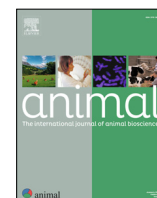




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Review: Improving residual feed intake modelling in the context of nutritional- and genetic studies for dairy cattle



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ABSTRACT

The residual feed intake (RFI) model has recently gained popularity for ranking dairy cows for feed efficiency. The RFI model ranks the cows based on their expected feed intake compared to the observed feed intake, where a negative phenotype (eating less than expected) is favourable. Yet interpreting the biological implications of the regression coefficients derived from RFI models has proven challenging. In addition, multitrait modelling of RFI has been proposed as an alternative to the least square RFI in nutrition and genetic studies. To solve the challenge with the biological interpretation of RFI regression coefficients and suggest ways to improve the modelling of RFI, an interdisciplinary effort was required between nutritionists and geneticists. Therefore, this paper aimed to explore the challenges with the traditional least square RFI model and propose solutions to improve the modelling of RFI. In the traditional least square RFI model, one set of fixed effects is used to solve systematic effects (e.g., seasonal effects and age at calving) for traits with different means and variances. Thereby, measurement and model fitting errors can accumulate in the phenotype, resulting in undesirable effects. A multivariate RFI model will likely reduce this problem, as trait-specific fixed effects are used. In addition, regression coefficients for DM intake on milk energy tend to have more biologically meaningful estimates in multitrait RFI models, which indicates a confounding effect between the fixed effects and regression coefficients in the least square RFI model. However, defining precise expectations for regression coefficients from RFI models or sourcing for accurate feed norm coefficients seems difficult, especially if the coefficients are applied to a wide cattle population with varying diets or management systems, for example. To improve multitrait modelling of RFI, we suggest improving the modelling of changes in energy status. Furthermore, a novel method to derive the energy density of the diet and individual digestive efficiency is proposed. Digestive efficiency is defined as the part of the efficiency associated with digestive processes, which primarily reflects the conversion from gross energy to metabolisable energy. We show the model was insensitive to prior values of energy density in feed and that there was individual variation in digestive efficiency. The proposed method needs further development and validation. In summary, using multitrait RFI can improve the accuracy of the ranking of dairy cows' feed efficiency, consequently improving economic and environmental sustainability on dairy farms.

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Implications

Residual feed intake is heavily used to rank dairy cows on their efficiency in nutrition and genetic studies. However, issues have

been raised regarding the biological interpretation of the model coefficients and how the model accounts for the fixed effects. We propose a multitrait modelling of residual feed intake, which can handle systematic effects better than traditional approaches, thereby obtaining more meaningful coefficients. Additionally, a novel method is proposed to derive feed energy density and individual variation in digestive efficiency. This review can lead to

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improved modelling of feed efficiency and, consequently, improve economic and environmental sustainability on dairy farms.

Introduction

The human population is expected to reach 9.7 billion by 2050 (United Nations, 2022). Consequently, the demand for food is expected to increase, and the demand for dairy products is expected to increase faster than the other main agricultural commodities (OECD/FAO, 2020). However, societal pressure to improve natural biodiversity is expected to decrease the area of arable farmland. Therefore, efficient use of farmland is required, and thus, feed efficiency in dairy cattle plays an important role in increasing dairy farm sustainability. On dairy farms, feed costs contribute more than half of the production costs (Connor, 2015). Dairy farmers are incentivised to improve their feed efficiency to improve their economic sustainability. Furthermore, improving feed efficiency might reduce the carbon footprint and environmental impact of dairy cattle. Manzanilla-Pech et al. (2022) stated that selection for feed-efficient animals would help to reduce methane emissions per produced unit, although Flay et al. (2019) found that feed-efficient dairy heifers did not emit less methane per day. In addition, improved management practices and the use of feed additives can reduce emissions of climate gases from dairy cattle (Fischer et al., 2020; Arndt et al., 2022).

The residual feed intake (RFI) model has recently gained popularity as a method for ranking the feed efficiency of individuals in various livestock species (Veerkamp et al., 1995; Aggrey et al., 2010; Berry and Crowley, 2013; Shirali et al., 2017; Olijhoek et al., 2020). Historically, literature reviews have covered the theory of different RFI models together with other feed efficiency definitions (Berry and Crowley, 2013), the mathematical properties and comparison between RFI and other feed efficiency measures (Tempelman and Lu, 2020), and the disentangling of the RFI model in Martin et al. (2021a). However, a recent study by Lidauer et al. (2023) questioned the biological interpretation of the regression coefficients from RFI models, especially from dry matter intake (DMI) on milk energy. The regression coefficients on energy sinks are often not biologically credible when considering nutrition theory. Tempelman et al. (2015) argued that regression coefficients of DMI on milk energy and metabolic body weight (MBW) were biologically meaningful when they were estimated per research farm. However, there was a high level of heterogeneity in the observed regression coefficients. In addition, Fischer et al. (2018a) showed that 41–47% of the variance in the residual ranking phenotype reflected measurement and model fitting errors in a residual energy intake model. Research has proposed multitrait (MT) modelling of RFI (Kennedy et al., 1993; Veerkamp et al., 1995; Islam et al., 2020; Martin et al., 2021b) as an alternative to the traditional least square method of RFI (Koch et al., 1963). Based on the aforementioned issues with the RFI model, this study aimed to explore ways to (1) avoid error accumulation in the phenotype from RFI models, (2) present the differences between the expected and the observed levels for regressions coefficients, and (3) propose solutions on data collection and model choice to improve or replace RFI models that can be used for genetic and nutrition purposes.

Background of residual feed intake models in nutrition and genetic studies

Over the last century, feed efficiency improvements have primarily been a side effect of the increase in production level that dilutes the feed requirements from maintenance (VandeHaar et al., 2016). However, even though modern dairy cows have a superior production efficiency, Potts et al. (2017) suggested that

there has been a decline in apparent digestive efficiency from 1970 to 2014. Further, with the current production levels of high-yielding dairy cows in most countries, an additional increase in milk yield would have only a limited effect on feed efficiency. In addition, it may adversely affect important life functions (e.g., fertility or metabolic disorders) and robustness (Roche et al., 2009; Oltenacu and Broom, 2010). Therefore, other options to further improve feed efficiency in dairy cattle populations are needed, such as genetic progress and dairy herd management improvements. From a management perspective, feed efficiency and feed intake phenotypes on the cow level could improve management decisions at culling, feeding, and reproduction. Fischer et al. (2020) showed that information on individual feed intake could increase herd efficiency through restricted feeding, bringing the least efficient cows closer to the most efficient ones.

The most efficient way to improve feed efficiency through genetic enhancement is by using RFI to directly include feed efficiency in the total merit indices (TMIs). In theory, feed efficiency is independent from the main drivers in a TMI (e.g., milk production). Thus, including feed efficiency in TMI would not require adjustments of economic weights for double counting, making it an elegant approach (Stephansen et al., 2021a). Another approach to include feed efficiency in a TMI is through the inclusion of DMI (Veerkamp et al., 2014; de Jong et al., 2016) in the TMI. On the trait level, the genetic evaluation of DMI is typically simpler than RFI because it only requires one phenotyped trait versus multiple phenotypes required for RFI equations (e.g., DMI, milk production, and BW). However, including feed efficiency in a TMI through DMI introduces challenges when setting the breeding goals because DMI is highly correlated to sub-traits in a TMI (e.g., milk production and BW). For the principle of independence from other important TMI traits, RFI is often included in a TMI in combination with maintenance requirements as “Feed Saved” (Pryce et al., 2015). Most genetic evaluation centres that have implemented a selection index for feed efficiency in a national TMI use Feed Saved (Jamrozik et al., 2021; Parker Gaddis et al., 2021; Stephansen et al., 2021b).

Residual feed intake reflects the cow's ability to convert feed into product without an effect on the individual cow's production level, body size, and energy status. Koch et al. (1963) first proposed the classical RFI model in beef cattle as the residual of regressions for DMI on different energy sinks with correction for fixed effects (e.g., seasonal and lactation periods). This least square regression analysis of RFI has been applied in nutrition (Guinguina et al., 2020; Olijhoek et al., 2020) and genetic studies (Veerkamp et al., 1995; Tempelman et al., 2015; Li et al., 2017), where the “energy sink model” provides a residual. That residual is used for the phenotypic ranking of animals and further as a phenotype in genetic models. This procedure to estimate breeding values for RFI is defined as the two-step method (Berry and Crowley, 2013; Tempelman et al., 2015). In most cases, the RFI phenotype is treated as longitudinal. Therefore, a permanent environmental effect is included in the genetic model step presented below:

$$1^{st} \text{ step} : DMI = \text{fixed effects} + \beta_i E_i + \varepsilon \quad [1]$$

$$2^{nd} \text{ step} : \varepsilon = a + pe + e \quad [2]$$

where DMI is the phenotype for DM intake; fixed effects cover seasonal, lactation stage, etc. effects; β_i is the regression coefficient of the i^{th} energy sink trait; E_i is the i^{th} energy sink trait; ε is the residual of the first step (“energy sink model”); a is the additive random effect of an animal; pe is the random permanent environmental effect; and e is the residual of the genetic model. Within the classical RFI models, a one-step procedure has been proposed for genetic evaluation (Tempelman et al., 2015). The two-step and one-step

classical RFI methods are highly correlated (Tempelman et al., 2015), meaning that the impact of model choice is limited for selection purposes.

When an RFI model considers all of the important life functions (i.e., energy sinks), the energy sink coefficients are estimated accurately with an animal effect, and all measurements are error-free, then the variation of the residuals will be zero in theory. In that situation, the model fits the data perfectly (Saviotto et al., 2014). However, in practice, variation will exist for the residuals of the model [1] because (1) measurement errors are highly likely to occur, (2) not all of the important life functions are easily measured at a large scale, (3) precise separation of different effects for vital life functions seems difficult, meaning the estimated coefficients do not correspond to the theoretically expected energy costs, and (4) individual variation exists on the efficiency of converting gross energy into available energy for the cow, and also on energy partitioning between different energy losses such as methane, urine, heat and faeces (Guinguina et al., 2020). The following section will explore how MT modelling of RFI can potentially reduce problems with error accumulation in the residual.

How to reduce problems with error accumulation in residual intake models?

To reduce problems with the accumulation of errors in RFI models [1], we propose an MT approach to model RFI, which has been demonstrated earlier (Kennedy et al., 1993; Veerkamp et al., 1995; Islam et al., 2020; Martin et al., 2021b). Kennedy et al. (1993) proposed a genetic MT RFI model, meaning the regression coefficients of the energy sinks are estimated from the genetic (co)variance matrix rather than from the phenotypic (co)variance matrix. However, the method of Kennedy et al. (1993) was based on a simpler MT model (repeatability) that ignores changes in variance over time. Martin et al. (2021b) proposed using an MT random regression model in a dynamic phenotypic RFI model to account for changes in variance over time. Stephansen et al. (2023) extended this model to include a genetic component. The advantage of an MT random regression model over the classical RFI model [1] is its ability to handle measurement errors separately for the different traits (e.g., DMI, energy-corrected milk (ECM), and BW). This can be seen from a simple MT example:

$$\begin{bmatrix} y_1 \\ y_2 \end{bmatrix} = \begin{bmatrix} X_1 \\ X_2 \end{bmatrix} \begin{bmatrix} \beta_1 \\ \beta_2 \end{bmatrix} + \begin{bmatrix} Z_1 \\ Z_2 \end{bmatrix} \begin{bmatrix} \alpha_1 \\ \alpha_2 \end{bmatrix} + \begin{bmatrix} \varepsilon_1 \\ \varepsilon_2 \end{bmatrix} \quad [3]$$

where y_i is the vector of observations for the i^{th} trait, β_i is the vector of fixed effects for the i^{th} trait, α_i is the vector of random animal effects for the i^{th} trait, ε_i is the vector of random residual effects for the i^{th} trait, and X_i and Z_i are the incidence matrices relating records of the i^{th} trait to the fixed and random animal effects, respectively (Mrode and Thompson, 2014). Equation [3] allows each trait to be modelled with specific fixed and random effects, while all traits in a least square Eq. [1] must be corrected by the same set of fixed and random effects.

Theoretically, the MT model is more flexible, which should reduce model fitting errors and measurement errors going into breeding values or animal effects. Tempelman and Lu (2020) recommended using the conditional MT theory proposed by Kennedy et al. (1993) over the least square regression. Tempelman and Lu (2020) argued that missing records were allowed in an MT RFI model for one or more traits, and it, therefore, mitigates the potential effect of measurement errors on the energy sink traits, which can distort partial regression estimates in a linear model. Veerkamp et al. (1995) also suggested that the difference in estimating fixed effects between the MT and least square RFI can result in different rankings of animals. Martin et al. (2021c) tested

the effect of combining datasets in an MT random regression RFI model. In addition, Martin et al. (2021c) compared RFI estimates between the MT random regression RFI model and the least square RFI model, where a correlation of 0.77 was reported, indicating reranking among animals. A high correlation (> 0.94) was obtained between variance components of the MT random regression RFI model on a merged dataset. This highlights that contemporary group corrections in the MT random regression RFI model adequately account for differences between the two feeding environments. Martin et al. (2021c) concluded the MT random regression RFI model can produce reliable residuals for ranking animals in pooled datasets when animals are raised in similar production systems.

Literature has demonstrated that the MT RFI is preferable to the least square RFI model. However, most genetic and nutrition studies have not adopted the MT modelling of RFI for different reasons: The least square modelling of RFI is easier and fits well in most readily available statistical software (e.g., R, SAS, and Python) and MT modelling requires more advanced and specialised software, which is mainly used by geneticists (e.g., DMU (Madsen and Jensen, 2013), BlupF90 (Misztal et al., 2002), and WOMBAT (Meyer, 2007)). Furthermore, in the case of intensive (nutrition) studies, the number of cows and records is limited. This can lead to an MT RFI model that provides estimates with high SEs or that will not converge. In that case, using either least square RFI or a feed conversion ratio will be preferable. To promote the use of software that can solve MT RFI models, we have generated a simple example using DMU (Supplemental Material S1) and WOMBAT (Supplemental Material S2), which have a no-fee license when used for research purposes.

An estimated co-variance matrix is generated as part of the DMU and WOMBAT output. The matrix notation in Kennedy et al. (1993) or Tempelman and Lu (2020) is followed to compute the regression coefficients from a repeatability analysis. In Supplemental Material S3, we have generated examples in R, Python, and SAS-IML to calculate the regression coefficients and the RFI phenotype from a repeatability MT analysis. In the case of MT random regression RFI modelling, the examples from Supplemental Material S3 can be extended to calculate regression coefficients and the RFI phenotype in different time periods. Matrix notifications are presented in Islam et al. (2020) or Martin et al. (2021b). In the following section, we will address the interpretation of the computed regression coefficient of RFI models for both least square and MT RFI models.

Do residual feed intake partial regression coefficients really need to match energy requirement values?

The traits included as energy sink variables in an RFI model are usually components of net energy (NE) outputs: milk production corrected for nutrient content, maintenance as metabolic BW, and BW gain or loss. Thus, in theory, in a perfect model where the NE content of the diet is known, the coefficients estimated in the RFI regression should be estimates of the biological efficiencies of these energy-consuming processes, i.e., the energy requirement values. However, as indicated below, this is often not the case. Whether the RFI model's partial coefficients must match the energy requirement values depends on the model's intended use. If the RFI model is intended to rank cows from low to high feed efficiency, the value of the corresponding energy requirement is negligible as long as the model ranks cows correctly.

There are different reasons for a mismatch between partial coefficients and energy requirement values. First, a multivariate linear regression is used as a residual model, but this relies on the assumption that the components are independent, which is

not the case for RFI model components (Martin et al., 2021b). Therefore, it is likely that some degree of collinearity will be present between components of the RFI model. The collinearity could alter the partial coefficient estimates, creating a deviation from the expected value for a given component. Another factor that will affect partial coefficients is an underlying assumption of the RFI models that the NE proportion of gross energy is fixed regardless of the DMI (Martin et al., 2021a). Further, the NE content of the diet might vary between and within herds. The type of feeding can affect the NE content (e.g., if the herd is divided into groups receiving different rations or if cows are fed a partial mixed ration with individual levels of concentrate allowance) or individual behaviour can create between-cow variation in concentrate intake and diet energy density. For example, Daniel et al. (2016) reported a CV of 6.35% for NE MJ/kg DM. Kristensen et al. (2015) reported the mean (SD) energy density in diets from Danish commercial herds with either Holstein, Jersey, or mixed breed cows of 6.45 (0.18) NE MJ/DM, 6.49 (0.22) NE MJ/DM, and 6.44 (0.19) NE MJ/DM, respectively. These differences in management and productivity of the population used for the RFI model might introduce noise, which could affect the partial coefficients to the point where they do not match the energy requirement values. Furthermore, the between-herd variation of NE might increase because of the assumptions and errors of the feeding system used, which differ between countries (Vermorel and Coulon, 1998). Even if the model could account for between-herd variation, the calculation of NE uses feeding system equations that differ between countries. These can generate a non-linear bias between the local feeding situation (e.g., diet composition and production level) and the general average that the feeding systems represent (e.g., Ellis et al. (2006)).

To partially overcome the issues with the NE as a proportion of gross energy, the RFI model could be changed to a residual energy intake model where DMI is substituted with NE intake. This approach was used by Fischer et al. (2018a), who calculated RFI from a linear regression model. In this alternative, NE intake for the individual can be estimated using a reference feeding system, ideally the same for the entire population used. If obtaining the NE intake is not possible, then only herds receiving a unique TMR for all lactating cows should be used to perform the residual ranking, as then the feedstuff effect will be accounted for in the random herd effect. This means the breeding values in other herds will be predicted without direct phenotypic data. However, this might create biased estimated breeding values in herds with more than 1 TMR or separate concentrate and forage feeding for lactating dairy cows.

The estimated values of the partial coefficients can be relevant if the partial coefficient has to be used for further analyses or if the estimated value affects the residuals and the ranking of the cows (Lidauer et al., 2023). Lidauer et al. (2023) have proposed to overcome this issue by assigning default coefficients to the components of the NE. Instead of the classic RFI regression on energy components, the DMI is regressed on the expected DMI (ReFI), which is calculated with fixed coefficients obtained from nutrition studies. This approach removes the issue of possible bias in the partial coefficients due to collinearity issues. Other alternatives for dealing with collinearity could be a partial component regression or a partial least square regression model. Furthermore, the issue with the possible discrepancy between NE intake and DMI (both between and within herds) is not solved by the ReFI approach if it is still based on DMI. Choosing the coefficients might also be an issue, especially when the ReFI model has to be applied to a broad and diverse population. Lidauer et al. (2023) estimated a negative genetic correlation between ReFI and ECM (-0.47 ± 0.22), meaning selecting for more efficient animals in terms of ReFI will give higher-yielding cows. As earlier addressed, including RFI or DMI in a TMI is economically equivalent. Residual feed intake is challenging to model but easy to implement in a TMI, whereas DMI

is easier to model but more challenging to implement in a TMI. In the TMI context, ReFI becomes an intermediate method. However, it requires all traits present for genetic evaluation on the exact same test day (as for classical RFI), accurate feed norm coefficients for the population, and an economic value that is corrected for the covariance structure to other traits in the proposed TMI. For these reasons, RFI or DMI is preferable to implement in a TMI over ReFI. However, it could be beneficial to fix one or more coefficients in the estimation process of MT RFI. This could be done for measures where both the measure and the energy content are accurate and precisely determined, such as milk production. A possible way to do this could be using the “desired gain” theory using Lagrange Multipliers, as seen in Nielsen et al. (2006). Preferably, the constraint(s) are implemented in the estimation process of the covariance structure in an MT RFI model. Random regression models with constraints on the polynomial correlation structure have been tested (McGowan et al., 2023). The following section will provide an overview of the observed regression coefficients from different types of RFI models.

Observed regression coefficients from residual feed intake models

For dairy cattle, several papers use RFI models that present regression coefficients from the “energy sink model” or the covariance structure of the model. However, the definition of the trait varies in these studies. We summarised regression coefficients in Table 1, standardising the traits for simplicity (see footnotes in Table 1). In the studies that do report regression coefficients, the regression coefficients for ECM, MBW, and change in BW (Δ BW) varied from 0.04 to 0.91 kg DMI/kg ECM, 0.006–0.22 kg DMI/kg MBW, and -0.002 – 14.2 kg DMI/kg Δ BW, respectively. Even within the same model, different research farms produced different estimates for the regression coefficients, but in general, for milk energy and maintenance, they agreed with NRC 2001 (Tempelman et al., 2015).

In addition to the effect of diets having different NE contents, another explanation for the observed heterogeneity in regression coefficients can be the traits used to account per se and inherent correlations between predictor traits (e.g., bigger cows produce more milk). Using Δ BW in an RFI model assumes the energy density of different body tissues (e.g., adipose and muscle) is equal in catabolic and anabolic processes. This assumption is incorrect, and according to Thorup et al. (2012), it is important to distinguish between energy coming from adipose tissue or protein tissue and whether these tissues are mobilised or deposited. Adipose tissue contains more energy and is considerably more efficient at storing energy than body protein. Studies have tried to overcome this issue by splitting Δ BW into loss and gain traits (Mehtiö et al., 2018; Fischer et al., 2018a). However, the assumption of homogenous energy density between adipose and protein tissue is still present when splitting Δ BW into loss and gain. The inability to appropriately model the change in energy status of dairy cows in a way that accounts for the different mobilisation and deposition properties of different tissues could cause a confounding effect with the other energy sinks. This can consequently provide heterogeneity in estimates of regression coefficients. Studies have tested different approaches for modelling body energy changes (Friggens et al., 2007; Hurley et al., 2016; Fischer et al., 2018b) but are often limited to a few animals and the use of visual subjective assessment of animals' adiposity levels.

From Table 1, studies using an MT approach over classical analysis of RFI had more biologically meaningful regressions for DMI|ECM and DMI|MBW, as they were closer to nutrition norms. This can be seen by comparing the US data from the study of

Table 1
Overview of regression coefficient levels from dairy cattle studies, estimated from different types of residual feed intake models using the energy sink traits for milk energy, maintenance and changes in BW, in nutritional and genetic studies.

Paper, model type	Number of cows, breed and parities	Regression coefficients		
		MilkE kg DM/kg MilkE	MBW kg DM/kg MBW	ΔBW kg DM/kg ΔBW
Connor et al. (2013), 2-step	287 MP HOL	0.22 ¹	0.096 ¹	1.33 ¹
Tempelman et al. (2015), 2-step	4 893 MP HOL	US: 0.45–0.59 ³ NL:0.39–0.63 ³ UK:0.47–0.48 ³	US: 0.08–0.16 NL:0.06–0.10 UK:0.06–0.07	US: 0.13–0.39 NL:0.07–0.27 UK:0.06–0.35
Veerkamp et al. (1995), 2-step	204 MP HOL	0.12 ²	0.06 ²	2.2 ²
Li et al. (2017), 1-step	747 PP HOL	Horizontal: 0.15 Partial:0.04–0.18 ³	Horizontal: 0.08 Partial:0.07–0.11 ³	Horizontal: 0.57 Partial: 0.0–1.1 ³
Tempelman et al. (2015), 1-step	4 893 MP HOL	US:0.40–0.50 ⁴ NL:0.24–0.61 ⁴ UK:0.24–0.27 ⁴	US: 0.10–0.14 NL:0.02–0.16 UK:0.05–0.07	US: 0.06–0.25 NL:0.08–0.32 UK:0.04–0.27
Martin et al. (2021b), pRFI	564 MP HOL	Partial: 0.22–0.30	Partial: 0.09–0.22	NR
Veerkamp et al. (1995), pRFI	204 MP HOL	0.10 ²	0.05 ²	1.5 ²
Khanal et al. (2022), gRFI	2 532 PP HOL	0.60 to 0.91 ⁴	0.11 to 0.16	–0.002 to 0.014 ⁵
	2 379 MP HOL	0.48 to 0.81 ⁴	0.12 to 0.14	–0.003 to 0.004 ⁵
Veerkamp et al. (1995), gRFI	204 MP HOL	0.15 ²	0.006 ²	14.2 ²

MilkE=milk energy, MBW=metabolic BW, ΔBW=change in BW, 2-step = two step RFI model, MP=Multi-Parous, HOL=Holstein, PP=Primi-Parous, 1-step = one step RFI model, pRFI=multitrait phenotypic RFI model, NR=Not Reported, gRFI=multitrait genetic RFI, ECM=energy corrected milk,

¹ Corrected from Mcal to kg DM by a 0.3545 Mcal/kg DM calculated from the average density in feed over the three parity groups in Connor et al. (2013).
² Corrected from MJ metabolisable energy to DM by a factor 11.725. The factor was calculated as the average energy density in feed ((11.55 + 11.90)/2) reported in Veerkamp et al. (1995).
³ Value obtained from Fig. 1 in Li et al. (2017).
⁴ Correction of Mcal to ECM by a factor of 1.3325 Mcal/kg ECM (4.184 Mcal/MJ divided by 3.14 MJ/kg ECM).
⁵ Corrected from metabolic body weight to BW by $(b \times 700^{0.75})/700$ kg BW.

Tempelman et al. (2015) with Khanal et al. (2022) and Li et al. (2017) with Martin et al. (2021b). This indicates that solving the RFI model in an MT random regression setting instead of a least square model will better handle measurement and model fitting errors, reduce confounding between the fixed effects and regression coefficients, and allow time-period-specific regression coefficient estimates.

Often, it is assumed that the relative importance of the biological mechanisms behind the RFI concept would be the same along lactation and across parities. However, this is not the case. Khanal et al. (2022) and Stephansen et al. (2023) indicated that improperly accounting for mobilisation caused a low genetic correlation between early and mid-to-late lactation. However, it is likely that in addition to the stage of lactation, different genes control how efficient animals are. In that case, Fig. 1 suggests that feed efficiency varies more over the lactation than milk production in a test-day model and BW (Khanal et al., 2022; Stephansen et al., 2023). It is important to understand where the variation in RFI originates and to understand this variability of RFI over the lactation. Fischer et al. (2018b) used frequent measurements to overcome the accumulation of errors in the RFI phenotype for dairy cattle. A limited contribution was seen from body reserves management when correcting the DMI phenotype for energy sinks. This indicates that the lack of modelling of mobilisation and deposition cannot entirely explain the negative genetic correlation between early and mid-to-late lactation of RFI. In Fischer et al. (2018b), the variation in RFI was related to the activity (26.5%), feeding behaviour (21.3%), unidentified activity (10.6%), rumen temperature, digestibility and body reserves management (0.5%), and others (41.1%). The largest variation source of residual energy intake was “others.” It is impossible to assess the extent to which “other” changes over lactation have a genetic basis relative to possible phenotypic changes through lactation. Indeed, the modelling of body reserve management by Fischer et al. (2018b) was based on the summed body condition

scores (BCSs) multiplied by the average BW during the experimental period. Using an indicator of body reserves management may not always be accurate enough to capture the full variability of the core trait. Richardson and Herd (2004) studied the biological basis of RFI in Angus steers and found the three main contributors were protein turnover, tissue metabolism, and stress, accounting for 37% of the variability. However, in growing animals, the early lactation dilemma is not present, which limits the generalisability to dairy cattle. To the authors' knowledge, there is sparse literature on how biological processes such as activity and feeding behaviour change over the lactation period from a genetic point of view, but few phenotypic studies have been conducted (Connor et al., 2013; Olijhoek et al., 2020; Thorup et al., 2023). Another reason for the changes in RFI throughout lactation could be the pollution of the residuals that arises from variation among individuals in digestibility (Martin et al., 2021a). The RFI concept is often referred to as metabolic efficiency, which assumes no population variation in the process of converting gross energy into metabolisable energy. However, Phuong et al. (2013) presented differences in each step of the conversion from one energy level to another. Significant variation in converting gross energy into metabolisable energy in the population might interfere with the RFI model. The observed variability on regression coefficients with the same model by Tempelman et al. (2015) could be caused by this non-identified variation in converting gross energy into metabolisable energy among cows. In theory, it seems attractive to include digestibility in the RFI equation, but from a practical point of view, it is challenging. The following section will address the practical and theoretical considerations of building an RFI model that includes digestibility.

Can residual feed intake models be improved?

This section explores and discusses how RFI models and data for this model can be improved in future research. The proposed RFI

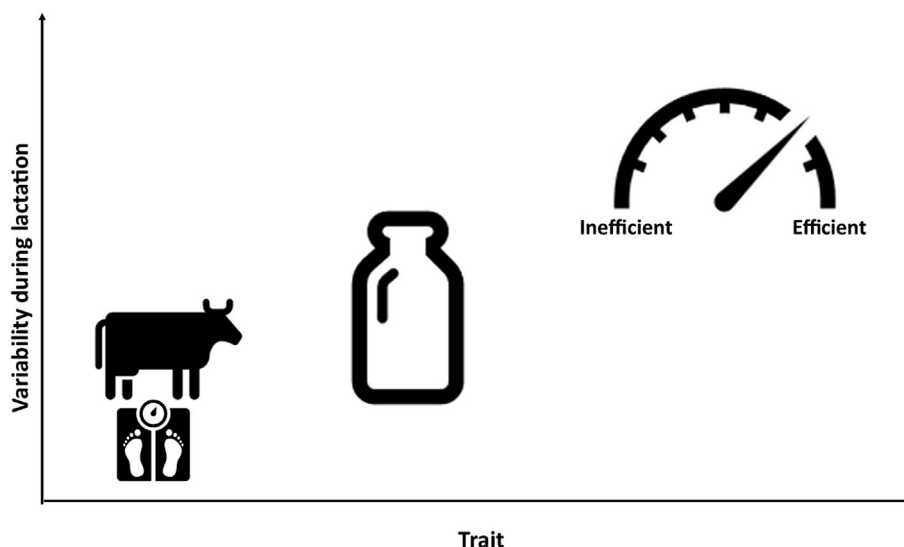


Fig. 1. Genetic variability of BW, milk production and feed efficiency during a lactation for dairy cattle.

model should be appropriate for use in nutrition and genetic studies, and also for genetic evaluation.

The ideal model should be informative on the ranking of animals according to their ability to utilise the energy input as efficiently as possible for the product and be applicable in practice. To make the model applicable in practice, we propose a model that can have a sufficient number of records to achieve satisfactory accuracy and simultaneously reflect the animals' efficiency with an acceptable degree of detail. Martin et al. (2021a) described the nature of the residuals from RFI models. Here, we extend their rationale. An important assumption for our model proposal is that the RFI model is an MT random regression to reduce error accumulation as earlier described, and also to model Δ traits as derivatives from the original traits, as described by Islam et al. (2020) and Martin et al. (2021b). The proposed model is as follows:

$$Elnt = \mu + \beta_1 MilkE + \beta_2 EBW + \beta_3 BL + \varepsilon \quad [4]$$

and

$$Elnt = eDIG \times DMI \quad [5]$$

where μ is the intercept of the model, Elnt is the energy intake, eDIG is the digestive efficiency, MilkE is the energy in milk, EBW is the empty body weight, BL is body lipids, and ε is the residual effect.

Elnt is the energy intake calculated from DMI and eDIG (digestive efficiency) phenotypes. Digestive efficiency is defined as the part of the efficiency associated with digestive processes and largely reflects the conversion from gross energy to metabolisable energy. The conversion from gross energy to metabolisable energy includes the loss of faeces, which alone results in digestible energy, and the loss of enteric methane and urine energy. Using DMI instead of digestible energy, metabolisable energy, and NE intake avoids making assumptions on variability among cows for digestive efficiency and energy lost as CH_4 , urine, and heat associated with feed, which is important because variations among cows in digestive efficiency (Phuong et al., 2013; Guinguina et al., 2020) and nitrogen efficiency (Phuong et al., 2013) have been documented. Thus, using DMI instead of digestible energy, metabolisable energy, or NE intakes gives the potential for a higher variance for the RFI index/phenotype. However, using DMI as a trait for energy intake assumes that methods of converting fresh matter into DMI do not introduce bias (Seymour et al., 2019). From

a practical perspective, DMI is a much less complex trait if the kg of feed on the individual level is available, whereas digestible energy, metabolisable energy, and NE require more complex analytic methods (NRC., 2001; Volden, 2011). Historically, feed intake has been recorded in research and nucleus herds using individual (either manual or automatic) feed intake registration methods. These methods are costly and labour-intensive. A novel method to record feed intake was proposed by Lassen et al. (2018) at the World Congress for Genetics Applied to Livestock Production. The developed Cattle Feed InTake technology has the potential to provide the data required to accurately assess feed efficiency in nutrition and genetic studies on a large scale (Lassen et al., 2018; Lassen et al., 2023; Manzanilla-Pech et al., 2023). However, the Cattle Feed InTake system measures the volume of feed (Lassen et al., 2023) but the current conversion method assumes a constant DM content when converting feed intake into DMI. That discrepancy could affect the analysis of Cattle Feed InTake data.

eDIG accounts for the variation among cows in digestive efficiency. It is important to note that when this is estimated within the framework of an RFI equation, eDIG expresses digestive efficiency as earlier defined, while digestive efficiency was not included in the Eq. [4]. It is captured in Eq. [5]. Martin et al. (2021a) have suggested a method to incorporate digestive efficiency into [4], which will be detailed later in this paper. To the author's knowledge, there is currently no cost-effective or easy method to measure digestibility accurately on a large scale. In the following section, we describe potential ways to measure, predict, or derive digestive efficiency on the cow level.

MilkE accounts for the energy used to produce milk. A phenotype for energy used for milk production can be formed in various ways (Sjaunja et al., 1990; NRC., 2001; Hall, 2023), but the general aim is to standardise milk for at least fat and protein content. Therefore, the energy needed for milk production between cows is comparable. The accuracy of different equations to calculate milk energy varies, and including more milk components increases the prediction accuracy of milk energy (Hall, 2023). The most accurate equations of milk energy included milk fat, protein, and lactose and used the respective energy values of the milk components as coefficients (Hall, 2023). The predicted energy in milk deviated the least from the measured milk energy in the following equations:

$$NASEM (2021): \text{Mcal/kg milk}$$

$$9.29 \times \text{fat, \%} + 5.5 \times \text{crude protein, \%} + 3.95 \times \text{lactose, \%}$$

Perrin (1958): kcal/100 g milk

$$9.11 \times \text{fat}\% + 37.4 \times (\text{total nitrogen}\% - \text{nonprotein nitrogen}\%) + 3.95 \times \text{lactose}\%$$

Sjaunja et al. (1990): kcal/kg milk

$$9.15 \times \text{fat, \%} + 5.78 \times \text{crude protein, \%} + 3.95 \times \text{lactose, \%} + 4.95$$

To further improve milk energy predictions, information from profiles of milk fat (fatty acids) and milk proteins (non-protein nitrogen, whey proteins) could potentially improve predictions (Hall, 2023). Most literature assumes a linear relationship between milk production and the energy for milk production. VandeHaar et al. (2016) projected the curve for dilution of maintenance on gross feed efficiency, showing a plateau at five times the maintenance intake requirements. However, this might be optimistic because the percentage of feed that is digested is depressed at high intakes. Here, Potts et al. (2017) found that apparent digestive efficiency decreased from 1970 to 2014 in US Holstein cows, but production efficiency increased during that period. In addition, at high intakes, the digestibility depression may neutralise the effect of dilution of maintenance, and overall efficiency may decline with increased intake (VandeHaar et al., 2016). That means that increasing feed intake for increased production levels could potentially reduce the overall efficiency of dairy cattle in the future. Breeding goals around the world typically place the highest emphasis on breeding values for milk production (Egger-Danner et al., 2015). However, this might not be ideal when selecting for the most efficient dairy cows. From the authors' view, large-scale recording of milk production is relatively easy and already feasible in the test-day recording schemes (ICAR, 2022). Furthermore, equipment in automatic milking systems and modern milking parlours can record milk production at each milking. However, to the authors' knowledge, accurate recordings of fat and protein content at the visit level are not currently available. However, some milking systems specify the level of fat, protein, and lactose (GEA, 2022; Lely, 2023).

EBW accounts for the energy to maintain the lean BW of the cow and potentially the changes in lean BW (through the derivative Δ trait), assuming that it is corrected for changes in body lipid as in Eq. [6]. Ideally, we could separate all the individual tissues (i.e., muscle, fat, or connective). However, that would require methods that are currently unavailable in large-scale recording. It is well-documented that protein and fat mass have very different maintenance requirements (Webster, 1981; Birnie et al., 2000). We propose the equation for standardising the BW into EBW from Martin et al. (2021a) to account for the maintenance of the lean body as a possibility:

$$EBW = (BW - RGF) \frac{1 - \beta(BCS - \alpha)}{1 - \beta(BCS_{std} - \alpha)} \quad [6]$$

where EBW is the empty body weight, BW is the measured body weight, RGF is the residual gut fill, α and β are assumed to be known and depend on the mature weight of the cows (Martin et al., 2021a), BCS is the observed value (assumed to be linearly related to body fat content), and BCS_{std} is the standardised BCS value (e.g., standardised to 3.00). The reason for including RGF is to avoid changes in lean BW hidden by an increasing gut fill, especially in early lactation. Residual gut fill can be calculated from the feed intake of the individual cow (Friggens et al., 2007), which allows individual variation among cows. Alternatively, RGF can be calculated as a function of days in milk (Thorup et al., 2018), which does not allow individual variation between cows. Introducing individual variation on RGF calculated from feed intake introduces potential issues with circularity because DMI will be on both sides of the RFI equation. If RGF is assumed to be constant across cows, RGF can be left out of the equation, and then Eq. [6]

will be a body fatness standardisation of BW. The standardisation for BCS was intended to avoid differences in BCS that could influence the maintenance of lean BW. Values that can be used to standardise BW for body fatness are α and β coefficients of 0.05 and 0.1 from Friggens et al. (2007), respectively. However, it should be noted that these coefficients are sensitive to the BCS scale being used. The core trait for data collection is BW. There are multiple ways to record the BW of lactating cows with scales or methods like tape (heart girth) and camera technology (Lidauer et al., 2019; Qiao et al., 2021). This phenotype can easily be recorded at least per milking and relatively cheaply compared to the other phenotypes recorded at dairy farms.

BL accounts for the maintenance of body lipids and changes in adipose tissue (through derivative Δ trait). Ideally, we could measure the body lipids of animals at a given time point in the lactation. However, that is not currently available for large-scale phenotyping. Historically, studies have used BCS in RFI models (Islam et al., 2020; Olijhoek et al., 2020; Martin et al., 2021b), which indicates the level of subcutaneous fat. We propose Wright and Russel (1984) equation to calculate a body lipid phenotype:

$$BL = EBW(\alpha + \beta BCS) \quad [7]$$

where EBW is empty BW that is not standardised for BCS, and α (kg of lipid/kg of EBW) and β (kg of lipid/kg of EBW/unit of BCS) are constants relating BCS to body fatness. Instead of BL, the raw BCS trait could have been modelled in Eq. [4]. However, that would require an interaction between EBW and BCS to account for the scaling factor between the two traits (e.g., bigger cows have more adipose tissue than smaller cows with the same BCS value). Therefore, BCS here is assumed to express the variation in body fatness among cows.

In a review of the role of adipose tissue in the transition period, Mann (2022) suggested a measure of subcutaneous fat might not be sufficient for calculating BL. Visceral fat has a higher lipolytic activity than subcutaneous fat, constituting a greater part of BL than subcutaneous fat (Raschka et al., 2016; Ruda et al., 2019; Szura et al., 2020). Furthermore, some evidence suggests that the correlation between BCS and visceral fat is only moderate (Drackley et al., 2014). Therefore, a measure of visceral fat is needed, but other methods for measuring BL do not seem easily applicable to large-scale phenotyping (Lerch et al., 2021). A few studies have investigated the possibility of ultrasound measurements (Mann, 2022). However, ultrasound measurements are labour intensive for large-scale recording and are equally prone to operator variation as BCS. An alternative approach could be modelling energy balance from changes in BW or in combination with BCS, which Thorup et al. (2018) demonstrated is robust. Recording of BCS for Eq. [7] is typically a subjective assessment. Research has shown that using camera technology to record BCS could reduce labour costs and accurately record objective phenotypes for BCS (Qiao et al., 2021).

ε is the residual of Eq. [4]. In principle, the residual is the final component of the breeding value in genetic studies and is the ranking parameter for efficient and non-efficient animals in nutrition studies. However, this residual contains variability in factors not included in the regression model. Fischer et al. (2018b) and Richardson and Herd (2004) studied factors that may explain some of the variation in the residual in lactating animals and beef steers, respectively.

Can we measure or model individual digestive efficiency?

Three different components of the energy losses determine digestive efficiency: faeces, methane, and urine. The largest component is the energy lost in faeces (Guinguina et al., 2020), which

defines the total tract digestibility. Usually, variation between individuals is not accounted for. Instead, total tract digestibility is estimated based on feed measures (Álvarez et al., 2020) and, therefore, environmental factors. Phenotyping variation between individuals for faecal energy losses would require a digestibility measure using an external or internal marker (Guinguina et al., 2019) (e.g., faecal sampling and analyses of the marker through chemistry (Mehtiö et al., 2019; Lacey et al., 2020) or NIR scans (Brognia et al., 2018)). Velásquez et al. (2018) showed that digestibility estimates with internal markers such as iNDF with spot faecal sampling can provide an equally accurate estimate of digestibility as total faecal collection. If a fast analysis of iNDF with NIRs (Brognia et al., 2018; Mehtiö et al., 2019) could be validated further on commercial farms and a limited number of spot samplings is sufficient for an accurate measure of the marker (iNDF) concentration, then there could be the potential for large scale digestibility recording. Methane is another component of the energy losses. Efforts to get large-scale measurements of methane production are increasing (De Haas et al., 2021), which is relevant given the variation in cows' methane emissions (Guinguina et al., 2020). Finally, measuring energy losses from urine is technically challenging (Tebbe and Weiss, 2018) and would contribute little to the between-cow variation in digestive efficiency (Guinguina et al., 2020). In a recent review of real-time sensor technologies of the rumen environment, oral injected boluses were mentioned as a possibility to evaluate metabolites (Han et al., 2022). Monitoring the yield and concentration of metabolites such as volatile fatty acids could potentially evaluate digestibility. However, current technologies cannot accurately measure metabolites in the biological range that is present in the rumen environment. Furthermore, rumen boluses might be developed to measure the concentration of volatile fatty acids in the rumen, but measuring the yield would be challenging. Research on developing boluses that could measure pH in commercial herds (e.g., long-lasting batteries or no drift) is increasing, and this development could also be seen for metabolites and biomarkers (Han et al., 2022). In the future, a less labour-intensive method could obtain phenotypes for digestibility on a large scale where commercial actors are already present (Moonsyst, 2023; Smaxtec, 2023). Furthermore, this technology also provides other opportunities for phenotyping on a large scale, such as rumen pH, activity, and temperature. These traits could be used to predict phenotypes for water intake and animal health and welfare (Han et al., 2022).

The problem with using DMI as the energy intake phenotype is that the β values in Eq. [4] become functions of both digestive and metabolic efficiency. Below, we propose a model, which is an extension of Martin et al. (2021a), to separate digestive and metabolic efficiency within an RFI model, as seen in models [4] and [5]. To do that, we start with the last equation of Martin et al. (2021a):

$$(ed_{true} + ded_i) \times DMI_i = \mu + (ed_{true} + ded_i) \times -\bar{DMI} + \beta_1 ECM + \beta_2 EBW + \beta_3 BL + \varepsilon \quad [8]$$

where ed_{true} was the true energy density of feed, ded_i was the individual variability of digestive efficiency, DMI_i was the individual variation in DM intake, μ was the intercept of the model, the term $(ed_{true} + ded_i) \times -\bar{DMI}$ was assumed to explain individual variability in digestive efficiency, $-\bar{DMI}$ was the mean DMI of the cohort, and the remaining parts are giving in the description of Eq. [4]. The next step is to estimate the parameters for digestive efficiency, where we will use Eq. [8] to estimate the random effects of ded_i with a mean of 0 and variance $\sigma_{ded_i}^2$ and the effect of ed_{true} :

$$(ed_{true} + ded_i) \times (\bar{DMI} + DMI_i) = \mu + \beta_1 ECM + \beta_2 EBW + \beta_3 BL + \varepsilon \quad [9]$$

We assume that $DMI_i \ll \bar{DMI}$ and $ded_i \ll ed_{true}$, meaning the effect of absolute feed intake is greater than the variation and that the energy density in the feed is greater than individual digestive differences. To separate the two parts of DMI into ed_{true} and individual variation on digestive efficiency, we have:

$$(ed_{true} + ded_i) \times (\bar{DMI} + DMI_i) = ed_{true} \times \bar{DMI} \times \left(1 + \frac{DMI_i}{\bar{DMI}}\right) \times \left(1 + \frac{ded_i}{ed_{true}}\right)$$

$$use : (1 + \epsilon_1) \times (1 + \epsilon_2) = (1 + \epsilon_1 + \epsilon_2 + \epsilon_1 \times \epsilon_2) \approx (1 + \epsilon_1 + \epsilon_2)$$

Then:

$$\begin{aligned} (ed_{true} + ded_i) \times (\bar{DMI} + DMI_i) &\approx ed_{true} \times \bar{DMI} \times \left(1 + \frac{DMI_i}{\bar{DMI}} + \frac{ded_i}{ed_{true}}\right) \\ &= ed_{true} \times \left(\bar{DMI} + DMI_i + \frac{\bar{DMI} \times ded_i}{ed_{true}}\right) \\ &= ed_{true} \times DMI_o + (\bar{DMI} \times ded_i) \end{aligned}$$

With $DMI_o = (\bar{DMI} + DMI_i)$ = observed individual feed intake.

For simplicity, we neglect the interaction between individual variation for intake and digestibility. We assume that if this interaction effect exists, it will end up in ded_i . That means we now have:

$$ed_{true} \times DMI_o + (\bar{DMI} \times ded_i) = \mu + \beta_1 ECM + \beta_2 EBW + \beta_3 BL + \varepsilon \quad [10]$$

Where $ed_{true} \times DMI_o$ is the energy intake and $(\bar{DMI} \times ded_i)$ is the individual digestive efficiency.

To start simply, we assume an initial value for ed_{true} (could be a prior from feeding tables) and no individual variation on digestive efficiency, $ded_i = 0$. Then:

$$ed_{true} \times DMI_o = \mu + \beta_1 ECM + \beta_2 EBW + \beta_3 BL + \varepsilon \quad [11]$$

Model [11] is a mixed model that, in a genetic context, could include a random animal effect and a permanent environment effect. From model [11], we can estimate μ and β values for the different predictors and the residual variance. If pedigree or genomic data are present, the additive and permanent environmental variances can be estimated, for example, by adding a genetic component to the random regression model in Martin et al. (2021b), which Stephansen et al. (2023) tested on an international dataset.

Then we can define:

$$\widehat{DMI}_{oi} = \hat{\mu} \times \frac{1}{ed_{true}} + \hat{\beta}_1 \times \frac{ECM}{ed_{true}} + \hat{\beta}_2 \times \frac{EBW}{ed_{true}} + \hat{\beta}_3 \times \frac{BL}{ed_{true}} + \varepsilon \quad [12]$$

But

$$\begin{aligned} E(DMI_{oi}) &= E(\bar{DMI} + DMI_i) = \bar{DMI} + E(DMI_i) \\ &= \bar{DMI} (\text{assuming } E(DMI_i) = 0) \end{aligned}$$

Then

$$\widehat{DMI} = (\text{weighted}) \text{average of } \widehat{DMI}_{oi}$$

Then, going back to Eq. [8], considering $\bar{DMI}$ known by replacing it with $\widehat{DMI}$ and moving it to the right-hand side:

$$ed_{true} \times DMI_o = \mu + \beta_1 ECM + \beta_2 EBW + \beta_3 BL + -\widehat{DMI} \times ded_i + \varepsilon \quad [13]$$

From model [13], we can estimate the μ , β values, $\sigma_{ded_i}^2$, and σ_e^2 . Furthermore, we can predict and calculate the animal effect or breeding values for $\widehat{ed}_i$.

But the solutions of [13] are correct only if ed_{true} is known. However, it is very unlikely to know ed_{true} on a larger scale, and therefore, it can be replaced by $\widehat{ed}_{true}$. $\widehat{ed}_{true}$ can be computed from [13] as a (weighted) average of the following terms:

$$\left(\frac{1}{DMI_o} \right) \times \left(\widehat{\mu} + \widehat{\beta}_1 ECM + \widehat{\beta}_2 EBW + \widehat{\beta}_3 BL + -\widehat{DMI} \times \widehat{ded}_i \right) \quad [14]$$

over all observations based on the same feeding regime.

To build the model, we have to iterate between models [12] (to compute updated $\widehat{DMI}$), [13] (to compute the variables of main interest: $\widehat{Int}$, $\widehat{\beta}_1$, $\widehat{\beta}_2$, $\widehat{\beta}_3$, $\sigma_{ded_i}^2$), and [14] (to compute updated $\widehat{ed}_{true}$). We analysed the feasibility of this method below as a simplified proof of concept.

Test of the proposed model to derive energy density in feed and individual digestive efficiency

This test was carried out in a simplified version of the proposed model using dairy cattle data from the Danish research herd DKC Foulum and the French research herd Le Pin. A description of DKC Foulum data can be found in Li et al. (2017) and a description of the French data in Fresco et al. (2023). The following five quality control steps were applied to the data: keep only (1) 1st parity Holstein cows, (2) data from ≥ 2010 , (3) data from 8 to 44 weeks in lactation, (4) minimum 14 weeks with data, and (5) minimum 10 records per herd $\times$ year $\times$ season level. Table 2 provides descriptive statistics of the data after quality control.

We used an MT model with the traits $\widehat{ed}_{true} \times DMI_o$, ECM, and BW:

$$\begin{bmatrix} y_1 \\ y_2 \\ y_3 \end{bmatrix} = \begin{bmatrix} X_1 \\ X_2 \\ X_3 \end{bmatrix} \begin{bmatrix} \beta_1 \\ \beta_2 \\ \beta_3 \end{bmatrix} + \begin{bmatrix} Z_1 \\ Z_2 \\ Z_3 \end{bmatrix} \begin{bmatrix} \alpha_1 \\ \alpha_2 \\ \alpha_3 \end{bmatrix} + \begin{bmatrix} \varepsilon_1 \\ \varepsilon_2 \\ \varepsilon_3 \end{bmatrix} \quad [15]$$

where y_i is the vector of phenotypes for the i^{th} trait ($\widehat{ed}_{true} \times DMI_o$, ECM, and BW), X_i is the incidence matrix relating observations with fixed effects, β_i represents the vector of fixed effects for the i^{th} trait (fixed effects of herd $\times$ year $\times$ season; season at Foulum were quarter $\times$ diet and season at Le Pin were month and the fixed effect of weeks in milk), Z_i is the incidence matrix relating observations with the random animal effect of the i^{th} trait, α_i is the vector of animal effect (no pedigree) for the i^{th} trait, and ε_i is the vector of residual effects for the i^{th} trait. The MT model was solved using the DMU software and the AI-REML algorithm (Madsen and Jensen, 2013). We tested three different starting values of $\widehat{ed}_{true}$ (1, 5, and 15) to test if the model was sensitive to prior values of $\widehat{ed}_{true}$. Updating

$\widehat{ed}_{true}$ through Eq. [14] was carried out in an R script (R Core Team, 2020) developed for this iterative process. We used the “dplyr” package (Wickham et al., 2023). The R script calculated regression coefficients based on the co-variance matrix output from DMU using the method described in Martin et al. (2021b). The intercept was the population mean of DMI_o . The phenotype $\widehat{ed}_{true} \times DMI_o$ was updated before a DMU run as the last part of the loop within the R script. We did not include the $-\widehat{DMI} \times ded_i$ term within the loop, as inclusion resulted in a DMU model that did not meet the converge criteria. We defined a criterion for convergence for $\Delta \widehat{ed}_{true}$, from cohesive runs to assess if the iterative process converged. When the value of $\Delta \widehat{ed}_{true}$ was below 1.0^{-4} , the model had converged.

From the converged model, we calculated $\widehat{DMI}$ as in Eq. [12]. We analysed fortnightly $\widehat{DMI}$ (DMI_{fort}) and lactation-based $\widehat{DMI}$ (DMI_{lact}). Fortnightly periods have previously been used in RFI models by Fischer et al. (2018a) and Martin et al. (2021c). We tested DMI_{fort} in the following univariate model in DMU:

$$DMI_{fort} = herd + animal + e$$

where herd was the fixed effect of either Le Pin or DKC Foulum, animal was the random animal effect (no pedigree), and e was the random residual effect. DMI_{lact} was not evaluated in the model, as it would become the effect of the animal since no pedigree was provided. However, we compared the animal solution of DMI_{fort} with average animal levels of DMI_{lact} , which showed a unity correlation in Le Pin ($r = 1.0$) and DKC Foulum ($r = 0.996$).

Output from the iterative process in R and DMU shows that the model reaches very small changes on the converge criteria after 30 iterations and converges after approximately 60 iterations (Fig. 2). The model in this setup was not sensitive to the prior value of $\widehat{ed}_{true}$ in terms of the number of iterations for convergence and the direction of convergence. The converged values of $\widehat{ed}_{true}$ were 7.55 MJ/kg DM for all scenarios. That is close to the level of MJ NE in a diet for high-producing Holstein cows. Kristensen et al. (2015) reported a range from 6.44 to 6.49 MJ NE/kg DM with an SD of 0.18–0.22 for different breeds in Denmark. Fresco et al. (2023) reported 6.7 MJ NE/kg DM for a TMR diet, where cows could eat up to 4 kg of additional concentrate with 7.9 MJ NE/kg DM.

To assess the animal solutions of DMI_{fort} , they were merged with animal solutions of the converged DMU model [15]. From the animal solutions, we built an RFI trait as

$$(\widehat{ed}_{true} \times DMI)_{sol} = \widehat{\beta}_1 ECM_{sol} + \widehat{\beta}_2 BW_{sol} + \varepsilon$$

where the residual was used to rank efficient, average, and inefficient animals. In Table 3, the three efficiency groups (each with two animals) had similar $\widehat{ed}_{true} \times DMI_o$ within the efficiency group but deviated on DMI_{fort} . It appears that within the efficiency group and at similar energy intake levels, there are substantial differences

Table 2

Descriptive statistics for weekly averages of DMI, ECM and BW collected from Holstein dairy cows at the research units at DCRC Foulum and Le Pin.

Item	Le Pin			Foulum		
	Mean	SD	N	Mean	SD	N
DMI, kg/day	23.5	2.8	1 902	19.9	2.1	21 311
ECM ¹ , kg/day	35.3	5.2	1 929	31.1	4.9	18 565
BW, kg	665.7	62.2	1 929	632.4	61.8	20 849
Cows, n	–	–	59	–	–	704

DCRC=Danish Cattle Research Center, DMI=DM Intake, ECM=Energy Corrected Milk.

¹ Energy Corrected Milk was calculated according to Sjaunja et al. (1990).

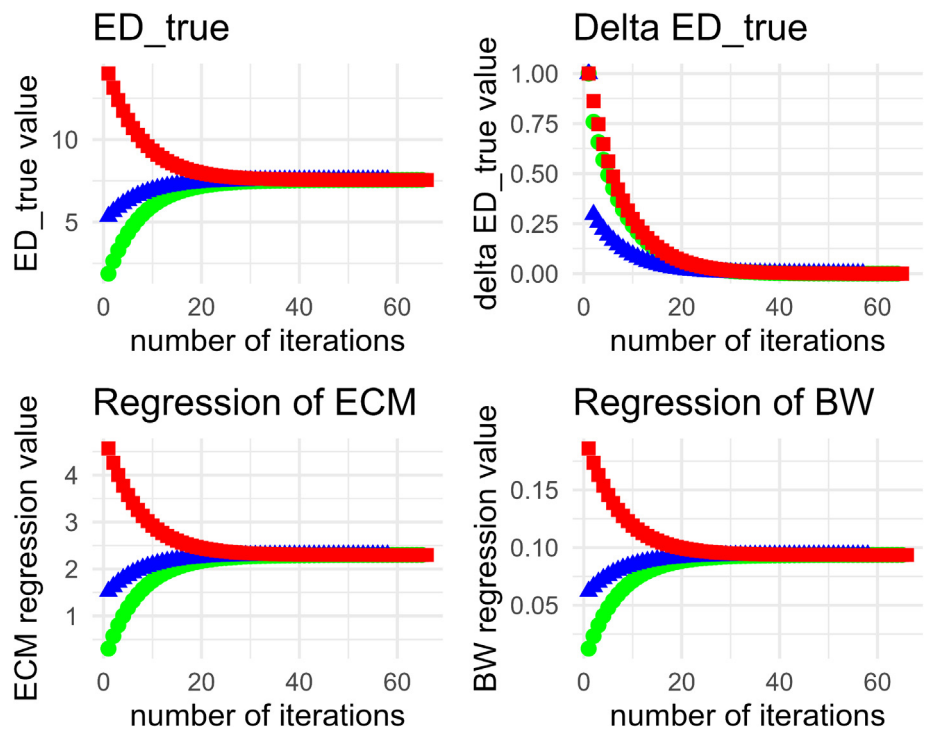


Fig. 2. Descriptive statistics of convergence over iterations in proposed model iterating over Eqs. [11] and [14], using the energy sink traits energy corrected milk (ECM) and BW from dairy cattle. Red square represents a prior value of energy density in the feed ($ED_{true} = ed_{true}$) at 15.0. Blue triangle represents a prior value of ed_{true} at 5.0. Green circle represents a prior value of ed_{true} at 1.0. Convergence was assessed by changes in ed_{true} ($\Delta ED_{true} = \Delta ed_{true}$) between cohesive iterations of the model.

Table 3
Animals solutions for two Holstein cows per category: efficient, average and inefficient. We formed the efficiency classes by the RFI phenotype and selected animals within efficiency group of similar energy intake values.

Group	ID	RFI	$ed_{true} \times DMI_o$	ECM	BW	DMI_{fort}
Efficient	1	−11.2	−11.8	0.4	−15.8	−1.4
	2	−11.2	−8.9	1.9	−23.4	1.5
Average	3	−0.6	0.8	−1.0	39.7	0.6
	4	−0.1	0.8	−4.7	127.2	−1.2
Inefficient	5	10.7	3.8	−2.9	−2.7	−1.8
	6	10.2	3.8	−1.4	−34.9	0.5

ID=renumbered animal ID, RFI=Residual feed intake (kg/day), DMI_o = observed DM Intake (kg/day), ed_{true} = estimated energy density in feed, ECM=Energy Corrected Milk (kg/day), DMI_{fort} = fortnightly averages of predicted DM intake (kg/day).

in DMI_{fort} animal solutions (range from 1.8 to 2.9 kg DM). This indicates that variation in individual digestive efficiency exists, and the difference in DMI_{fort} for these extreme animal solutions corresponds to 9–14% of the DMI across the population in this study.

The results from this test indicate we can estimate energy density in a joint Holstein dairy cattle dataset. However, additional studies are needed to validate these results and further develop the model to estimate herd-specific ed_{true} . We recommend using a Bayesian approach in the future development of this model, which would enable the use of posterior SDs to assess statistically significant differences, for example, if herd-specific ed_{true} are significantly different.

Summary

This review aims to explore ways to reduce error accumulation in the modelling of RFI, present differences between observed and expected regression coefficients of RFI models, and propose solutions to improve modelling and data collection in an MT RFI sce-

nario. We suggest using a MT RFI model that can handle fixed effects better than the traditional least square RFI method, which is supported by the literature. We showed that heterogeneity exists in regression coefficient estimates for the different energy sinks in published RFI models. Sourcing accurate coefficients to fix all coefficients in RFI models from feed norm tables is difficult and inappropriate in a broad population with different diets. We have proposed ways to collect phenotypes for a MT RFI model and improve the fitting of such a model. In particular, improving the modelling of changes in adipose and protein tissue is recommended. In addition, we propose a novel way to derive the energy density of the diet and individual variation in digestive efficiency within the MT modelling of RFI. The preliminary results look promising regarding the convergence of the estimated energy density in feed, and variation exists in individual digestive efficiency. The method was tested on a small scale and needs further development and validation before it can be determined whether the approach can be widely adopted. The authors suggest that modelling a feed efficiency trait to rank animals in nutritional and genetic contexts should be carried out using a MT RFI concept.

Supplementary material

Supplementary material to this article can be found online at <https://doi.org/10.1016/j.animal.2024.101268>.

Ethics approval

The data used were part of the research institute's current databases and the data were collected in the collection period in accordance with national guidelines. Therefore, no approval statement from national institutions of animal care and use committee were necessary.

Data and model availability statement

The data used to support the finding in this study are confidential and therefore not officially stored in a repository.

Declaration of Generative AI and AI-assisted technologies in the writing process

During the preparation of this work the author(s) did not use any AI and AI-assisted technologies.

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Declaration of interest

None.

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