy production efficiency-related traits, the target of achieving an average productive lifespan of 5.5 lactations will not be achieved in the near future unless changes, such as increasing the emphasis on longevity or including traits important to survival in older cows, are made to current breeding programs. Based on the current phenotypic trends for lactation length and longevity (Figure 6.1 and 6.2), Holstein-Friesian heifers born in 2020 that achieve five lactations would be expected to lactate for 305 days, however, it will be 2031 before newly born Holstein-Friesian heifers would be expected to achieve an average productive life of 5.5 lactations. In contrast to longevity, based on two recently published Irish studies (Evers et al., 2021; Berry and McCarthy, 2021), Irish dairy cows are already close to achieving an average of one kg of milk solids per kg of body
weight, which is the third dairy production efficiency target frequently cited by Irish dairy producers (Chapter 1).

Despite lactation length not being included in the Irish dairy cow breeding goal, phenotypic and genetic merit for lactation length of Holstein-Friesian cows have both improved (Figure 6.1; Chapter 3). The improvement observed in lactation length to date, which was also observed in the difference between the average lactation length in Chapter 3 (288 days) and the average lactation length (265 days) reported by Evans et al. (2006) fourteen years earlier, may reflect the improvement achieved in fertility with Irish dairy cows now calving earlier and being dried-off later each year (Figure 6.3). The fertility sub-index of the total merit index for Irish dairy cows, which includes calving interval and survival, is favourably correlated with both calving date ($r=0.16$) and dry-off date ($r=0.10$) in multiparous Holstein-Friesian cows. This suggests that current breeding objectives may be improving lactation length without directly selecting for it. These correlations suggest that Irish Holstein-Friesian cows

**Figure 6.2.** Phenotypic trend for longevity of Holstein-Friesian dairy cows born between 2000 and 2008 (blue) and the expected phenotypic trend for longevity for Holstein-Friesian dairy cows born between 2009 and 2025 estimated using linear extrapolation from the previous ten years (purple).
with high fertility sub-index values are more likely to calve earlier and be dried off later than cows with low fertility sub-index values.

Although, the average lactation length of Irish dairy cows is 288 days (Chapter 3), the phenotypic trend for the lactation length of Holstein-Friesian cows reaching fifth parity has almost reach the target of 305 days (Figure 6.1). Nevertheless, the lactation length of other dairy cow breeds is expected to be up to 5 days shorter than Holstein-Friesian (Chapter 3), consequently, consideration should be given to improving both the phenotypic and genetic merit for lactation length. Substantial exploitable genetic variation in lactation length was identified in Chapter 3. In fact, based on the genetic standard deviation of 3.3 days for lactation length (Chapter 3), the top 10% of cows on genetic merit for lactation length would be expected, on average, to have an 11.6-day longer lactation than cows in the bottom 10% for genetic merit for lactation length. Nonetheless, due consideration should be given to ensuring lactation length is not extended to the detriment of calving interval, particularly in seasonal pasture-based production systems where extending calving intervals beyond 365 days would make farms less efficient and profitable. In addition to genetic selection, the plethora of management factors associated with lactation length (Chapter 3) could also represent opportunities to lengthen lactations quickly and these management factors could also serve as a checklist for extension officers when exploring why a given herd reports relatively short lactations.
In contrast to lactation length, some measure of dairy cow survival/longevity is already included in most dairy cow breeding objectives globally (Egger-Danner et al., 2015; Cole and VanRaden, 2018; Chapter 1); hence, the year-on-year improvement in phenotypic longevity could be expected (Figure 6.2). At present, the rate of survival from one parity to the next tends to decrease as parity increases (Chapter 5) with survival ranging from 0.85 (survival from second to third parity) to 0.60 (survival from ninth to tenth parity). Therefore, if dairy cow longevity targets are to be achieved, the rate of survival from one parity to the next will need to improve, particularly in older parities. If the same proportion of cows could survive to each subsequent parity, an average of 5.5 lactations per cow could be achieved with a common survival rate of 86.6%. In Chapter 5, 84% and 85% of cows survived from first to second parity and from second to third parity, respectively. Therefore, increasing survival to the next parity to 86.6% should be rapidly achievable, at least in young cows. Conversely, only 65% of cows survived from eighth to ninth parity. Thus, achieving a survival rate of 86.6% in older parities will require achieving a much greater rate of improvement.

Improving the proportion of cows that survive from one parity to the next, particularly in older parities, would fundamentally rely on identifying how the factors

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**Figure 6.3.** Median calving date (blue) and dry-off date (purple) for spring-calving Irish Holstein-Friesians calving between 2000 and 2020.
contributing to culling differ between parities and potentially changing how survival is genetically selected for, particularly in older parities. Multiple studies have suggested that survival is not the same genetic trait throughout the lifetime of a dairy cow (Veerkamp et al., 2001; van Pelt et al., 2015), corroborated by the results in Chapter 5. Therefore, the factors that govern survival likely vary between parities. If longevity targets are to be achieved, dairy cows will need to live longer. In fact, 27% of cows would need to reach tenth parity in order to achieve an average herd productive lifespan of 5.5 lactations, assuming an 86.6% survival rate in each parity. Hence, due consideration should be given to improving the genetic and phenotypic merit for traits associated with culling in older dairy cows.

Age-related deterioration in health and fitness traits is common across many animal species (Padilla et al., 2021) including dairy cows (Costagliola et al., 2016; Jamali et al., 2018). The differences in the reported culling reasons for older dairy cows compared to younger dairy cows reflects this deterioration, with older cows more likely to be culled due to high SCS, or mastitis, than younger cows (Pinedo et al., 2010; Kerslake et al., 2018; Wondatir Workie et al., 2021). Therefore, reducing the incidence of high SCS and mastitis could improve the trajectory of survival in older cows. The eigenfunctions and EBV for parity-specific SCS identified in Chapter 4 could be used to select for dairy cows than maintain low SCS even in old parities thereby hopefully improving survival for one parity to the next in older cows.

Eigenvalues and associated eigenfunctions of the additive genetic covariance matrix provide some insight into the feasibility of altering the profile of a repeated trait through genetic selection (Kirkpatrick and Heckman, 1989). The size of the eigenvalue is indicative of how quickly the change depicted by the associated eigenfunction could happen if the eigenvalue is under selection (Berry et al., 2007b). Eigenvalues and eigenfunctions have been identified as potential strategies to improve the profiles of a wide range of longitudinal animal traits, including lactation persistency in both dairy cows (Van der Werf et al., 1998; Togashi and Lin, 2006) and dairy goats (Arnal et al., 2020), as well as growth trajectories in multiple species (Mice: Kirkpatrick et al., 1990; Beef cattle: Van der Werf, 2001; Goats: Ghiasi and Mokhtari, 2018). In Chapter 4, the eigenfunction associated with the largest eigenvalue of the additive covariance matrix of SCS was relatively constant across all ages. Therefore, this eigenfunction is responsible for scaling the profile of SCS without altering the shape of the profile. This
eigenfunction could certainly be used to improve the genetic merit for SCS across all parities, but if the goal was to improve the genetic merit for SCS in older parities, where culling due to SCS and mastitis is a greater issue, the second or third eigenfunctions may be useful. If selection pressure was exerted on the third eigenfunction for SCS, SCS could be reduced between fifth and eighth parity. Nevertheless, given that the genetic variation associated with the third eigenfunction for SCS was limited (4%), in order to alter the shape of the SCS through selection, a greater weight would have to be imposed on this eigenfunction. An alternative approach to improve both the height and shape of the SCS profile would be to combine multiple eigenvalues into an eigenvector index, similar to that proposed by Togashi and Lin (2006) to improve milk yield and persistency. In addition to improving the genetic merit for SCS in older parities with eigenvalues and eigenfunctions, the linear type traits that became more strongly genetically correlated with survival in older parities in Chapter 5 had previously been associated with high SCS and/or mastitis (Seykora and McDaniel, 1986; Němcová et al., 2007; Bobbo et al., 2019), providing further support to the hypothesis that traits associated with resistance to high SCS and mastitis are more important to survival in older parities.

This thesis also highlights the potential value of using random regression models to account for the variation in the relationships among repeated records for milk production, SCS, and survival over the lifetime of dairy cows (Chapters 4 and 5). Random regression models have also been used to model test-day milk production (Jamrozik et al., 2002), growth traits (Ghiasi and Mokhtari, 2018), and dairy cow survival (Veerkamp et al., 1999). Fitting random regression models to longitudinal animal traits could improve the accuracy of predictions of the genetic merit of a multitude of traits, including milk production traits (Chapter 4), SCS (Chapter 4), and survival (Chapter 5) in older dairy cows. Test-day models are already routinely used in Irish dairy cow genetic evaluations for modelling milk yield and SCC within a lactation.

6.2.2 The importance of validating genetic correlations

The disparity between the proportion of the genetic merit for DMI that linear type traits were expected to explain and the proportion of the actual genetic merit for DMI explained from multitrait genetic evaluation of linear type traits highlighted the
need to validate genetic correlations (Chapter 2). For example, the genetic correlation between DMI and chest width suggested that differences in the genetic merit for chest width could explain 39% of the genetic variance in DMI; when, however, the genetic merit for DMI was estimated using multitrait genetic evaluations, no such predictive ability transpired. This discrepancy called into question the validity of suggesting proxy traits for difficult or expensive to measure traits based on estimated genetic correlations alone. If genetic correlations between two traits cannot be successfully validated, the relationship between the traits may be non-linear, which could inhibit validation if the means of the traits differ between populations. For example, if the relationship between two traits is curvilinear, the shape of the estimated genetic correlation could differ depending on where in the trajectory the population lies. Nevertheless, multiple studies, including those presented in Table 6.1, estimated moderately strong genetic correlations between feed intake and linear type traits, and based on these genetic correlations suggested linear type traits would be suitable proxy measures for the genetic merit for feed intake.

Table 6.1. Previous studies that suggested linear type traits may be suitable proxy measures for feed intake or feed efficiency.

<table>
<thead>
<tr>
<th>Reference</th>
<th>Country</th>
<th>Number of animals</th>
</tr>
</thead>
<tbody>
<tr>
<td>Veerkamp and Brotherstone, 1997</td>
<td>UK</td>
<td>527</td>
</tr>
<tr>
<td>Parke et al., 1999</td>
<td>Canada</td>
<td>36,115</td>
</tr>
<tr>
<td>Vallimont et al., 2010</td>
<td>USA</td>
<td>970</td>
</tr>
<tr>
<td>Manafiazar et al., 2016</td>
<td>Canada</td>
<td>260</td>
</tr>
<tr>
<td>Manzanilla-Pech et al., 2016</td>
<td>Netherlands</td>
<td>2,283</td>
</tr>
<tr>
<td>Manzanilla-Pech et al., 2016</td>
<td>USA</td>
<td>1,924</td>
</tr>
</tbody>
</table>

The assumption that genetic correlations between two traits provides an accurate reflection of the ability for one trait to predict the genetic merit of the other is not restricted to identifying proxy measures for the genetic merit for feed intake. Indeed, it is common for studies to propose that easy to measure traits may be suitable proxies for predicting the genetic merit for a wide variety of difficult-to-measure traits without validating their genetic correlations (Boettcher et al., 1998; Zwald et al., 2004; Urioste et al., 2012).
6.2.3 Recommendations and limitations of this thesis

Several recommendations that have the potential to improve the production efficiency of Irish dairy cows could be made based on the results of this thesis. Firstly, based on the small proportion of Irish dairy cows that achieve 305-day lactations, as determined in Chapter 3, the use of estimated 305-day yields in dairy cow genetic evaluations in questionable. Ideally, actual milk yield rather than estimated 305-day yields should be used in genetic evaluations, or alternatively, lactation length should be included in addition to the estimated 305-day yields to more accurately reflect actual milk production. Secondly, a checklist could be developed using the management factors associated with lactation length in Chapter 3 to enable extension officers to easily identify reasons for short lactations and offer suggestions as to how lactation lengths could be improved on individual dairy farms. Additionally, based on the results of Chapter 5, if longevity targets are to be achieved improving survival in older parities will be essential; it may be appropriate to include an alternative survival trait that focuses on survival in older parities in dairy cow breeding objectives given the results of Chapter 5 suggest that survival is not the same genetic trait during the lifetime of dairy cows. Nevertheless, it is worth noting that some of these recommendations are speculative and further research should be conducted prior to altering the national breeding program or management practices.

In light of the above recommendations, the limitations of this thesis should also be considered. One of the primary limitations of this thesis is the potential errors that may exist in the data due to nature and origin of the information. Although every effort has been made to remove erroneous records, given the majority of the data utilised in this thesis was farmer recorded there are potential that some erroneous records remain. Additionally, although the DMI records used in Chapter 2 represent the largest national dataset of grass DMI records globally, the dataset was still relatively small and if additionally records were available the results may have varied, particularly with regards to the statistical significance of the correlations between the breeding values for DMI predicted from linear type traits and the phenotypic DMI. Prior to altering current dairy breeding programs based on the results of Chapters 4 and 5, consideration should be given to the likelihood that some of the correlations between traits (e.g., survival and milk yield) in different parities may have been estimated through pedigree relationship rather that solely on repeated measures for the same individual.
6.3 Further Research

Although this thesis focused on dairy cows exclusively, many of the principles and methods proposed to improve production efficiency could also be employed to improve the efficiency of other dairy species, such as dairy goats or sheep, or other mature lactating non-dairy animals, such as mature beef cows. The lack of individual grazing dairy cow feed intake measurements has limited the estimation of precise genetic parameters for feed intake and related efficiency metrics and, in turn, limited the ability to include feed intake and efficiency traits in dairy total merit selection indexes. Unlike the ICBF Cattle Progeny Test Centre, which was established to estimate the genetic potential of beef bulls, there is no equivalent centre dedicated to collecting dairy cow feed intake and efficiency phenotypes in Ireland, with all currently available measures of dairy cow feed intake originating from experiments limited to research herds.

It could be speculated that if linear type trait information was available for the entire validation population in Chapter 2, then more accurate EBV for feed intake could have been generated from linear type trait phenotypes, as was the case when body weight phenotypes of the validation population were used. Therefore, if additional feed intake measurements and linear type traits were recorded on the same cows, the genetic evaluations from Chapter 2 should be repeated. It was not possible to consider the linear type trait phenotypes of the validation population in the present work, as only 309 cows had both linear type trait and feed intake data, only 77 of which were in the validation population used for the genetic evaluations (Chapter 2). If additional feed intake and linear type trait phenotypes became available, it would also be of interest to attempt to validate the genetic correlations between feed intake and linear type traits in each stage of lactation, particularly in early lactation when DMI is often not sufficient to meet the total energy demands of the cow. Given that the genetic correlations between DMI and some of the composite linear type traits defined in Chapter 2 were strongest in early lactation, if these genetic correlations were validated, these traits could be used to generate breeding values for DMI for a large population of dairy cows. These EBV could assist producers to select for cows with greater intake capacity in early lactation, potentially negating the complications associated with negative energy balance.
Considering recent advancements in imaging analyses and automation technology, routine recording of body weight (Song et al., 2018) and linear type traits (Martins et al., 2020) may soon be a reality on many farms. More regular recording of linear type traits using imaging analysis (Martins et al., 2020) would remove the requirement to subjectively score linear type traits, as well as likely providing a more accurate reflection of each animal’s type as they age. Nonetheless, as imaging and automation technology improves it may be possible to predict feed intake directly from imaging and/or video analyses (Lassen et al., 2022), removing the need to predict feed intake from proxy measures, such as linear type traits.
Chapter 7: References


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 HARNER III, A. D. WRIGHT, AND S. I. SMITH. 2013. Invited review:


Chapter 8: Publications and Contributions
8.1 Peer Reviewed Publications


8.2 Conferences


### 8.3 Other Publications


8.4 Industry Dissemination


Williams, M. 2022. *Genetic differences exist in the rate of maturity among grazing dairy cows.* In: VistaMilk TP 6 stakeholder meeting. Online. 12th of April 2022.

8.5 Research Awards

Journal of Dairy Science, Editor’s Choice Article, April 2022. *Exploiting genetic variability in the trajectory of lactation yield and somatic cell score with each progressing parity.*
8.6 Courses Attended

- Data Analysis with R, Cork Institute of Technology, Bishopstown, Co. Cork, 1\textsuperscript{st} February - 24\textsuperscript{th} May 2019.
- Communicating Your Research, Cork Institute of Technology, Bishopstown, Co. Cork, Ireland, 3\textsuperscript{rd} – 17\textsuperscript{th} April 2019.
- Research Skills Development, Cork Institute of Technology, Bishopstown, Co. Cork, 18\textsuperscript{th} October – 13\textsuperscript{th} December 2019.
- Research Integrity in Natural and Physical Sciences, Epigeum, Online, 25\textsuperscript{th} November 2019.
- Introduction to Data Science for Life Scientists, Genomics CRT, National University of Galway, Online, 16\textsuperscript{th} April – 28\textsuperscript{th} May 2020.
- PhD Writing Essentials, Dr Dan Soule (Professional Writing Academy), Online, 5\textsuperscript{th} May 2020.
- Early Stage Career Planning, Cork Institute of Technology, Online, 5\textsuperscript{th} May – 15\textsuperscript{th} July 2020.
- Story Telling Training, Whipsmart Media, Online, 15\textsuperscript{th} October 2020.
- Issues in Research Integrity, Munster Technological University, Online, 4\textsuperscript{th} March – 13\textsuperscript{th} May 2021.
Chapter 9: Appendices
**Appendix A.** Number of observations (n), mean, genetic standard deviation ($\sigma_g$), heritability ($h^2$; standard error in parenthesis) for dry matter intake (kg), body weight (kg), and daily milk yield (kg) in early, mid and late lactation.

<table>
<thead>
<tr>
<th></th>
<th>Early lactation</th>
<th></th>
<th>Mid lactation</th>
<th></th>
<th>Late lactation</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>n</td>
<td>mean</td>
<td>$\sigma_g$</td>
<td>$h^2$(se)</td>
<td>n</td>
<td>mean</td>
</tr>
<tr>
<td>Dry matter intake</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>DMI¹</td>
<td>2,789</td>
<td>15.98</td>
<td>0.728</td>
<td>0.13 (0.042)</td>
<td>3,205</td>
<td>17.33</td>
</tr>
<tr>
<td>DMI AdjBW</td>
<td>2,789</td>
<td>15.98</td>
<td>0.681</td>
<td>0.12 (0.039)</td>
<td>3,205</td>
<td>17.33</td>
</tr>
<tr>
<td>Body weight</td>
<td>2,789</td>
<td>500.82</td>
<td>31.124</td>
<td>0.51 (0.071)</td>
<td>3,205</td>
<td>520.4</td>
</tr>
<tr>
<td>Daily milk yield</td>
<td>2,789</td>
<td>26.36</td>
<td>0.93</td>
<td>0.07 (0.046)</td>
<td>3,205</td>
<td>21.59</td>
</tr>
</tbody>
</table>

¹DMI – unadjusted dry matter intake; DMI AdjBW – dry matter intake adjusted for phenotypic differences in body weight.
### Appendix B. Phenotypic correlations (standard error in parenthesis) between DMI measured in early, mid, and late lactation (unadjusted and adjusted for phenotypic differences in body weight) body weight (BW), milk yield, and linear type traits.

<table>
<thead>
<tr>
<th>Trait</th>
<th>Early Lactation</th>
<th>Mid Lactation</th>
<th>Late Lactation</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>DMI</td>
<td>DMI AdjBW</td>
<td>BW</td>
</tr>
<tr>
<td>BW</td>
<td>0.29</td>
<td>-</td>
<td>0.41 (0.024)</td>
</tr>
<tr>
<td>Milk yield</td>
<td>0.38 (0.019)</td>
<td>0.34 (0.021)</td>
<td>0.29 (0.026)</td>
</tr>
<tr>
<td>BD</td>
<td>0.11 (0.063)</td>
<td>0.02 (0.065)</td>
<td>0.15 (0.040)</td>
</tr>
<tr>
<td>CW</td>
<td>0.16 (0.063)</td>
<td>0.06 (0.065)</td>
<td>0.25 (0.040)</td>
</tr>
<tr>
<td>STA</td>
<td>0.13 (0.057)</td>
<td>0.01 (0.060)</td>
<td>0.19 (0.035)</td>
</tr>
<tr>
<td>CWBD</td>
<td>0.20 (0.066)</td>
<td>0.06 (0.068)</td>
<td>0.28 (0.040)</td>
</tr>
<tr>
<td>CWSTA</td>
<td>0.15 (0.063)</td>
<td>0.02 (0.068)</td>
<td>0.28 (0.035)</td>
</tr>
<tr>
<td>BDSTA</td>
<td>0.15 (0.063)</td>
<td>0.07 (0.067)</td>
<td>0.37 (0.037)</td>
</tr>
<tr>
<td>CWBDSTA</td>
<td>0.22 (0.066)</td>
<td>0.05 (0.072)</td>
<td>0.30 (0.036)</td>
</tr>
</tbody>
</table>

1DMI – unadjusted DMI; DMI AdjBW – dry matter intake adjusted for phenotypic differences in body weight; BD – body depth; CW – chest width; STA – stature; CWBD – chest width x body depth; CWSTA – chest width x stature; BDSTA – body depth x stature; CWBDSTA – chest width x body depth x stature
Appendix C. The genetic correlations (above diagonal; standard error in parenthesis) and phenotypic correlations (below diagonal; standard error in parenthesis) between the traditional linear type traits and novel composite traits.

<table>
<thead>
<tr>
<th>Trait</th>
<th>BD</th>
<th>CW</th>
<th>STA</th>
<th>CWBD</th>
<th>CWSTA</th>
<th>BDSTA</th>
<th>CWBDSTA</th>
</tr>
</thead>
<tbody>
<tr>
<td>BD¹</td>
<td>0.54</td>
<td>0.23</td>
<td>0.92</td>
<td>0.80</td>
<td>0.47</td>
<td>0.75</td>
<td></td>
</tr>
<tr>
<td></td>
<td>(0.035)</td>
<td>(0.034)</td>
<td>(0.013)</td>
<td>(0.022)</td>
<td>(0.013)</td>
<td>(0.011)</td>
<td></td>
</tr>
<tr>
<td>CW</td>
<td>0.37</td>
<td>0.26</td>
<td>0.43</td>
<td>0.75</td>
<td>0.90</td>
<td>0.72</td>
<td></td>
</tr>
<tr>
<td></td>
<td>(0.004)</td>
<td>(0.047)</td>
<td>(0.009)</td>
<td>(0.018)</td>
<td>(0.040)</td>
<td>(0.022)</td>
<td></td>
</tr>
<tr>
<td>STA</td>
<td>0.83</td>
<td>0.89</td>
<td>0.34</td>
<td>0.88</td>
<td>0.72</td>
<td>0.92</td>
<td></td>
</tr>
<tr>
<td></td>
<td>(0.006)</td>
<td>(0.06)</td>
<td>(0.04)</td>
<td>(0.017)</td>
<td>(0.010)</td>
<td>(0.024)</td>
<td></td>
</tr>
<tr>
<td>CWBD</td>
<td>0.58</td>
<td>0.87</td>
<td>0.66</td>
<td>0.85</td>
<td>0.87</td>
<td>0.97</td>
<td></td>
</tr>
<tr>
<td></td>
<td>(0.002)</td>
<td>(0.001)</td>
<td>(0.006)</td>
<td>(0.012)</td>
<td>(0.024)</td>
<td>(0.008)</td>
<td></td>
</tr>
<tr>
<td>CWSTA</td>
<td>0.85</td>
<td>0.49</td>
<td>0.77</td>
<td>0.74</td>
<td>0.75</td>
<td>0.92</td>
<td></td>
</tr>
<tr>
<td></td>
<td>(0.002)</td>
<td>(0.005)</td>
<td>(0.003)</td>
<td>(0.002)</td>
<td>(0.013)</td>
<td>(0.004)</td>
<td></td>
</tr>
<tr>
<td>BDSTA</td>
<td>0.79</td>
<td>0.80</td>
<td>0.60</td>
<td>0.94</td>
<td>0.93</td>
<td>0.88</td>
<td></td>
</tr>
<tr>
<td></td>
<td>(0.002)</td>
<td>(0.002)</td>
<td>(0.004)</td>
<td>(0.001)</td>
<td>(0.001)</td>
<td>(0.002)</td>
<td></td>
</tr>
</tbody>
</table>

¹BD – body depth; CW – chest width; STA – stature; CWBD – chest width x body depth; CWSTA – chest width x stature; BDSTA – body depth x stature; CWBDSTA – chest width x body depth x stature
Appendix D. The percentage achieved as well as the genetic standard deviation ($\sigma_g$), heritability estimate ($h^2$; standard error in parenthesis), repeatability (t; standard error in parenthesis), and heritability estimate on the underlying liability scale ($h^2_L$) of binary lactation length traits where all cows calved in January, February, March, and April and May combined; lactation length ≥150 days (LL150), lactation length ≥200 days (LL200), lactation length ≥240 days (LL240), lactation length ≥270 days (LL270), lactation length ≥305 days (LL305).

<table>
<thead>
<tr>
<th></th>
<th>Percentage achieved, %</th>
<th>$\sigma_g$</th>
<th>$h^2$</th>
<th>t</th>
<th>$h^2_L$</th>
</tr>
</thead>
<tbody>
<tr>
<td>January</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>LL150</td>
<td>99.61</td>
<td>0.000</td>
<td>0.0000 (0.0000)</td>
<td>0.0000 (0.0000)</td>
<td>0.000</td>
</tr>
<tr>
<td>LL200</td>
<td>99.42</td>
<td>0.001</td>
<td>0.0002 (0.0011)</td>
<td>0.0002 (0.0011)</td>
<td>0.004</td>
</tr>
<tr>
<td>LL240</td>
<td>98.88</td>
<td>0.003</td>
<td>0.0007 (0.0016)</td>
<td>0.0168 (0.0085)</td>
<td>0.009</td>
</tr>
<tr>
<td>LL270</td>
<td>95.21</td>
<td>0.021</td>
<td>0.0126 (0.0036)</td>
<td>0.0361 (0.0077)</td>
<td>0.058</td>
</tr>
<tr>
<td>LL305</td>
<td>51.62</td>
<td>0.078</td>
<td>0.0373 (0.0057)</td>
<td>0.0479 (0.0076)</td>
<td>0.059</td>
</tr>
<tr>
<td>February</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>LL150</td>
<td>99.64</td>
<td>0.001</td>
<td>0.0002 (0.0005)</td>
<td>0.0002 (0.0005)</td>
<td>0.006</td>
</tr>
<tr>
<td>LL200</td>
<td>99.31</td>
<td>0.001</td>
<td>0.0003 (0.0005)</td>
<td>0.0006 (0.0036)</td>
<td>0.006</td>
</tr>
<tr>
<td>LL240</td>
<td>97.92</td>
<td>0.009</td>
<td>0.005 (0.0013)</td>
<td>0.0149 (0.0037)</td>
<td>0.041</td>
</tr>
<tr>
<td>LL270</td>
<td>84.09</td>
<td>0.036</td>
<td>0.0146 (0.0022)</td>
<td>0.0423 (0.0035)</td>
<td>0.033</td>
</tr>
<tr>
<td>LL305</td>
<td>24.93</td>
<td>0.035</td>
<td>0.0100 (0.0017)</td>
<td>0.0102 (0.0033)</td>
<td>0.019</td>
</tr>
<tr>
<td>March</td>
<td></td>
<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>LL150</td>
<td>99.51</td>
<td>0.002</td>
<td>0.0009 (0.0013)</td>
<td>0.0009 (0.0013)</td>
<td>0.022</td>
</tr>
<tr>
<td>LL200</td>
<td>98.68</td>
<td>0.006</td>
<td>0.0027 (0.0019)</td>
<td>0.0330 (0.0109)</td>
<td>0.031</td>
</tr>
<tr>
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<td>89.56</td>
<td>0.022</td>
<td>0.0075 (0.0028)</td>
<td>0.0095 (0.0104)</td>
<td>0.021</td>
</tr>
<tr>
<td>LL270</td>
<td>49.42</td>
<td>0.045</td>
<td>0.0134 (0.0035)</td>
<td>0.0397 (0.0091)</td>
<td>0.021</td>
</tr>
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<td>LL305</td>
<td>12.22</td>
<td>0.022</td>
<td>0.0064 (0.0026)</td>
<td>0.0064 (0.0026)</td>
<td>0.017</td>
</tr>
<tr>
<td>April and May</td>
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<td>99.19</td>
<td>0.000</td>
<td>0.0000 (0.0000)</td>
<td>0.5457 (0.0157)</td>
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<tr>
<td>LL200</td>
<td>93.62</td>
<td>0.028</td>
<td>0.0165 (0.0068)</td>
<td>0.2725 (0.0238)</td>
<td>0.063</td>
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<tr>
<td>LL240</td>
<td>66.17</td>
<td>0.039</td>
<td>0.0127 (0.0056)</td>
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<td>LL270</td>
<td>36.34</td>
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<td>0.0049 (0.0039)</td>
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</tr>
<tr>
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<td>0.002</td>
<td>0.0001 (0.0026)</td>
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Appendix E. The proportion of cows reaching maximum 305-day milk, fat, and protein yield, highest average fat and protein percentage and highest average somatic cell score in each parity.

<table>
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<tr>
<th>Parity</th>
<th>Milk yield</th>
<th>Fat yield</th>
<th>Protein yield</th>
<th>Fat percentage</th>
<th>Protein percentage</th>
<th>Somatic cell score</th>
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<td>0.959</td>
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</tr>
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<td>0.834</td>
<td>0.005</td>
<td>0.001</td>
<td>0.000</td>
</tr>
<tr>
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<td>0.004</td>
<td>0.010</td>
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<td>0.001</td>
</tr>
<tr>
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<td>0.000</td>
<td>0.003</td>
<td>0.000</td>
<td>0.011</td>
<td>0.000</td>
<td>0.010</td>
</tr>
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<td>0.013</td>
<td>0.013</td>
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Appendix F. Genetic correlations and their respective standard errors between 305-day fat yield (kg) in different parities (above diagonal) and 305-day protein yield (kg) in different parities (below diagonal).

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<th>5</th>
<th>6</th>
<th>7</th>
<th>8</th>
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<td>0.97</td>
<td>0.92</td>
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<td>0.87</td>
<td>0.84</td>
<td>0.75</td>
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<tr>
<td></td>
<td>(0.004)</td>
<td>(0.01)</td>
<td>(0.01)</td>
<td>(0.01)</td>
<td>(0.02)</td>
<td>(0.02)</td>
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<td>0.91</td>
<td>0.78</td>
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</tr>
<tr>
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<td>(0.001)</td>
<td>(0.003)</td>
<td>(0.004)</td>
<td>(0.01)</td>
<td>(0.01)</td>
<td>(0.01)</td>
<td>(0.02)</td>
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<tr>
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<td>0.93</td>
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<tr>
<td></td>
<td>(0.01)</td>
<td>(0.001)</td>
<td>(0.000)</td>
<td>(0.001)</td>
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</tr>
<tr>
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<td>(0.01)</td>
<td>(0.004)</td>
<td>(0.001)</td>
<td>(0.000)</td>
<td>(0.000)</td>
<td>(0.002)</td>
<td>(0.01)</td>
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<tr>
<td></td>
<td>(0.02)</td>
<td>(0.01)</td>
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<td>(0.000)</td>
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<tr>
<td>6</td>
<td>0.60</td>
<td>0.80</td>
<td>0.86</td>
<td>0.89</td>
<td>0.93</td>
<td>0.97</td>
<td>0.96</td>
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<tr>
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<td>(0.02)</td>
<td>(0.01)</td>
<td>(0.01)</td>
<td>(0.004)</td>
<td>(0.002)</td>
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<td>0.69</td>
<td>0.75</td>
<td>0.84</td>
<td>0.94</td>
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<tr>
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<td>(0.03)</td>
<td>(0.02)</td>
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**Appendix G.** Pairwise genetic correlations (standard errors in parentheses) between survival adjusted for 305-day milk yield (above diagonal) and their respective standard errors (below diagonal) between survival in first to ninth parity.

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