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Novel genetic parameters for genetic residual feed intake in dairy cattle using time series data from multiple parities and countries in North America and Europe

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ABSTRACT

Residual feed intake is viewed as an important trait in breeding programs that could be used to enhance genetic progress in feed efficiency. In particular, improving feed efficiency could improve both economic and environmental sustainability in the dairy cattle industry. However, data remain sparse, limiting the development of reliable genomic evaluations across lactation and parity for residual feed intake. Here, we estimated novel genetic parameters for genetic residual feed intake (gRFI) across the first, second, and third parity, using a random regression model. Research data on the measured feed intake, milk production, and body weight of 7,379 cows (271,080 records) from 6 countries in 2 continents were shared through the Horizon 2020 project Genomic Management Tools to Optimise Resilience and Efficiency, and the Resilient Dairy Genome Project. The countries included Canada (1,053 cows with 47,130 weekly records), Denmark (1,045 cows with 72,760 weekly records), France (329 cows with 16,888 weekly records), Germany (938 cows with 32,614 weekly records), the Netherlands (2,051 cows with 57,830 weekly records), and United States (1,963 cows with 43,858 weekly records). Each trait had variance components estimated from first to third parity, using a random regression model across countries. Genetic residual feed intake was found to be heritable in all 3 parities, with first parity being predominant (range: 22–34%). Genetic residual feed intake was highly correlated across parities for mid- to late lactation; however, genetic correlation across parities was lower during early lactation, especially when comparing first and third parity. We estimated a genetic correlation of 0.77 ± 0.37 between North America and Europe for dry matter intake at first parity. Published literature on genetic correlations between high input countries/continents for dry matter intake support a high genetic correlation for dry matter intake. In conclusion, our results demonstrate the feasibility of estimating variance components for gRFI across parities, and the value of sharing data on scarce phenotypes across countries. These results can potentially be implemented in genetic evaluations for gRFI in dairy cattle.

Key words: genetic residual feed intake, variance component estimation, random regression, multitrait analysis

INTRODUCTION

Genetic improvement of feed efficiency represents a promising way to increase the environmental and economical sustainability of the dairy cattle industry. Over the last century, the feed efficiency of the dairy cattle industry has mainly improved as an indirect effect of selection for milk production, which improves produc-

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tion efficiency. This effect is termed the "dilution of maintenance effect" (Bauman et al., 1985; VandeHaar et al., 2016). In other words, the "costs" of maintenance are diluted with increasing output (milk or meat). However, along with the strong selection for milk production, antagonistic tradeoffs for functional traits have been documented in the last 2 decades (Rauw et al., 1998; Oltenacu and Broom, 2010). Therefore, any future index for feed efficiency must improve both, efficiency and at the same time avoid antagonistic tradeoffs for robustness and resilience.

The main limitation for developing reliable genomic breeding values for feed efficiency is the expensive system required to measure and record the feed intake of individual animals. Most feed intake data are obtained from research farms, where animals are typically used in nutritional experiments. Therefore, collaborations across country borders are needed to improve the number of records used to estimate the breeding values for feed efficiency (de Haas et al., 2012, 2015; Berry et al., 2014). The Resilient Dairy Genome Project (**RDGP**) consortium aims to enhance sustainability in the dairy cattle industry through genetically improving feed efficiency. At present, this consortium has the largest joint database on Holstein cows with feed intake measured for individual animals (12,687 cows; van Staaveren et al., 2024).

Berry and Crowley (2013) classified feed efficiency traits for genetic selection into 2 groups: (1) feed conversion ratios (commonly used in poultry and pigs), and (2) residual traits, based on a linear regression. In dairy cattle breeding systems, residual feed intake (**RFI**) is often referred to as the desirable trait for use in genetic selection for feed efficiency (Pryce et al., 2015; VandeHaar et al., 2016). Residual feed intake was first proposed by Koch et al. (1963), as the phenotypic regression for an animal's feed intake related to its energy sinks (yield, maintenance, mobilization, pregnancy, and so on). Thus, RFI is phenotypically uncorrelated with the energy sinks in the model. Few genetic evaluation centers routinely estimate the breeding values for feed efficiency traits in dairy cattle (de Jong et al., 2019; Jamrozik et al., 2021; Parker Gaddis et al., 2021; Stephansen et al., 2021a). Many of these institutions use RFI typically in context with the feed saved definition (Pryce et al., 2015).

Kennedy et al. (1993) proposed a genetic RFI (**gRFI**) model, in which the genetic correlations between the feed intake of a cow and its energy sinks are considered to be zero. The main advantage of gRFI is that the trait, in theory, is not genetically correlated with its energy sinks (Stephansen et al., 2021b) compared with phenotypic RFI (Veerkamp et al., 1995). Furthermore, in classical phenotypic RFI models, model fitting errors, and measurement errors form the residual, which potentially ends up in EBV. For instance, Fischer et al. (2018) showed that 41% to 47% of variance in the RFI phenotype reflects model fitting errors and measurement errors. Li et al. (2017) also analyzed the importance of taking mobilization into consideration in a classical phenotypic RFI model, using partial regression coefficients on DMI. This model was extended by Martin et al. (2021a), who proposed a nongenetic dynamic RFI multitrait model. The partial regression coefficients on milk energy in RFI models also differ significantly through lactation (Li et al., 2017; Khanal et al., 2022). This can support the phenomenon, that dairy cows mobilize body reserves to compensate the rate of energy demand toward milk production by a lower rate of energy intake (Roche et al., 2009). However, the estimation of the changing partial regression on milk energy over lactation could potentially be influenced by the confounding effects among multiple partial regressions in an RFI model. The phenotypic multitrait approach suggested by Martin et al. (2021a) could help avoid the accumulation of errors in the phenotype and subsequent estimated breeding values for RFI. The feasibility of a gRFI model, with a zero genetic correlation to energy sinks, has earlier been studied within parity or parity groups (Islam et al., 2020; Khanal et al., 2022), but not with a covariance structure across parities.

However, a knowledge gap exists on modeling gRFI in a dynamic RFI multitrait model and across the first, second, and third parity. The novelty in this study consists of modeling gRFI with a covariance structure across parities. Thus, here, we aimed to estimate variance components for a dynamic multitrait and multiparity gRFI model using time series and feed intake data from multiple countries in North America and Europe.

MATERIALS AND METHODS

Data from Denmark, France, and the Netherlands were shared as a part of the Horizon 2020 project GenTORE project (https://www.gentore.eu). Data from the United States, Canada, and Germany were shared as a part of the RDGP (https://genomedairy.ualberta.ca/; http://www.resilientdairy.ca/). The data used in this study are briefly described here. A detailed description of RDGP data is provided in van Staaveren et al. (2024). A detailed overview of the number of cows, number of records, and recording period is provided in Table 1. Only data from the first 3 lactations were used for this analysis. All data used were from existing databases, where studies were in accordance with na-

Table 1. Frequency of the number of cows, lactation, average number of records per lactation, and data collection period for each country

Country	No. of cows	Lactations	Weekly records	Average weekly records per lactation	Years of data collection
Canada	1,053	1,269	47,130	37.1	2015–2021
Denmark	1,045	2,000	72,760	36.4	2003–2021
France	329	441	16,888	38.3	2014–2020
Germany	938	1,146	32,614	28.5	2015–2021
The Netherlands	2,051	2,402	57,830	24.1	1991–2019
United States	1,963	2,198	43,858	20.0	2007–2021
Total	7,379	9,456	271,080	28.7	1991–2021

tional guidelines. Therefore no approval statement from national institutions of animal care and use committees was necessary.

Denmark

Data from 1,045 Danish Holstein cows, with 2,000 lactations (mean: 36.4 records/cow per lactation) were collected from 2003 to 2021 at the Danish Cattle Research Center (**DKC**; Foulum, Denmark). Detailed information on the housing conditions and feeding before 2020 is provided in Li et al. (2017). During 2020, the cows were moved to the new DKC facilities, where cows were milked in a milking parlor (SAC, Kolding, Denmark). Individual feed intake was measured in feed boxes (RIC system, Insentec, Marknesse, the Netherlands). Cows were not offered concentrates in the milking parlor. Thus, from 2020 onward, they were fed ad libitum TMR. Cows were automatically weighed after milking on a scale.

The Netherlands

Data on 2,051 Dutch Holstein cows with 2,402 lactations (mean: 24.1 records/cow per lactation) were collected from 1990 to 2019 at multiple research farms in the Netherlands. All cows were housed in commercial herds for nutritional experiments. All cows were kept in freestall barns with cubicles, and were offered a TMR ad libitum in feed boxes (RIC system). For a detailed description of basic parameters, the nutrition experiments, and descriptions of data collection, please see Heida et al. (2021) and references therein.

France

Data from 329 French Holstein cows were collected from 2014 to 2020 at 2 facilities. Data on 158 cows were collected at Le-Pin-Au-Haras INRAE facility, with 208 lactations (mean 39.7 records/cow per lactation; INRAE, 2021). Data from 171 cows were collected at Méjusseaume INRAE facility, with 236 lactations (mean: 37.1 records/cow per lactation; INRAE, 2022). At both farms, cows were fed ad libitum using a TMR with an electronic gate feeding system and ear-tag identification to record individual feed intake. For detailed descriptions, see Fischer et al. (2018), Martin et al. (2021b), and Lefebvre et al. (2022).

Germany

Data were collected from 938 German Holstein cows between 2015 and 2021 at 4 research farms in Germany. These farms included: Iden (208 cows with 236 lactations; mean 23.6 records/cow per lactation), Karkendamm (195 cows with 262 lactations; mean 35.9 records/cow per lactation), Neumuehle (171 cows with 199 lactations; mean 22.4 records/cow per lactation), and Riswick (364 cows with 449 lactations; mean 29.3 records/cow per lactation). Cows were housed in freestall barns, with no access to pasture. The cows were milked 2 to 3 times per day using herringbone (DeLaval, GEA), parallel (DeLaval), and rotary systems (GEA). Weekly milk weight was measured automatically. Samples were collected in the morning and evening to obtain data on fat, protein, MUN, lactose, and SCC. Animals were fed grass and corn silage based on TMR (Iden and Neumuehle) or partial mixed ration (Riswick and Karkandamm). Feed intake records were collected for both primiparous and multiparous cows. Daily feed intake weight was collected over 24 h, and was aggregated to a single daily feed intake. Daily records were averaged over 44 wk of lactation to obtain weekly records. At 3 farms (Karkendamm, Neumuehle, and Riswick), BW data were collected after returning from the parlor twice per day using an automated electronic weighing system. At the farm in Iden, BW was recorded manually once a month, from which daily weight was calculated by linear interpolation. Detailed descriptions of the facilities and feeding of the different research herds are provided in van Staaveren et al. (2024).

Canada

Data from 1,053 Canadian Holstein cows were collected from 2015 to 2021 by 3 institutions. These were the University of Alberta (Dairy Research and Technology Centre, DRTC; 285 cows with 337 lactations; mean 33.3 records/cow per lactation), University of Guelph (Elora) research farms (510 cows with 666 lactations; mean 40.3 records/cow per lactation), and a commercial farm (SUNALTA; 258 cows with 266 lactations; mean 34.0 records/cow per lactation). Detailed information on the facilities and feeding regimens of the various research herds is provided in van Staaveren et al. (2024).

United States

Data on 1,963 Holstein cows were collected at 6 research farms from 2007 to 2021 in the United States. Specifically Beltsville (510 cows with 665 lactations; mean: 28.7 records/cow per lactation), University of Florida (494 cows with 527 lactations; mean: 17.6 records/cow per lactation), Iowa State University (353 cows with 354 lactations; mean: 22.5 records/cow per lactation), Michigan State University (88 cows with 89 lactations; mean: 20.8 records/cow per lactation), University of Wisconsin (425 cows with 450 lactations; mean: 19.8 records/cow per lactation), and the Purina Animal Nutrition Center (93 cows with 113 lactations; mean: 25.2 records/cow per lactation). Detailed information of the facilities and feeding regimens at the various research herds is provided in van Staaveren et al. (2024).

Phenotypes and Data Editing

Energy-corrected milk was calculated for statistical analysis according to the formula by Sjaunja et al. (1990):

$$\text{ECM (kg)} = \text{raw milk (kg)} \times [(0.383 \times \text{fat content } (\%) + 0.242 \times \text{protein content } (\%) + 0.7832)/3.140].$$

The combined dataset was filtered to remove outliers. The following steps were used to clean using SAS software version 9.4 (SAS Institute Inc.): (1) extreme values were set to missing if DMI was not in the range of 5 to 40 kg/d, milk yield was not in the range of 5 to 100 kg/d, fat percentage in milk was not in the range of 1% to 10%, protein percentage in milk was not in the range of 1% to 10%, and BW was not in the range of 300 to 1,100 kg, (2) outliers were set to missing, defined of the range of mean ± 3 standard deviations, (3) nonsensical records were set to missing if one of the traits (DMI, ECM, and BW) exceeded a change of 5, 10, and 50 kg, respectively, in time windows of ± 1 wk, (4) data from lactations with less than one-third of test-days were excluded (minimum 14 wk with data per cow during parity), (5) if lactations were not cohesive for a cow, only the first lactation was kept, and (6) records were excluded when herd × year × season (calving) or experiment and country × year × month groups were smaller than 5 records.

The filtered data consisted of 9,456 lactations from 7,379 cows and a total of 271,080 weekly records from first to third parity. Unfiltered data consisted of 20,703 lactations from 14,871 cows and a total of 405,292 weekly records. The required 14 wk minimum with data per cow was the criterion that caused the largest reduction in the number of records. On average, filtering reduced the number of records by 31%, and affected France, Denmark, Germany, the Netherlands, Canada, and United States by 1%, 6%, 21%, 27%, 38%, and 56%, respectively. The filtering criteria was used to reduce problems with “Runge’s phenomenon.” Runge’s phenomenon describes problems with polynomials placing overly high emphasis on observations at the extremes of lactation (Meyer, 2005). A filtering criterion for the minimum number of weeks in records is typically used when developing phenotypic multitrait RFI models (Martin et al., 2021a). Lidauer et al. (2015) also excluded cows with no data at the beginning of first lactation in a test-day evaluation.

Pedigree

Pedigrees were provided directly from the partners in the GenTORE project, whereas a common pedigree was available for partners in the RDGP database. All pedigrees were combined to form a common pedigree (Figure 1). In the process of forming the common pedigree, different quality checks (sire and dam in the pedigree, correct wrong birth years, insert genetic groups) were performed to ensure a high-quality pedigree. The pedigree was pruned to 5 generations for animals with phenotype data, using DMU trace software (version 2, July 2020, Madsen, 2012). All noninformative animals were excluded from the pedigree. The full pedigree contained information on 118,646 individuals; after pruning, the pedigree contained 29,537 animals. For animals with missing parent(s), genetic groups were assigned, taking into account the effect of country (Denmark, France, Canada, Unites States, the Netherlands, Germany, other European countries, and other countries), breed (Ayrshire + Red Dairy Cattle + Montbéliarde + Brown Swiss,

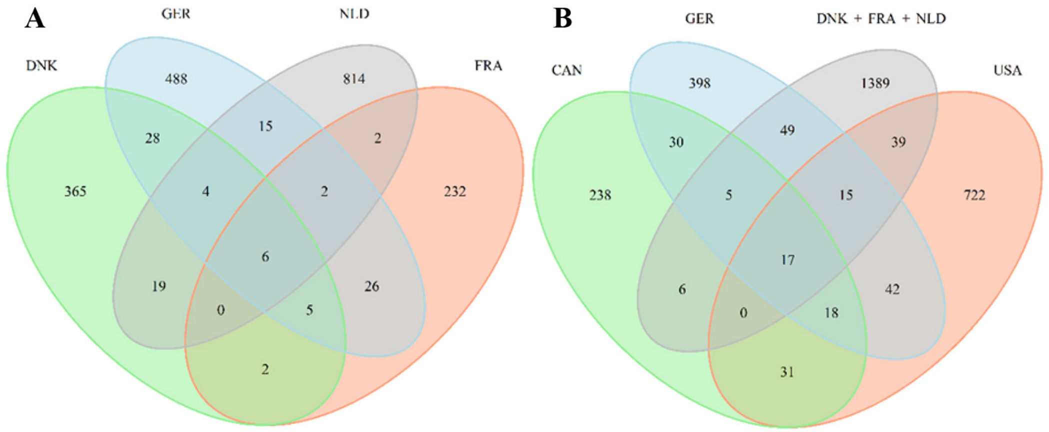

Figure 1. Venn diagram showing the number of sires and grandsires with at least one offspring across countries. Plot A shows common sires and grandsires between European countries. Plot B shows common sires and grandsires between continents. CAN = Canada; DNK = Denmark; FRA = France; GER = Germany; NLD = the Netherlands; USA = United States of America.

Holstein, and other breeds), and 3 birth-year classes (1: <1990, 2: 1990–2005, 3: >2005). Ayrshire, Red Dairy Cattle, Montbéliarde, and Brown Swiss were grouped into one breed group, as they individually would have been too small. In addition, the breeds are a part of the population structure in the Nordic Red Dairy breed (SEGES Livestock Innovation Cattle, 2021). Furthermore, the authors did not include an effect of sex in the genetic groups, as we did not expect an effect of selection for RFI. Figure 1A shows the common sires and grandsires in European countries. Most sires and grandsires had progeny in one country; however, genetics overlapped between European countries for 6 sires and grandsires, which had progeny in all European countries (Figure 1A). The same pattern was recorded for the Unites States and Canada (Figure 1B). Germany was grouped independently from the other European countries, because most sires and grandsires were common with the United States and Canada. Seventeen sires and grandsires had offspring in all countries, where Denmark, France and the Netherlands were grouped (Figure 1B).

Statistical Analysis

The statistical software DMU (Madsen and Jensen, 2013) was used for variance component estimation using AI-REML and EM-REML algorithms. We used for the random effect part a linear (DMI and ECM) or quadratic (BW) random regression models. We did not use higher orders because of convergence issues. For the fixed regressions on age at calving we used linear and quadratic equations. The random regression models by parity were as follows:

$$y_{ijclmnopq} = \mu + CHYS_i + \sum_{k=0}^{x} W_{jkl}\Phi_k + \beta_1 ACC_c + \beta_2 ACC_c^2 + \sum_{k=0}^{m} a_{kc}\Phi_{kc} + \sum_{k=0}^{m} pe_{kc}\Phi_{kc} + EXP_{no} + CYM_p + e_{ijclmnopq}, \quad [1]$$

where $y_{ijclmnopq}$ is the phenotypes for DMI, ECM, or BW for cow c on week of lactation j (j = 1, 2, . . . , 44); μ is the intercept; $CHYS_i$ is the ith fixed effect of calving herd × year × season (933 levels; seasons were separated into quarters from date of calving); W_{jkl} is the kth fixed regression of the jth week of lactation and is nested within herd × 5-yr period l (23 levels; 5-yr periods were only used for Danish and Dutch data); Φ_k is the term of the xth order Legendre polynomial (**LP**) for week of lactation; β_1 and β_2 are the fixed regressions on age at calving (ACC_c) and ACC_c^2 for cow c, respectively; a_{kc} is the kth regression coefficient of the mth order LP for the random additive genetic effect for the cth cow; pe_{kc} is the kth regression coefficient of the mth order LP for the random permanent environmental effect for the cth cow; Φ_{kc} is the term of the mth order LP for a_{kc} and pe_{kc}, where time is the week of lactation; EXP_{no} is the random effect of the nth trial nested in the oth herd x × year × month (2,866 levels; year and month are defined from record date); CYM_p is the random effect of the pth country × year × month (898 levels; country groups: Denmark, France, Canada, the United States [except Florida], Germany, the Netherlands, the state of Florida [the United States]; year and month are defined from record date); and $e_{ijclmnopq}$ is the random residual error, modeled as heterogeneous by country and the qth lactation period (1: 1–4 wk of lactation [**WOL**], 2: 5–36 WOL, 3: 37–44 WOL), with 20 levels in total.

It was assumed that $\mathrm{var}(\boldsymbol{a}) = \mathbf{A} \otimes \widehat{\boldsymbol{K}(\boldsymbol{a})}$, $\mathrm{var}(\boldsymbol{pe}) = \mathbf{I} \otimes \widehat{\boldsymbol{K}(\boldsymbol{pe})}$, and $\mathrm{var}(\boldsymbol{e}) = \mathbf{I} = \mathbf{R}$, where $\mathbf{A}$ is the numerator relationship matrix, $\otimes$ is the Kronecker product, and $\widehat{\boldsymbol{K}(\boldsymbol{a})}$ is the genetic covariance matrix between the LP coefficients and $\widehat{\boldsymbol{K}(\boldsymbol{pe})}$ is the permanent environmental covariance matrix between the LP coefficients (first order for DMI and ECM, and second order for BW). The fixed lactation curve was fitted with an xth order LP that was 2 orders higher than that of the $\boldsymbol{a}$ and $\boldsymbol{pe}$ effects.

To construct the covariance for all 9 traits (3 traits × 3 lactations), 36 bivariate analyses were performed. For analyses that did not meet the convergence criteria with AI-REML in DMU, an EM-REML analysis was implemented with the priors from the AI-REML analysis. The models were analyzed as bivariate multitrait:

$$\begin{bmatrix}\mathbf{y}_1\\ \mathbf{y}_2\end{bmatrix} = \begin{bmatrix}\mathbf{X}_1\\ \mathbf{X}_2\end{bmatrix}\begin{bmatrix}\mathbf{b}_1\\ \mathbf{b}_2\end{bmatrix} + \begin{bmatrix}\mathbf{Z1}_1\\ \mathbf{Z1}_2\end{bmatrix}\begin{bmatrix}\mathbf{a}_1\\ \mathbf{a}_2\end{bmatrix} + \begin{bmatrix}\mathbf{Z2}_1\\ \mathbf{Z2}_2\end{bmatrix}\begin{bmatrix}\mathbf{pe}_1\\ \mathbf{pe}_2\end{bmatrix} + \begin{bmatrix}\mathbf{e}_1\\ \mathbf{e}_2\end{bmatrix},$$

where $\mathbf{y}$ is the vector of the phenotypes, $\mathbf{b}$ is the vector of the fixed effects, $\mathbf{X}$ is the incidence matrix relating observations with fixed effects, $\mathbf{a}$ is the vector of additive genetic effects, $\mathbf{Z1}$ is the incidence matrix relating observations with random additive effects, $\mathbf{pe}$ is the vector of permanent environmental effects, $\mathbf{Z2}$ is the incidence matrix relating random permanent environmental effects with observations, and $\mathbf{e}$ is the vector of residual effects.

Across-Continent Analysis

For an across-country model [1] to improve genetic evaluations of feed efficiency in the participating countries, the genetic correlation among countries must be high. To analyze this, an across-continent analysis was carried out for DMI during first parity between North America (Canada and the United States) and Europe (Denmark, France, Germany, and the Netherlands). A filtered dataset was used that only contained data from 4 to 24 wk of lactation and data from 2005 to 2021. This selection was implemented to harmonize the recording period within lactation and over years between North America and Europe. The filtered dataset contained 3,538 cows in first lactation, with 31,422 records from North America and 29,726 records from Europe. The bivariate model was solved with DMU AI-REML, and was presented as follows:

$$\mathrm{y}_{\mathrm{ijclnopq}} = \mu + \mathrm{CHYS}_{\mathrm{i}} + \sum_{\mathrm{k}=0}^{3}\mathrm{W}_{\mathrm{kl}}\Phi_{\mathrm{k}} + \beta_1\mathrm{ACC}_{\mathrm{c}} + \beta_2\mathrm{ACC}_{\mathrm{c}}^2 + a_c + Pe_c + \mathrm{EXP}_{\mathrm{no}} + \mathrm{CYM}_p + \mathrm{e}_{\mathrm{ijclnopq}}. \qquad [2]$$

See the description of model 1 for interpretation. However, in this model, heterogeneous residual variance was nested within lactation periods per fourth week of lactation. The residual and permanent environmental covariance between the 2 continents were assumed to be 0. The asymptotic standard error on the genetic correlation between continents was calculated according to Jensen and Madsen (2002).

Deriving the Outputs for Genetic and Phenotypic RFI

The concept of deriving gRFI solutions and output for further analysis was extended in comparison to the approaches of Kennedy et al. (1993), Islam et al. (2020), and Martin et al. (2021a). Variance components from the previous 36 bivariate trait analyses were combined using the iterative summing method developed by Mäntysaari (1999), as described in Henshall and Meyer (2002). The iterative summing method ensured that the final variance component matrix was positive definite. The genetic covariance $\left(\hat{\boldsymbol{G}}\right)$ matrix for t points over the 12 trajectories was derived as $\hat{\boldsymbol{G}} = \boldsymbol{\Phi}\widehat{\boldsymbol{K}(\boldsymbol{G})}\boldsymbol{\Phi}'$, where $\boldsymbol{\Phi}$ has dimension $t \times k$, $\widehat{\boldsymbol{K}(\boldsymbol{G})}$ has dimension $k \times k$, and $\hat{\boldsymbol{G}}$ has dimension $t \times t$. When setting up the $\boldsymbol{\Phi}$ and $\hat{\boldsymbol{K}}$, these parameters were sorted by parity and the variable order DMI, ECM, and BW. Covariance components of change in BW ($\boldsymbol{\Delta}\mathbf{BW}$) were derived from the fitted slope of BW within parity. That was done by constructing the $\boldsymbol{\Phi}$ matrix as Equation 3 in Islam et al. (2020). The permanent environment covariance matrix $\left(\widehat{\boldsymbol{Pe}}\right)$ was derived as $\hat{\boldsymbol{G}}$ by replacing $\widehat{\boldsymbol{K}(\boldsymbol{G})}$ with the respective solution matrix. The dimensions of $\hat{\boldsymbol{G}}$ and $\widehat{\boldsymbol{Pe}}$ were 528 × 528.

The residual ($\mathbf{R}$) matrix was constructed as a block diagonal matrix for each week of lactation. Each block contained residual (co)variance for DMI, ECM, BW, and ΔBW for each parity, resulting in a matrix of 528 × 528. The transformation matrix within each parity was defined according to Islam et al. (2020):

$$\boldsymbol{t_{wp}} = \begin{bmatrix}1 & 0 & 0 & 0 & 0 & 0\\ 0 & 1 & 0 & 0 & 0 & 0\\ 0 & 0 & 1 & 0 & 0 & 0\\ 0 & 0 & -1 & 0 & 0 & 1\end{bmatrix},$$

where $\boldsymbol{t_{wp}}$ is the transformation matrix for the wth week of lactation ($w = 1, 2, \ldots, 44$) and the pth parity ($p = 1, 2, 3$) to derive the residual variance for ΔBW. The first 3 rows of $\boldsymbol{t_{wp}}$ represent the residual variance for DMI, ECM, and BW. The fourth row represents the residual variance for ΔBW. $\mathbf{R_{0,wp:w+1p}}$ represents the block diagonal matrix with the residual variance estimates for the 2 adjacent weeks of lactation in the pth parity, resulting in a dimension of 6 × 6. The residual matrix for the wth week of lactation and pth parity is derived as follows:

$$\mathbf{R_{wp}} = \mathbf{t_{wp}}\mathbf{R}_{0,\mathbf{wp:w+1p}}\mathbf{t}_{\mathbf{wp}}^{'}, \quad [3]$$

where the dimension of the first matrix (week of lactation = 1, parity = 1) $\mathbf{R_{11}}$ is 6 × 6. The final $\mathbf{R}$ matrix is a block diagonal matrix with a dimension of 528 × 528. The phenotypic (co)variance matrix is defined as $\mathbf{P} = \mathbf{G} + \mathbf{Pe} + \mathbf{R}$. The genetic and phenotypic regression coefficients for each parity are calculated as

$$\boldsymbol{\beta_{Gwp}} = \boldsymbol{B}_{\boldsymbol{G}:21}\left(\boldsymbol{wp}\right)\boldsymbol{B}_{\boldsymbol{G}:22}^{-1}\left(\boldsymbol{wp}\right)\text{and } \boldsymbol{\beta_{Pwp}} = \boldsymbol{B}_{\boldsymbol{P}:21}\left(\boldsymbol{wp}\right)\boldsymbol{B}_{\boldsymbol{P}:22}^{-1}\left(\boldsymbol{wp}\right). \quad [4]$$

The genetic and phenotypic regressions are a 3 × 1 vector for wth week of lactation and pth parity. $\mathbf{B_{G:22}}$ is a 3 × 3 matrix of genetic (co)variance for ECM, BW, and ΔBW from each week of lactation and each parity. $\mathbf{B_{G:21}}$ is a 3 × 1 matrix of genetic covariance for DMI on ECM, BW, and ΔBW from each week of lactation and each parity. $\mathbf{B_{P:22}}$ is a 3 × 3 matrix of phenotypic (co)variance for ECM, BW, and ΔBW from each week of lactation and each parity. $\mathbf{B_{P:21}}$ is a 3 × 1 matrix of phenotypic covariance for DMI on ECM, BW, and ΔBW from each week of lactation and each parity.

A $\hat{\boldsymbol{G}}$ (co)variance) matrix, containing gRFI, could be obtained from $\boldsymbol{B\hat{G}B'}$. The $\hat{\boldsymbol{G}}$ matrix was derived earlier, and the $\mathbf{B}$ matrix represents a block matrix for genetic regressors:

$$\boldsymbol{B_{Gwp}} = \begin{bmatrix} 1 & 0 & 0 & 0 \\ 1 & -\beta_{Gwp:ECM} & -\beta_{Gwp:BW} & -\beta_{Gwp:\Delta BW} \\ 0 & 1 & 0 & 0 \\ 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 1 \end{bmatrix},$$

where $\boldsymbol{B_{Gwp}}$ is the regression matrix for the wth week and pth parity, $-\beta_{Gwp:i}$ is the genetic regression coefficient for wth week and pth parity for the ith trait. The $\boldsymbol{B_{G11}}$ matrix has a dimension of 5 × 4; $\boldsymbol{B\hat{G}B'}$ has a dimension of 660 × 660. The $\hat{\boldsymbol{P}}$ (co)variance matrix containing RFI could be easily derived as $\hat{\boldsymbol{G}}$ by replacing $\boldsymbol{B_{Gwp}}$ with $\boldsymbol{B_{Pwp}}$. Thus, the heritability of gRFI could be obtained as the diagonal elements from $\mathbf{BGB'}$ divided by the diagonal elements from $\mathbf{BPB'}$.

Standard errors for heritability and genetic correlations were calculated according to the approximate method of Fischer et al. (2004). Approximate asymptotic standard errors were calculated as described by Fischer et al. (2004), using the appropriate elements of the inverse of the average information matrix.

RESULTS

Descriptive Statistics for Records and Phenotypes

The overview of records per week (Figure 2) showed that the recording strategy differed among the involved countries. Most data across countries were recorded from 0 to 30 wk of lactation. For all countries, the number of records declined during late lactation, particularly in the United States and the Netherlands. With increasing parity number, the number of records per week of lactation also decreased (Figure 2).

Descriptive plots of phenotypes for DMI, ECM, and BW are presented in Supplemental Figures S1, S2, and S3 (https://doi.org/10.7910/dvn/sxxdcy; Stephansen, 2023). Average DMI was lowest at first parity, with peak feed intake occurring at a later time point for first parity compared with later parities (Supplemental Figure S1). Feed intake only declined after the peak in later parities for Denmark, France, Germany, and the Netherlands. The average DMI was highest in Canada and the United States, and lowest in the Netherlands. The lower feed intake in the Netherlands have been affected by the longer recording period (Table 1). For DMI, the average ECM was lower for first-parity cows compared with later parities (Supplemental Figure S2). The lactation curve for ECM was less steep for first-parity cows after peak production compared with later parities. The highest producing Holstein cows were those in Canada and the United States, whereas the lowest producing cows were in the Netherlands, reflecting the pattern obtained for DMI. For BW, the heaviest cows across parities were in Canada, while the lightest cows were in the Netherlands (Supplemental Figure S3). For all countries and parities, the expected pattern of mobilization during early lactation and deposition in mid and late lactation was observed.

Variance Component Estimates

Heritability and additive variance estimates for ECM, BW, and ΔBW are shown in Supplemental Figure S4 (https://doi.org/10.7910/dvn/sxxdcy; Stephansen,

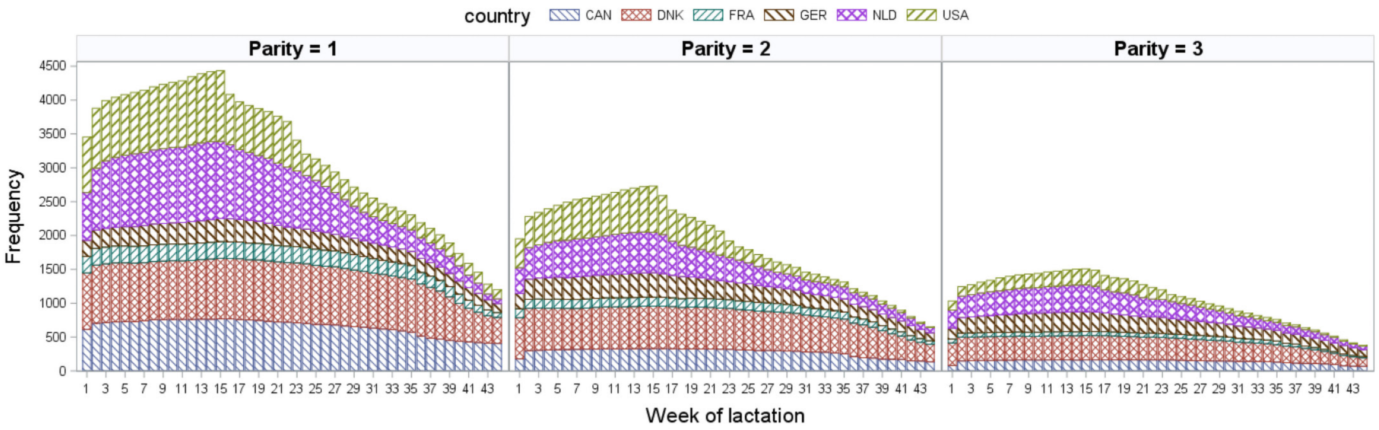

Figure 2. Number of records per week of lactation within parity, and grouped by country. Each bin represents the individual number of records for each specific week of lactation. CAN = Canada; DNK = Denmark; FRA = France; GER = Germany; NLD = the Netherlands; USA = United States of America.

2023) and heritability approximate standard errors are shown in ST1. The highest heritability was observed for ECM at first parity (range: 22–34%, depending on lactation week). Additive variance increased more at the end of lactation for ECM in second and third parity compared with first parity. For BW, heritability was highest in first parity (range: 39–52%). Extreme "tails" on additive variance were only present for BW in third parity. The derivative trait ΔBW showed a low level of heritability (<2%) in all parities (Supplemental Figure S4).

Heritability and additive variance estimates were obtained for DMI and gRFI (Figure 3). Stable additive variance was estimated for DMI in first and second parity; however, an extreme tail was reported at the end of third parity. Additive variance had a similar pattern for gRFI (Figure 3). The highest average heritability for DMI was estimated in first parity (range: 20–37%). Heritability for DMI in third parity was moderate at early and mid lactation, but was moderately high at late lactation. Third parity had the largest approximate standard errors (**ASE**) for DMI heritability. Additive variance and heritability had a similar pattern for DMI and gRFI (Figure 3); however, numerical values were lower for gRFI. Approximate standard errors for heritability tended to be larger for gRFI compared with DMI, and were highest at third parity (Table 2).

Phenotypic and Genetic Regression for DMI on Energy Sinks

The calculated genetic (Figure 4) and phenotypic (Figure 5) regression coefficients from Equation 4 were obtained for lactation during first, second, and third parity. The genetic regression coefficients for DMI|ECM was stable in all parities, and was highest in third par-

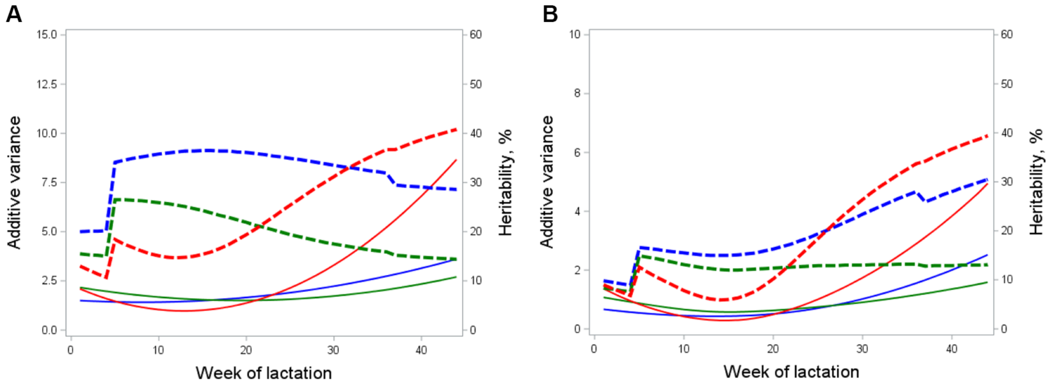

Figure 3. Plot showing additive variance (left y-axis), heritability (right y-axis), and week of lactation (x-axis) for DMI (A) and genetic residual feed intake (B). Solid line = additive variance; dashed line = heritability; blue = first parity; green = second parity; red = third parity.

Table 2. Approximate SE for DMI and genetic residual feed intake (gRFI), presented as 10th, 50th, and 90th quantiles (P10, P50, and P90, respectively)

	DMI			gRFI		
Parity	P10	P50	P90	P10	P50	P90
First	0.03	0.06	0.10	0.05	0.10	0.15
Second	0.02	0.05	0.11	0.02	0.03	0.04
Third	0.06	0.15	0.26	0.09	0.18	0.26

ity. Genetic regression coefficients for DMI|ECM were higher than the phenotypic regression coefficients for these traits. The genetic regression for DMI|BW was stable over the lactation period and 3 parities (mean: 0.012, 0.012, and 0.021 for first, second, and third parity, respectively). Phenotypic regression coefficients showed a similar pattern for DMI|BW (mean: 0.014, 0.015, and 0.014 for first, second, and third parity, respectively). The regression coefficients for DMI|ΔBW were close to zero for the phenotypic values (Figure 5); however, there was variation for the genetic regression coefficients of DMI|ΔBW (Figure 4). The pattern across lactation for the genetic regression coefficients of DMI|ΔBW was similar in first and second parity, but differed in third parity.

Estimated Genetic Correlation Across Lactation and Among Parities

Heatmaps showing the structure of genetic correlation within lactation and across parities are presented for ECM, BW, and ΔBW in Supplemental Figures S5, S6, and S7 (https://doi.org/10.7910/dvn/sxxdcy; Stephansen, 2023). For ECM (Supplemental Figure S5), the heat map shows that ECM was almost the same trait throughout first parity. In later parities, ECM changed during lactation, and the genetic correlation between early and late lactation was close to zero. Across parities on the same test day, ECM was highly correlated. The heatmap for BW showed that the trait was very stable, and was highly correlated both within lactation and across parities (Supplemental Figure S6). For ΔBW, a moderately high negative genetic correlation was obtained for all 3 parities between early and late lactation (Supplemental Figure S7). Across parities on the same test day, a moderate to moderately high genetic correlation was observed, showed that mobilization and deposition were genetically correlated across parities.

The genetic correlation structure for DMI (Figure 6) showed that DMI was stable during first and second parity. Early and late lactation were moderately to highly correlated. However, third parity showed more variability, with early and late lactation being moderately to highly negatively correlated. Across parities on the same test day, a moderate high correlation was observed, especially for consecutive parities.

The genetic correlation structure for gRFI (Figure 7) across parities showed that gRFI was highly correlated in mid to late lactation. The genetic correlation between early lactation and the later periods showed a zero to moderately high negative correlation within parity, particularly in third parity. The genetic correlation between parities for gRFI was presented with ASE (Figure 8). Genetic correlations with the lowest ASE were obtained between first and second parity, whereas the highest ASE was obtained between second and third parity. The highest genetic correlations were obtained between consecutive parities, and for the mid and late lactation periods.

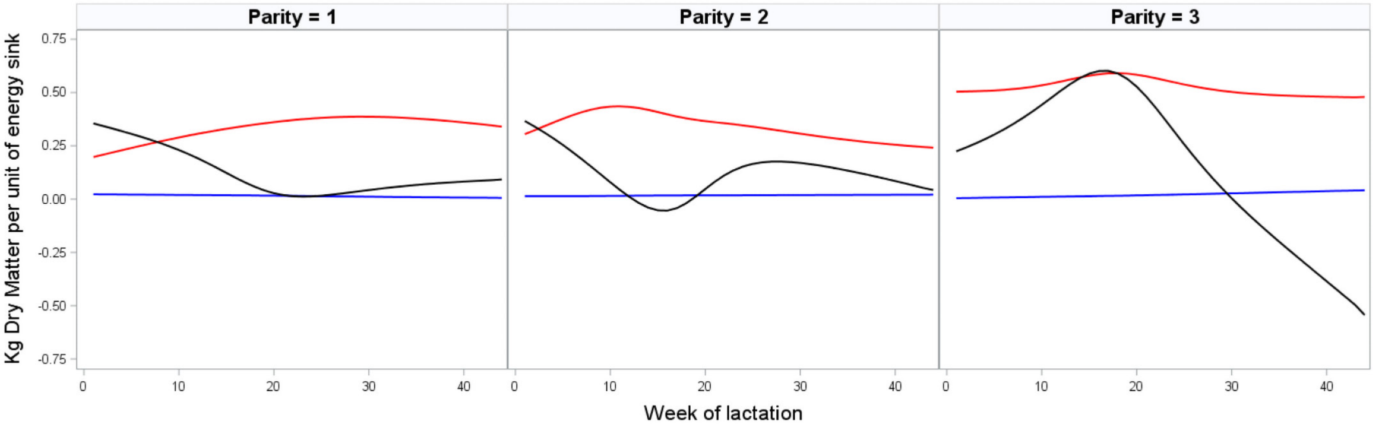

Figure 4. Plot showing genetic regression coefficients for the first to third parity. Red = ECM; blue = BW; black = change in BW.

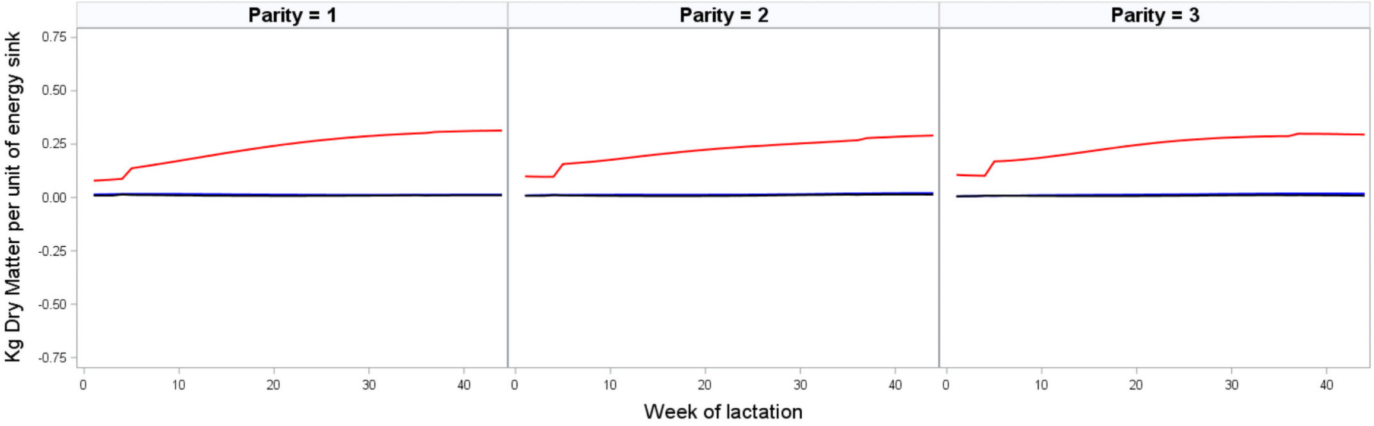

Figure 5. Plot showing phenotypic regression coefficients for the first to third parity. Red = ECM; blue = BW; black = change in BW.

Genetic Correlations Across Continents

Bivariate analysis between North America and Europe showed a high genetic correlation for DMI in first parity (0.77). The asymptotic standard error associated with the genetic correlation was 0.37.

DISCUSSION

Methodology of gRFI

Most breeding goal traits are genetically evaluated taking parity into account; however, some traits are

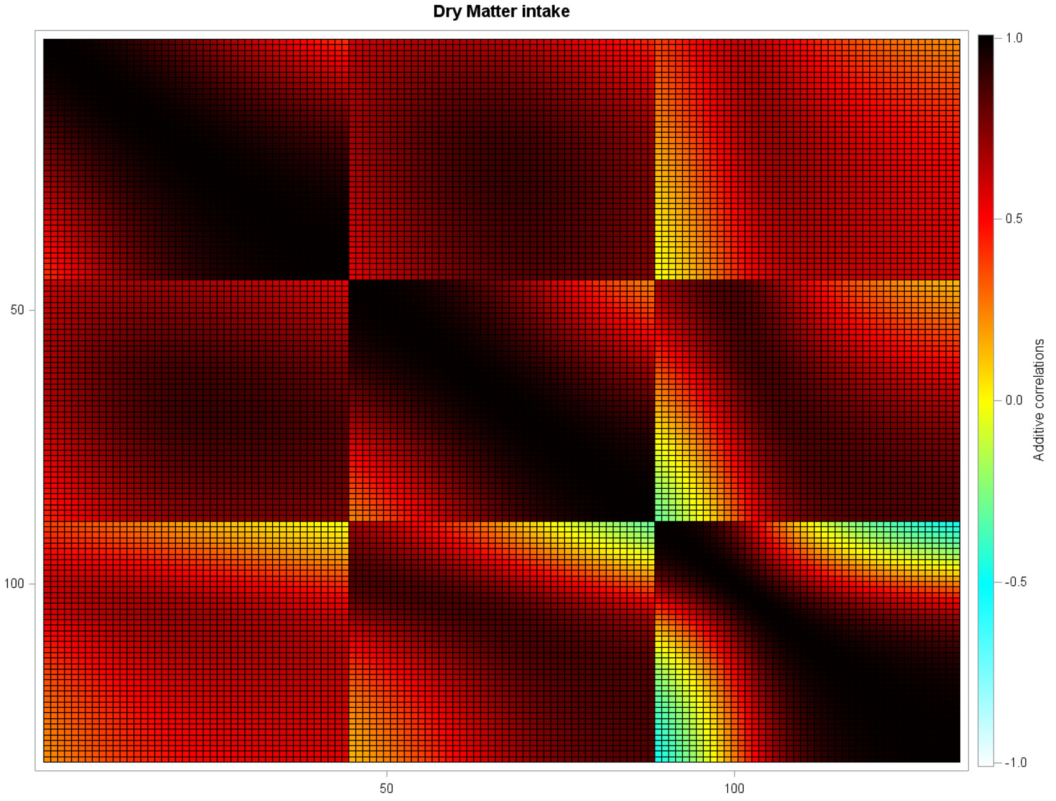

Figure 6. Genetic correlations across lactation for DMI in the first, second, and third parity. First, second, and third parity are shown in the upper left box, middle box, and lower right box, respectively. The genetic correlation between parities is presented in the off-diagonal boxes. Each pixel represents 1 wk of lactation (132 wk of lactation in total, when combining all 3 parities).

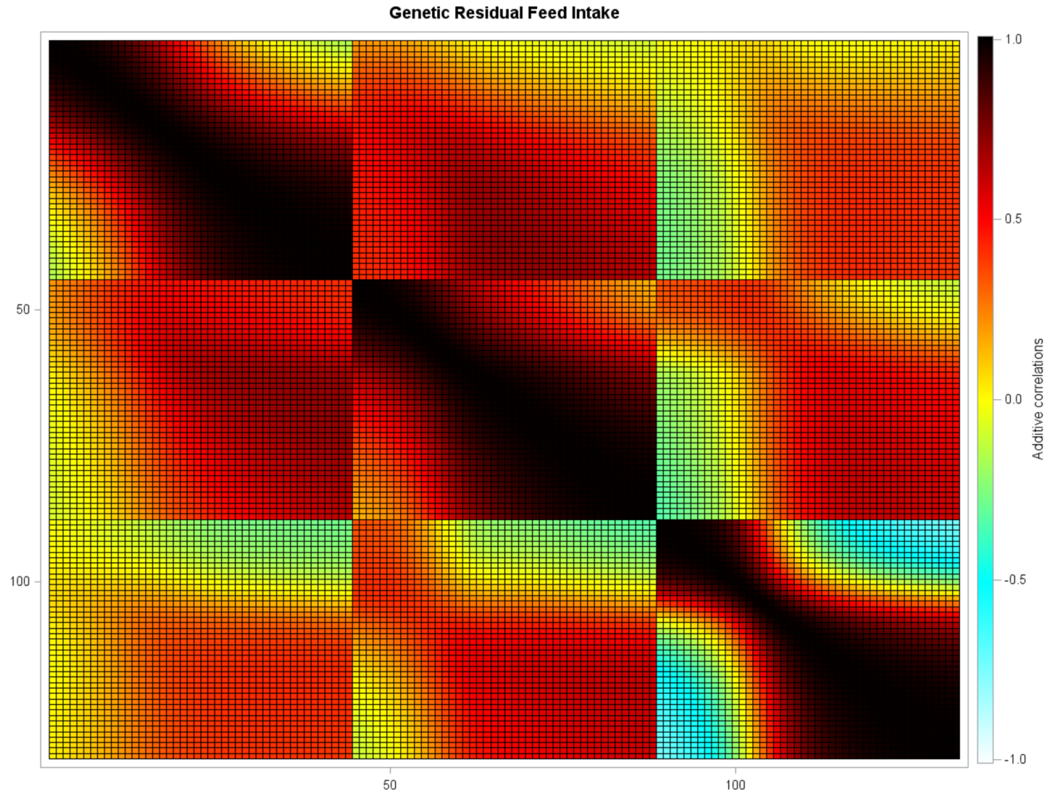

Figure 7. Genetic correlations across lactation for genetic residual feed intake (gRFI) during the first, second, and third parity. First, second, and third parity are shown in the in upper left box, middle box, and lower right box, respectively. The genetic correlation between parities is presented in the off-diagonal boxes. Each pixel represents 1 wk of lactation (132 wk of lactation in total, when combining all 3 parities).

evaluated using random regression models (**RRM**), such as milk production (https://interbull.org). This approach is used because most traits change genetically with respect to lactation and parity. However, feed intake data tend to be sparse, limiting the use of advanced statistical methods to estimate breeding values for RFI. Here, we constructed a model that had similarities to models used for test-day evaluations (Lidauer et al., 2009; Oliveira et al., 2019) and Manzanilla Pech et al. (2014). However, the mentioned studies on production traits, used higher orders of LP (3–5) on the random additive effect and estimated the variance components in a multitrait model. It is a limitation in this study that we could not model higher orders of LP and estimate variance components in a multitrait model due to the limited number of cows and records with individual DMI. The calving herd × year × season (CHYS) effect was calving season within a herd and has been used to assess the effect of herd × year × season in test-day evaluations (Lidauer et al., 2009; Oliveira et al., 2019). Random experiment nested within herd × year × month (EXP) was used in the current study to combine the 2 random effects of EXP and year × month (YM) used in Manzanilla Pech et al. (2014). Consequently, the random effect of EXP in this study captured monthly changes within the herd and experiment (e.g., changes to feed or management). The random effect of country × year × month (CYM) was used to capture the effects of monthly changes within each country. The research herd in Florida (United States) was treated as an independent country, because it is in a subtropical climate compared with the other research herds in the United States.

Some genetic evaluation centers use an across parity classical 2-stage evaluation of RFI (Parker Gaddis et al., 2021; Stephansen et al., 2021a) to estimate breeding values in a subindex for feed saved. The classical RFI model works well on small datasets with a small number of herds, but has some limitations. For instance, the handling of model fitting and measurement errors (Fischer et al., 2018) with respect to phenotypic RFI is not genetically uncorrelated to energy sinks, which is preferable as a breeding goal (Stephansen et al., 2021b). These problems could be addressed by using a multitrait approach in combination with RRM. For instance, Shirali et al. (2017) first used a multitrait gRFI RRM

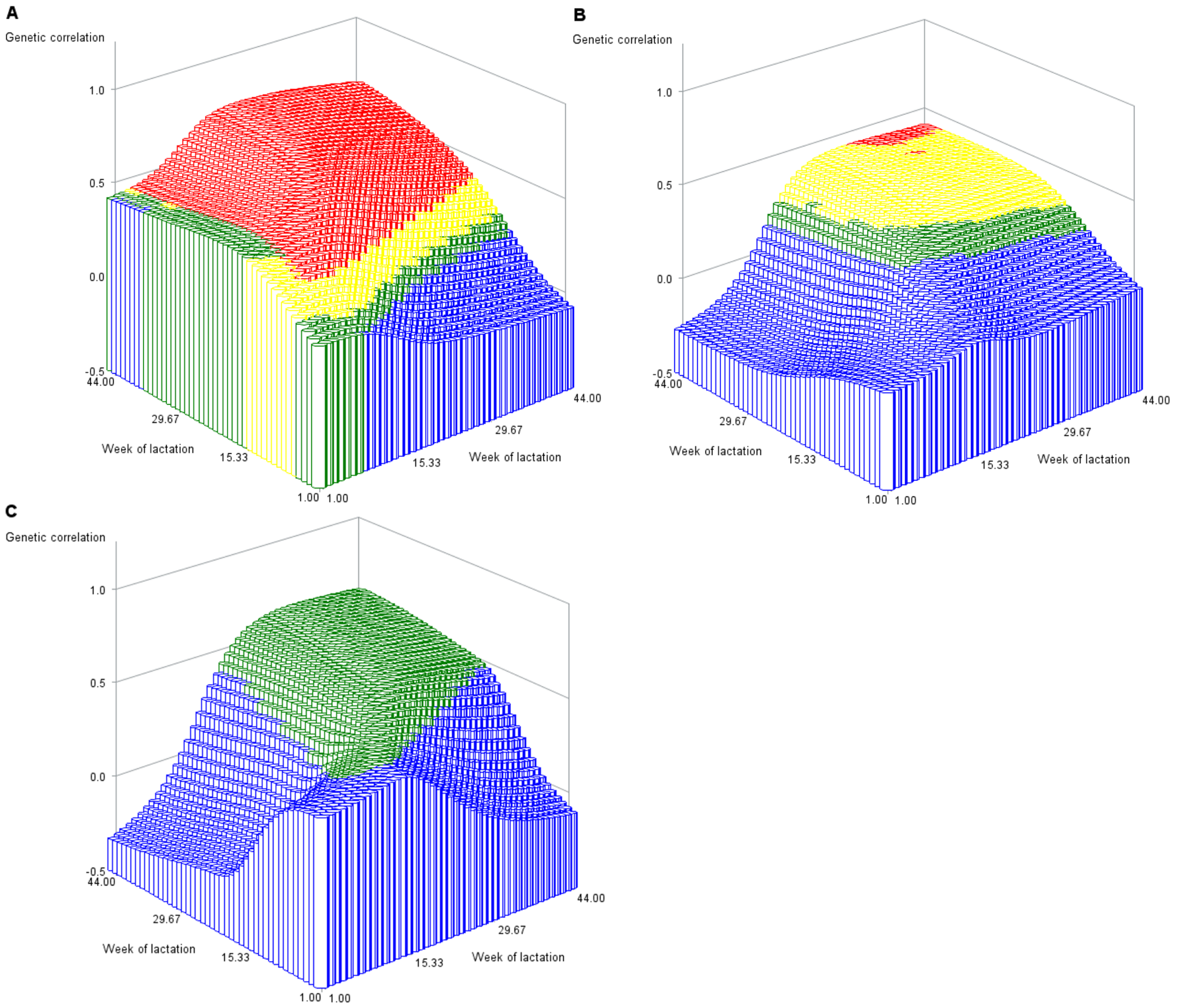

Figure 8. Genetic correlations and approximate SE between parities for genetic residual feed intake (gRFI). Plots are rotated by 40° compared with Figure 7. Genetic correlations between (A) first and second parity, (B) first and third parity, and (C) second and third parity. Colors indicate the level of approximate SE: black: SE >0.20; red: SE 0.20–0.40; yellow: SE 0.40–0.60; green: SE 0.60–0.80; blue: SE <0.80.

in pigs, while Islam et al. (2020) included ΔBW as derivative of BW in a multitrait gRFI RRM for dairy cattle. A requirement for data from first parity probably helps to avoid selection bias on variance component estimates, as shown by Lidauer et al. (2015). However, introducing this requirement to individual feed intake data in the present study would reduce the quantity of usable data significantly.

The ASE used here was based on the approximate method of Fischer et al. (2004). However, asymptotic standards errors provided directly from variance component estimation software would have been preferable. However, a full multitrait model that includes all traits (9 traits and 21 variance components) did not converge with the current dataset. Therefore, bivariate models were used in combination with the interactive summing method (Henshall and Meyer, 2002). Future research should focus on multitrait analyses of gRFI with RRM that provide asymptotic standard errors from REML analysis or Bayesian analysis presenting posterior standard deviations. However, using a Bayesian approach in a large-scale multitrait analysis of gRFI could be infeasible in terms of computational power.

Variance Component Estimate Results

Published data on RRM of gRFI remain sparse, with no studies presenting covariance between parities for gRFI. Several studies have estimated variance components for ECM and BW or metabolic body weight (**MBW**), as energy sink traits in gRFI. Body weight was used over MBW to reduce the number of traits in the model. The concept of reducing the gRFI model for one trait, was earlier described in Islam et al. (2020), by deriving ΔBW from BW. Furthermore, Tempelman and Lu (2020) demonstrated that BW was nearly a linear function of MBW, which also was stated in Khanal et al. (2022). However, an effect can be found in comparison of maintenance requirements for a very small (e.g., 500-kg Holstein cow) and a very heavy (e.g., 1,000-kg Holstein cow) cow. As earlier discussed, BW was used instead of MBW to reduce the number of traits in the variance components estimation. Tempelman and Lu (2020) suggested BW to be incorporated in a TMI, as it is already included in the Net Merit Index. The heritability for energy toward milk production ranged from 22% to 43% in first-parity Dutch cows in a study by Manzanilla Pech et al. (2014), which was supported by the current study. The current study obtained similar results to Khanal et al. (2022) with respect to the level and pattern of energy for milk production (Supplemental Figure S4). Specifically, first-parity cows had the highest heritability (30–38%), with this level being lower for later parities (13–24%). However, Khanal et al. (2022) only modeled milk energy from 50 to 200 DIM, and did not consider very early and late lactation.

Body weight has the highest heritability, with various studies showing ranges of 25% to 48% (Manzanilla Pech et al., 2014), 50% to 70% (Islam et al., 2020), 59% to 65% and 46% to 57% (Khanal et al., 2022) for first and later parities, respectively. The results of the current study supported these ranges (Supplemental Figure S4). In our study, the derivative trait of BW had very low weekly heritability, similar to Islam et al. (2020), with heritability being close to zero in Khanal et al. (2022). However, Khanal et al. (2022) showed that lactation-based heritability for ΔBW was 11% and 13% for primiparous and multiparous cows, respectively. Islam et al. (2020) obtained higher additive variance for ΔBW compared with the current study. Additive variance of ΔBW might have been higher in Islam et al. (2020) due to a higher level of additive variance for BW, and a higher acceleration for additive variance at the end of lactation.

Manzanilla Pech et al. (2014), Islam et al. (2020), and Khanal et al. (2022) reported similar levels for the heritability of DMI in first-parity Holsteins, with the results from the current study supporting these findings (Figure 3). For later parities, Khanal et al. (2022) reported heritability ranging from 13% to 24% at from 50 to 200 DIM, with our data also providing similar results (Figure 3). Covariance functions for DMI using RRM were first reported in the late 1990s (Koenen and Veerkamp, 1998; Veerkamp and Thompson, 1999). Only Islam et al. (2020) reported the level of additive variance for DMI, with extremely high levels being obtained at the end of lactation. This phenomenon was only observed for DMI in late lactation for third parity in the current study (Figure 3), thus we should be careful with the interpretation of these results. The extremely low or high additive variance level at the end of lactation has earlier been obtained by RRM (Bohmanova et al., 2008). This is because RRM places high emphasis on observations at the extremes of the time period for the measured trait, especially high order LP (Meyer, 2005).

Islam et al. (2020) and Khanal et al. (2022) reported the heritability for gRFI using partial regression coefficients (range: 10–15% and 3–13%, respectively). Veerkamp et al. (1995) and Difford et al. (2020) also reported heritability from repeatability analysis (range: 5–14%). For first-parity Holstein cows, additive variance was reported to vary around 0.5 in Islam et al. (2020), and 0.48 for Denmark and 0.27 for the Netherlands in Difford et al. (2020). In the current study, average additive variance was 0.95, 0.90, and 1.6 for first, second, and third parity, respectively. No studies have reported the level of additive variance in later parities for gRFI. The higher heritability of gRFI reported in the current study might be caused by the construction of gRFI. The genetic variance of gRFI is not affected by the residual covariance between feed intake and energy sink traits, as obtained for phenotypic RFI (Islam et al., 2020). Therefore, phenotypic RFI is expected to have higher heritability compared with gRFI, with some exceptions (Islam et al., 2020). In the current study gRFI explained 43% and 48% (range: 28–70%) of additive variance in DMI for first parity and later parities, respectively, on average. Islam et al. (2020) reported a lower range (15–40%). Difford et al. (2020) found that gRFI explained 17% and 42% of the additive variance in DMI for Danish and Dutch Holstein cows, respectively. In a symposium review, Tempelman and Lu (2020) estimated that 35% of gRFI explained DMI, which represents unexplained genetic variation of DMI. In comparison to the percentage of gRFI explaining DMI in the current study, the studies by Difford et al. (2020), Islam et al. (2020), and Tempelman and Lu (2020) showed clear heterogeneity; however, all studies showed that ECM and

BW accounted for at least half of variance in DMI, on average.

RFI Regression Coefficients

Difford et al. (2020) reported genetic regression coefficients to calculate gRFI in Danish Holstein cows as 0.31 for DMI|ECM and 0.016 for DMI|BW. An energy sink for change in body tissue was not included. In Islam et al. (2020), partial genetic regressions showed that DMI|ECM increased during lactation (from 0.2 to 0.5). Khanal et al. (2022) reported the levels of DMI|milk energy (Tempelman et al., 2015) in first parity (from 0.5 to 0.7) versus later parities (from 0.4 to 0.6) during the lactation period from 50 to 200 DIM. The pattern and level of genetic regression for DMI|ECM (Figure 4) obtained in the current study was similar to that obtained by Islam et al. (2020). In contrast, Khanal et al. (2022) obtained higher level and more fluctuating regression coefficients during first parity. This higher level might be explained by differences in the definition of energy in milk between studies. The levels for second and third parity in the current study were similar to the level of later parities obtained in Khanal et al. (2022); however, the pattern fluctuated more during lactation in Khanal et al. (2022). The genetic regression for DMI|BW or DMI|MBW was stable in all studies. The genetic regression for DMI|ΔBW differed with respect to the level and pattern during lactation in the same studies. In addition, the level of the DMI|ΔBW in all weeks of lactation in this study, was lower than feeding norms reported from NRC (2001). This inconsistency for DMI|ΔBW and feeding norms, has earlier been found in Tempelman et al. (2015), Li et al. (2017), and Islam et al. (2020). This difference might be because it is difficult to model changes in different body tissues and change in gut fill, which could mask changes in body tissue. Thorup et al. (2012) reported that the mobilization of proteins and lipids in the body generated 13.5 MJ/kg protein and 39.6 MJ/kg lipid, respectively. Deposition of proteins and lipids in the body required 50 MJ/kg protein and 56 MJ/kg lipid, respectively. Adipose tissue is the most efficient tissue; however, it is important to distinguish between the 2 body tissues, along with mobilization and deposition. Furthermore, Thorup et al. (2018) showed that residual gut fill during early lactation could mask up to 30 kg empty BW.

Phenotypic regression coefficients were similar across studies for gRFI, whereby DMI|ECM was low during early lactation and subsequently increased over the entire period. The phenotypic regression coefficients for DMI|BW or DMI|MBW were at a stable and low level. Furthermore, the phenotypic regression coefficient for DMI|ΔBW or DMI|ΔMBW varied minimally along lactation when compared with the genetic regression coefficients.

Genetic Structure Within and Across Parities

The estimated genetic correlations within lactation and across parities for energy sink traits per week are presented in Supplemental Figures S5, S6, and S7. For ECM in first parity, there was a high genetic correlation between the weeks of mid to late lactation, and a moderate to moderately high genetic correlation between the weeks of early and mid to late lactation. This result supported those of Manzanilla Pech et al. (2014) and Khanal et al. (2022). Second and third parity showed similar results to first parity; however, the genetic correlation between early and mid to late lactation was close to zero. Khanal et al. (2022) did not estimate covariance between parities for ECM, preventing comparison. The current study obtained high genetic correlations between parities for ECM (Supplemental Figure S5) on the same test day, similar to the covariance obtained by genetic evaluation centers (De Roos et al., 2001; NAV, 2022). For BW, genetic correlation was high across lactation and parities in the current study (Supplemental Figure S6), supporting Manzanilla Pech et al. (2014) and Khanal et al. (2022). This high genetic correlation for BW across parities was similar with the results in Mehtiö et al. (2021).

The current study is the first to report how genetic correlation is structured across lactation and parities for ΔBW (Supplemental Figure S7). The same pattern was found in all parities, with cows that intensively mobilize ΔBW during early lactation also intensively depositing it during mid to late lactation. Biologically, recovery is logical after a mobilization period in cows. Across parities, a moderate to moderately high genetic correlation was recorded on the same test day. Thus, intensive mobilization early in life and at later life stages appears to be genetically correlated in cows.

Genetic correlations per week for DMI (Figure 6) showed a high genetic correlation between mid and late lactation, and a moderate correlation between early and mid to late lactation for first and second parity. A high genetic correlation was obtained for mid and late lactation, whereas a moderately high negative correlation was obtained between early and mid to late lactation for third parity. Of note, third parity had the fewest records for estimating variance components. Manzanilla Pech et al. (2014) obtained a negative genetic correlation between early and mid to late lactation for first parity. Khanal et al. (2022) obtained a high genetic correlation between days in mid lactation for DMI within parity (in Supplemental File S1 in Khanal et al, 2022).

Genetic correlations per week for gRFI (Figure 7) showed a genetically stable trait at mid to late lactation, whereas gRFI seemed to be another trait during early lactation. Based on the definition of RFI, this trait should be stable through lactation. Genetic RFI might have differed in early lactation to mid/late lactation because different genes control it along the lactation. Alternatively, this difference might be due to the difficulty in modeling mobilization and deposition. Komaragiri and Erdman (1997) showed that adipose tissue stores energy more efficiently compared with muscle tissue. Thus, gRFI models need to be developed that distinguish between mobilization and deposition in different tissues to account for this complexity.

This study is the first to evaluate genetic correlations between parities for gRFI in an RRM. This novel finding is of high importance for breeding dairy cattle that are more feed efficient and climate friendly. This is because it allows us to select feed efficient cattle at mid to late lactation during first parity, with our data indicating that they would likely also be efficient in second and third parity. Furthermore, genetic correlation structure per week showed that early lactation is separate trait to mid and late lactation. When assessing between parities on the same test day, a moderate to moderately high correlation was obtained for gRFI. Thus, some of the animals that are efficient during the early part of first parity are expected to be efficient in the early part of second parity.

Across Country Estimates

In our study, we assumed a genetic correlation of one across countries in the analyses. For energy sink traits, a high genetic correlation across countries for Holstein cows is expected. For milk production, Interbull previously reported genetic correlations between countries for Holstein (median: 0.79; range 0.60–0.99; Interbull, 2021). For BW, a very high genetic correlation is expected between countries. Interbull previously reported high genetic correlations between countries (median: 0.79–0.91; Interbull, 2021) for conformation traits used to calculate body size composition (stature, chest width, body depth, angularity, and rump width; Parker Gaddis et al., 2021).

In our study, we expected energy sink traits in gRFI to have high genetic correlations across countries; however, Interbull provides no information on DMI. Typically, records exist for thousands of cows across countries on milk production and BW or body size traits; however, DMI is different. Few studies have investigated genetic correlation across countries for DMI (de Haas et al., 2012, 2015; Berry et al., 2014). The current study obtained a high genetic correlation (0.77 ± 0.37) between North America and Europe, supporting the results of Berry et al. (2014) (genetic correlations: 0.76–0.84). de Haas et al. (2015) calculated genetic correlations between separate research herds. Using a dendrogram, the herds were placed in 3 groups: (1) heifers and lactating animals in Australia, Ireland, and New Zealand; (2) lactating animals in Denmark, Germany, and the United States; and (3) lactating animals in Canada and the Netherlands. The genetic correlations between groups 2 and 3 were not estimated with sufficient accuracy to establish whether they should be treated as different traits. Of note, the accuracy of genomic predictions showed that all countries benefited from sharing phenotypes for DMI collaboratively. Thus, sharing phenotypes for DMI and energy sink traits represents an important next step together with improving the model, to achieve reasonable accuracy for breeding values of gRFI.

CONCLUSIONS

This study estimated variance components for gRFI and its component traits. We used a multitrait model where traits were modeled by parities, with data from multiple countries. We used a REML procedure to estimate the variance components with random regression methodology. Our results showed that gRFI is heritable, and that the genetic correlation structure was highly genetically correlated between lactation weeks in mid and late lactation within each parity. However, the genetic correlation between early and mid/late lactation showed low, or even negative, correlations within each parity. A moderately high genetic correlation was estimated across parity in mid and late lactation, but this correlation was low to moderate low in early lactation. Our study demonstrates that it is possible to estimate variance components for gRFI using a multitrait RRM, and that this trait is genetically correlated across parities in mid and late lactation. However, more focus needs to be placed on early lactation. In conclusion, it is feasible to select for feed efficiency in different parities without affecting the production and size of the cows, conforming with global feed saved evaluations.

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ish Columbia. As per the research agreement, researchers maintained independence in conducting their studies, own their data, and report the outcomes, regardless of the results. The decision to publish the findings rests solely with the researchers. The authors have not stated any conflicts of interest.

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