

Modelling metabolic efficiency – Do we need to understand the biological meaning of residual feed intake breeding values?

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Abstract

Selecting dairy cattle that are efficient in utilizing feed is topical for many reasons discussed widely. Residual feed intake (RFI) is a trait that can capture the metabolic efficiency of a dairy cow in a broad sense including the abilities to digest feed, to have low energy loss through methane exhalation, and to use metabolizable energy for production. In 2020 the countries Denmark, Finland and Sweden have included the traits metabolic body weight and RFI into the Nordic Total Merit indices for Holstein, Nordic Red and Jersey dairy cattle. When adding more data from commercial farms to the genomic prediction for RFI, it was recognized that partial regression coefficient estimates may vary significantly across environments and parities. In this study we applied different approaches to predict breeding values for metabolic efficiency in Jersey dairy cows to assess the implications of using RFI breeding values for selection. The approaches were: A) similar to the current Nordic RFI evaluation where firstly dry matter intake (DMI) is regressed on energy sinks to get RFI observations that are subsequently used for predicting breeding values. B) was otherwise same as A) but instead of regressing DMI on energy sinks, DMI was regressed on expected DMI, where expected DMI values were calculated by utilizing energy requirement estimates from dairy nutrition studies. C) also otherwise same as A) but RFI observations were the difference between DMI and expected DMI. D) a random regression breeding value prediction model where DMI was regressed on expected DMI (ReFI). Estimated heritability was 0.14, 0.16, 0.10 and 0.10, and estimated additive genetic standard deviation was 0.89 kg, 1.02 kg, 0.95 kg and 5.4 % when applying approach A, B, C and D, respectively. Metabolic efficiency was unfavourable correlated with yield traits when applying A or B. In contrast, metabolic efficiency was favourable correlated with yield traits when applying C or D. We found that with approach A and B it was not possible to model the expected feed intake properly, which caused the discrepancy between the breeding values. Consequently, when selecting the genetically 10% best cows based on approach A, then these cows had only a 4% higher feed conversion efficiency compared to average cows, but when selection was based on approach D, then the cows had highest yield and 12 % higher feed conversion efficiency compared to average cows. Results indicate that using RFI as a trait to improve metabolic efficiency in dairy cows should be reconsidered if the modelling of partial regression coefficients for the energy sinks is not satisfying.

Keywords: feed efficiency, residual feed intake, regression on expected feed intake, Jersey

Introduction

Improving resources efficiency of dairy cows not only by selecting for the traits commonly included in total merit indices but preferable by also including efficiency traits into total merit indices has been studied intensively. Pryce et al. (2015) proposed to include a subindex that accounts for feed saved due to lower feed requirement for maintenance and higher metabolic efficiency of the cow. In this regard, the metabolic efficiency of a cow is understood in a broad sense that includes the abilities to digest feed, to have low energy loss through methane exhalation and to use metabolizable energy for the different energy pathways, and all that can be modelled by residual feed intake (RFI) (Koch et al., 1963). For breeding value estimation purposes, it is common that RFI observations are modelled from the same data that is used for estimating the breeding values. Therefore, dry matter intake (DMI) is modelled by partial regression analyses and obtained deviations from the expectations, i.e., the residuals, are used subsequently as observations for estimating RFI breeding values (Berry & Crowley, 2013). Alternatively, RFI can be described by a linear function of feed intake and energy sink traits breeding values from a multivariate analysis (Kennedy et al., 1993), which also can be tailored to complex multiple-trait random regression models (Islam et al., 2020).

In 2020 Nordic Cattle Genetic Evaluation (NAV) has included a Saved feed index into the Nordic Total Merit for selecting Holstein, Nordic Red and Jersey dairy cattle in Denmark, Finland and Sweden (Stephansen et al., 2021). The Saved feed index considers the animal's genomic breeding value for metabolic body weight (MBW) to account for the feed needed for maintenance, and the animal's genomic breeding value for RFI to accounts for the metabolic efficiency of the cow. Research on improving genomic predictions for both traits has been continued with the aim to increase the reliabilities of the genomic breeding values. For the MBW evaluation carcass weight will be included as correlated trait and for RFI more data from commercial herds with the CFIT 3D camera system (Lassen et al., 2018) are used. In this attempt, we have recognized that partial regression coefficient estimates from the first step of the RFI evaluation may vary significantly across environments and parities. Furthermore, partial regression coefficients also differed from regression coefficients developed in nutrition studies (Agnew et al., 2003). This was observed both on research farm data and CFIT data. In an earlier study (Mehtiö et al., 2018) it was also found that the partial regression coefficients, when estimated from the data, may deviate significantly from those obtained in nutrition studies. Moreover, we noticed that the varying of partial regression coefficient estimates has a noteworthy effect on RFI breeding values. Therefore, a better understanding of the implications of using RFI breeding values for genetic improvement of dairy cattle is needed.

An alternative approach (Lidauer et al., 2022) that allows modelling regression coefficients to be close to their biological expectations, is regression on feed intake (ReFI), where DMI is regressed on expected DMI (eDMI). For this approach, eDMI is calculated by using energy requirement (ER) coefficients that are estimated in nutrition studies (e.g., Agnew et al., 2003) rather than estimating partial regression coefficients simultaneously while estimating breeding values for RFI. The aim of this study was to contrast estimated breeding values (EBV) obtained from a RFI model like that applied by NAV with those obtained from the ReFI model. To dissect differences between the two approaches, we modelled metabolic efficiency by two additional approaches and estimated the genetic correlations between these metabolic efficiency traits and the production traits milk yield (MY), fat yield (FY), and protein yield

(PY). We also contrasted phenotypes of selected superior cows, when selection is based on the four alternative EBV.

Material and methods

Data

For this study Jersey feed efficiency data were extracted from the NAV genetic evaluation. The data were collected on four herds between January 2019 and December 2021 and included 46,822 records up to the sixth parity of 1,211 Jersey cows (Table 1). Weekly averages of daily DMI and body weight (BW) predictions were attained by the CFIT 3D camera system (Lassen et al., 2018). The BW predictions were used to calculate daily MBW and daily BW change (Δ BW). The milk yield data were from the official milk recording scheme and were used to form for each intake record an energy corrected milk (ECM), MY, FY and PY observation. All data was cleaned from outliers.

Table 1. Descriptive statistics for dry matter intake (DMI), metabolic body weight (MBW), energy corrected milk (ECM), milk yield (MY), fat yield (FY) and protein yield (PY) given for 1,211 Jersey cows by first (1) and later (2+) parities.

Parity	N		DMI	MBW	ECM	MY	FY	PY
1	18,221	Mean	21.3	95.0	28.9	22.0	1.3	1.0
		Std	3.2	5.5	5.6	4.9	0.3	0.2
2+	28,588	Mean	24.5	103.3	37.1	28.5	1.7	1.2
		Std	3.3	5.1	6.1	5.6	0.3	0.2

Approaches for estimating metabolic efficiency breeding values

The RFI approach and ReFI approach are conceptually rather different. Despite that the ReFI approach utilizes coefficients from ER studies, also the applied model is rather different. To better understand the source of differences in EBV from both approaches, we also included two intermediate approaches.

Approach A: Currently used residual feed intake model (RFI_A).

The approach involved two steps. In a first step DMI was regressed on energy sinks to get RFI observations:

$$\text{DMI} = c_1 \times A + c_2 \times A^2 + \text{LP} + \text{LYS} + \text{HYS} + \gamma_1 \times \text{ECM} + \gamma_2 \times \text{MBW} + \gamma_3 \times \Delta\text{BW} + \text{rfi} \quad (1)$$

where c_1 and c_2 are regression coefficients to model the calving age (A) effect of the cow; LP is lactation month nested within first and later parities; LYS is lactation period nested within year and season; HYS is the herd \times year \times season contemporary effect; γ_1 , γ_2 and γ_3 are the coefficients for the partial regressions on the energy sinks ECM, MBW and Δ BW, respectively that are nested within LP classes; and rfi is the model residual and was regarded

as a raw RFI observations. The raw rfi observations were adjusted for heterogeneous variance to accommodate a single trait evaluation in the second step (Stephansen et al., 2021). The final RFI observations used in the second step were formed by adding to the adjusted rfi observations the LYS and HYS solutions from model (1) to avoid that genetic variation would be lost in step 1. For the second step the applied breeding value estimation model was:

$$\text{RFI} = \text{LYS} + \text{HYS} + \text{pe} + \text{a} + \text{e} \quad (2)$$

where LYS and HYS are same fixed effects as described for model (1); pe is the cow's random permanent environmental effect; a is the random additive genetic animal effect; and e is the random residual.

Approach B: Residual feed intake with regression on feed requirement (RFI_B).

The approach was otherwise identically with approach A, but the model for the first step was modified:

$$\text{DMI} = c_1 \times \text{A} + c_2 \times \text{A}^2 + \text{LP} + \text{LYS} + \text{HYS} + \varphi \times \text{eDMI} + \text{rfi}, \quad (3)$$

where all effects in the model are the same as in model (1) but the model included instead of partial regressions on energy sinks a regression on eDMI, where φ is a regression coefficient nested within LP classes. Calculating for each record the eDMI value was done by firstly calculating ER:

$$\text{ER} = 4.81 \times \text{ECM} + 0.603 \times \text{MBW} - 27.6 \times \text{BW_Loss} + 38.3 \times \text{BW_Gain} \quad (5)$$

where the coefficients are metabolizable ER in mega joules for producing 1 kg ECM, maintaining 1 kg^{0.75} MBW, utilizing energy from 1 kg BW loss, and gaining 1 kg BW. The applied coefficients were the averages of the estimates reported by Agnew et al. (2003). Then, ER values were scaled so, that the obtained eDMI covariables should yield φ regression coefficient estimates that have on average an expectation of unity:

$$\text{eDMI} = \text{ER} \times \text{mean}(\text{DMI}) / \text{mean}(\text{ER}). \quad (6)$$

Approach C: Requirement residual feed intake (RFI_C).

Again, the approach was otherwise identically with approach A, but a raw RFI observation was calculated as a difference:

$$\text{rfi} = \text{DMI} - \text{eDMI} \quad (7)$$

Approach D: Regression on expected feed intake (ReFI).

This approach only requires modelling of DMI by a random regression model that regresses DMI on eDMI:

$$\text{DMI} = \beta \times \text{eDMI} + \eta \times \text{eDMI} + \psi \times \text{eDMI} + \alpha \times \text{eDMI} + \varepsilon \quad (8)$$

where β is a fixed regression coefficient nested within herd \times year \times parity classes, η is a random regression coefficient nested within herd \times year \times month classes, ψ is a random regression coefficient nested within permanent environmental classes, α is a random regression coefficient nested within additive genetic animal classes, and ε is the random residual.

Estimation of variance components and breeding values

The relationships between animals were modelled by setting up the numerator relationship matrix (**A**). Therefore, the pedigree of all cows with observations was pruned including five generations at most, which resulted 4,223 informative animals in the pedigree. Univariate analyses were carried out to estimate variance components for the four metabolic efficiency approaches by applying model (2) for the RFI approaches (A, B and C) and model (8) for the ReFI approach (D). The genetic correlations between the four metabolic efficiency traits and the production traits MY, FY and PY were estimated by multivariate analyses using as observations yield deviations (YD) and applying a multiple-trait repeatability animal model that included a mean and the random permanent environmental, random animal and random residual effects. The YD observations were obtained by firstly carrying out a multivariate analysis for the yield traits and univariate analyses for metabolic efficiency by the approaches A, B, C and D, and followed by summing solutions for the permanent environmental, additive genetic, and residual effects. For the genetic correlation study only first parity data was used.

All data were used for the prediction of EBV based on model (2) for the RFI approaches (A, B and C) and model (8) for the ReFI approach (D). Cows with at least 5 observations in the first parity were ranked alternatively based on the four different sets of EBV, and the first parity phenotypic means of the genetically 10 % best cows were contrasted against the phenotypic means of all cows.

Results and Discussion

Variance component estimates

The estimated heritability was 0.14, 0.16, 0.10 and 0.10, and the estimated additive genetic standard deviation was 0.89 kg, 1.02 kg, 0.95 kg and 5.4 % for RFI approach A, B, C and ReFI approach, respectively. Considering that the average DMI was 23.2 kg, the genetic standard deviations estimated by approach A, B and C can be expressed in efficiency percentages to make it comparable to ReFI. Thus, the genetic standard deviations for RFI by approach A, B, and C relate to 3.8 %, 4.1 % and 5.2 %, respectively, which all are lower than that one estimated by ReFI. Even estimated genetic variance was higher for RFI_C and ReFI, the heritability was lower. This was because RFI_C and ReFI resulted higher residual variance estimates compared to those from RFI_A and RFI_B.

The genetic correlation between metabolic efficiency by the four approaches and yield traits are given in Table 2. For RFI_A and RFI_B we obtained moderate positive (unfavourable) correlations with the yield traits. This was unexpected, because RFI observations are corrected for yield. In contrast, for RFI_C and ReFI we obtained moderate negative correlations with FY and PY, which indicates a favourable genetic association between metabolic efficiency and milk content traits, in particular with fat %.

Table 2. Genetic correlations between metabolic efficiency by approach A (RFI_A), B (RFI_B), C (RFI_C) and D (ReFI), and the yield traits milk (MY), fat yield (FY) and protein yield (PY).

Yield trait	RFI_A	RFI_B	RFI_C	ReFI
MY	0.47	0.43	-0.01	0.02
FY	0.17	0.24	-0.20	-0.28
PY	0.31	0.30	-0.16	-0.10

Regression coefficients for modelling feed intake expectations

The differences in the estimated genetic correlations between the yield traits and metabolic efficiency by the four approaches are a result on how the expected DMI is modelled. For RFI_A the expectations were obtained by the estimated partial regression coefficients for the three energy sink traits ECM, MBW and Δ BW (Table 3). For RFI_B only one single regression coefficient (ϕ) was fit for each class, instead of fitting a partial regression coefficient triplet. For approach RFI_C no regression coefficients were estimated, and for the ReFI approach regression coefficients (β) were estimated within a different set of classes because regression coefficients also modelled the contemporary group effect.

Table 3. Means of regression coefficient estimates across lactation month classes (RFI_A, RFI_B) and across herd \times year classes (ReFI) by first (1) and later (2+) parities. Energy sink traits: energy corrected milk (ECM), metabolic body weight (MBW), body weight change (Δ BW), and expected dry matter intake (eDMI).

Parity	RFI_A			RFI_B	ReFI
	ECM	MBW	Δ BW	eDMI	eDMI
	γ_1	γ_2	γ_3	ϕ	β
1	0.307	0.159	-0.277	0.463	1.036
2+	0.179	0.196	-0.244	0.322	1.013

The mean estimates given in Table 3 indicate that there is a discrepancy between the estimated partial regression coefficients and the coefficients reported in ER studies (e.g., Agnew et al., 2003). Considering that ER regression coefficients applied in equation (5) are sufficiently close to the ER of the cows in this study, and that the average energy density of the feed was 9.80 megajoule / kg DMI, then it can be expected that on average a cow would have required 0.49 kg, 0.062 kg, and 3.91 kg DMI to produce 1 kg ECM, maintain 1 kg^{0.75} MBW and increase BW by 1 kg, respectively. However, the partial regression coefficient estimates for ECM were on average 37% and 63% lower in first and later parity, respectively. The partial regression coefficients for MBW were 2.6 and 3.2 times larger in first and later parity, respectively, and the partial regression coefficients for Δ BW were on average even negative. Consequently, for high yielding cows the modelled feed intake expectations were far too low and such cows received a positive RFI observation, which explains the unfavourable correlation between RFI_A and yield traits. The estimated regression coefficients for RFI_B were significantly lower than the expected value of 1.0. Therefore,

similarly to RFI_A, for high producing cows the modelled feed intake expectations were too low, which resulted also in unfavourable correlations with the yield traits. For the ReFI approach the estimated regression coefficients were on average close to the expected value of 1.0 (Table 3), which supports that the estimated favourable correlations with yield traits might be closer to the true genetic association between metabolic efficiency and yield. The finding for the ReFI approach were supported by the RFI_C approach, which did not require to estimate regression coefficients from the data.

Phenotypes of genetically superior cows based on four alternative breeding values

The four different sets of EBV for metabolic efficiency differed considerably. We obtained a correlation between EBV from the approach A with EBV from approaches B, C and D of 0.92, 0.69 and 0.61, respectively. Consequently, groups of genetically superior cows were rather different when selecting based on the different sets of EBV. In Table 4 the first parity phenotypic means of the four different cow groups are tabulated against the first parity phenotypic means of all cows with at least five first parity observations.

Table 4. Phenotypic means of first parity dry matter intake (DMI), metabolic body weight (MBW), energy corrected milk (ECM), milk yield (MY), fat yield (FY), protein yield (PY) and feed conversion efficiency (FCE=ECM/DMI) for all cows with at least 5 observations and for 10% best cows with at least 5 observations selected based on EBV estimated by four Approaches. Approach A (RFI_A), B (RFI_B), C (RFI_C) and D (ReFI).

		DMI	MBW	ECM	MY	FY	PY	FCE
All cows		21.2	94.9	28.7	21.8	1.30	0.946	1.35
10% best cow	Method							
	RFI_A	18.6	94.7	26.3	18.8	1.22	0.860	1.41
	RFI_B	18.4	92.8	25.3	18.3	1.17	0.833	1.38
	RFI_C	19.9	93.1	29.1	21.5	1.34	0.966	1.46
	ReFI	19.8	93.9	29.8	22.0	1.37	0.982	1.51

When the 10 % best cows were selected based on RFI_A and RFI_B then these cows had lowest DMI but also lower yields compared to average cows. In contrast, when the 10 % best cows were selected based on ReFI, then these cows had lower DMI as average cows but highest yields. Consequently, when selecting based on RFI_A, then the feed conversion efficiency of the 10 % best cows was only 4 % higher than that one of average cows, but the feed conversion efficiency was 12 % higher when selection was based on ReFI.

Conclusion

In this study we compared different approaches to predict breeding values for metabolic efficiency in dairy cows. With the currently used approach, which models metabolic efficiency by a residual feed intake model, genetically superior cows were only moderately better in feed efficiency but had lower production. In contrast, when applying an alternative approach, where dry matter intake is regressed on expected dry matter intake, then superior cows were clearly more efficient and had also significantly higher production. The poor

performance of the residual feed intake model in this study was due to the inability of the model to estimate the partial regression coefficients for the energy sinks properly.

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