

Alternative Residual Feed Intake (RFI) expressions in dairy cattle

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Abstract

Residual Feed Intake (RFI) is commonly defined as residuals from linear regression of feed intake on energy sinks, expressed on the phenotypic scale. Estimates of partial regression coefficients are obtained by Least Squares, and RFIs are subsequently used as phenotypes in a genetic evaluation model. Alternatively, regression coefficients for RFI can be derived directly from phenotypic covariances among feed intake and the energy sinks, and EBVs for RFI can be formulated as reparameterizations of EBVs for feed intake and energy sinks from a multiple-trait (MT) model. This is equivalent to the recursive model (RM) approach, with EBVs calculated as system parameters. Using RM as operational tools, RFI can be defined and the respective parameters calculated, for overall and any individual source of random variation covered by the MT model for feed intake and energy sinks, i.e., genetic, PE, residual. Different definitions of RFI result in independence of RFI from energy sinks on different levels of variability. These concepts are illustrated by application of the genetic evaluation model for feed efficiency of Canadian Holsteins. A six-trait MT model for Dry Matter Intake (DMI), Energy Corrected Milk (ECM) and Metabolic Body Weight (MBW) in two DIM intervals of 1st lactation was fitted to approximately 100,000 weekly records on 5,000 cows, with 9,000 genotyped animals in the pedigree via MC-EM-REML and Single-Step GBLUP, for the purpose of co-variance component estimation and genomic evaluation. Four different expressions of RFI in 61 – 305 DIM in lactation (phenotypic = pRFI, genetic = gRFI, permanent environmental = eRFI and residual = rRFI) were defined and examined as potential selection criteria or as tools for optimizing management, with respect to estimates of genetic parameters and GEBV. Standardized regression coefficients of DMI on sinks differed among RFI definitions, but the relative impact of sinks was similar. Heritabilities of RFIs ranged from 0.05 (gRFI) to 0.15 (rRFI). Genetic and phenotypic expressions of RFI were genetically correlated at 0.84. Genetic correlations between pRFI and energy sinks were 0.62 for ECM and 0.04 for MBW (versus 0.00 for gRFI). Genetic correlations with DMI were 0.37 and 0.59 for gRFI and pRFI, respectively. Correlations between GEBV, for official sires (N = 298), ranged from 0.64 (gRFI and pRFI) to 0.99 (pRFI and eRFI). Results illustrate substantial differences among definitions of RFI in dairy cattle and consequences of using different definitions for genetic evaluation and selection. Generalizations to other traits are straightforward.

Key words: RFI, feed efficiency, single-step genomic evaluation

Introduction

Feed represents a significant proportion of dairy cattle production expenses. To reduce costs, genetic selection for feed efficiency has recently become more widely used across different dairy populations. Examples include the Canadian Holstein genetic evaluation for

metabolic feed efficiency (Jamrozik et al., 2022), and US genetic evaluation for feed saved (Parker Gaddis et al., 2021). Both North American approaches are based on the concept of Residual Feed Intake, as a measure of feed efficiency independent of an animal's body size and production level. It is considered to

represent the inherent variation in metabolic processes to describe efficiency.

Residual Feed Intake (**RFI**) was initially proposed by Koch et al. (1963) as the residuals from linear regression of feed intake on various energy sinks, expressed on the phenotypic scale. For simplicity, let Energy Corrected Milk (**ECM**) and Metabolic Body Weight (**MBW**) be the only energy sinks acting on Dry Matter Intake (**DMI**).

The equation for linear regression can be represented as:

$$DMI_i = \mathbf{x}_i' \mathbf{b} + c_M * ECM_i + c_W * MBW_i + e_i,$$

with \mathbf{b} being a vector of selected systematic (fixed) effects acting on DMI.

Estimates of the covariable regression coefficients c_M and c_W are obtained by Least Squares (**LS**) and phenotypes for RFI are defined as residuals (e_i) from the above model. These residuals are subsequently used as observations in genetic and genomic evaluation models for RFI.

Alternatively and equivalently, c_M and c_W can be derived as partial regression coefficients from phenotypic co-variances between DMI and the energy sinks. Define $\mathbf{C} = [C_{ij}]$ (2x2) phenotypic co-variance matrix for ECM and MBW, $\mathbf{w} = [w_{ij}]$ vector of phenotypic co-variances between sinks and DMI. Then $[c_M \ c_W]' = \mathbf{C}^{-1} \mathbf{w}$ (Kennedy et al., 1993).

The calculation of phenotypes for RFI from LS, to be used for further (i.e. genetic) analyses, faces challenges from conceptual, statistical, and practical perspectives (Lu et al., 2015):

1. RFI is not an observable trait and hence it may be difficult to explain to farmers,
2. Any regression analysis used to derive RFI implicitly assumes that all covariates (i.e., energy sinks) are recorded and known without any measurement error,
3. If any of the energy sink covariates are completely missing for a particular animal, none of the records on that animal can be used to derive the animal's RFI, and

4. The presence of non-zero genetic and residual correlations between DMI and the energy sink traits distorts heritability estimates for RFI (Kennedy et al., 1993) and interpretation of the inferences.

Materials and Methods

Use of mixed model methods for RFI

Genetic parameters and EBVs for RFI can be obtained without directly using phenotypes for RFI. The mixed linear model associated with the i -th multivariate record for ECM, MBW and DMI can be written as:

$$\mathbf{y}_i = \mathbf{X} \mathbf{b} + \mathbf{a}_i + \mathbf{p}_i + \mathbf{e}_i, \text{ where}$$

\mathbf{y}_i is a vector of observations on subject i for DMI and the two energy sink measurements, \mathbf{b} is a vector of fixed effects, \mathbf{a}_i is a vector of animal additive genetic effects, \mathbf{p}_i is a vector of permanent environmental (**PE**) effects, \mathbf{e}_i is a vector of residuals, \mathbf{X} is an incidence matrix. Assumptions are that: $v(\mathbf{a}_i) = \mathbf{G}$, a genetic covariance (3x3) matrix; $v(\mathbf{p}_i) = \mathbf{E}$, a covariance (3x3) matrix for the PE effects; $v(\mathbf{e}_i) = \mathbf{R}$, a residual covariance matrix. Phenotypic co-variance matrix (**P**) can be defined as $\mathbf{P} = \mathbf{G} + \mathbf{E} + \mathbf{R}$.

Let $\mathbf{a} = [a_1, a_2, a_3]'$ refer to EBV for ECM, MBW and DMI, respectively. To obtain phenotypic independence between an RFI variable (not yet defined) and the energy sinks, a linear re-parameterization of the EBV for ECM, MBW and DMI can be postulated as:

$$\mathbf{a}^* = \mathbf{\Lambda} \mathbf{a}, \text{ with}$$

$$\mathbf{\Lambda} = \begin{bmatrix} 1 & 0 & 0 \\ 0 & 1 & 0 \\ -L_{31} & -L_{32} & 1 \end{bmatrix}$$

Non-zero elements of $\mathbf{\Lambda}$, L_{31} and L_{32} , can be expressed as functions of elements of phenotypic co-variance matrix \mathbf{P} as:

$$L_{31} = (p_{12} * p_{23} - p_{13} * p_{22}) / (p_{12} * p_{12} - p_{11} * p_{22})$$

$$L_{32} = (p_{12} * p_{13} - p_{11} * p_{23}) / (p_{12} * p_{12} - p_{11} * p_{22}),$$

and they are partial phenotypic regression coefficients of DMI on ECM and MBW. The EBV of ECM and MBW remain unchanged, and EBV for DMI is transformed into an EBV for RFI:

$$a_3^* = a_3 - L_{31} a_1 - L_{32} a_2.$$

This definition for RFI can be interpreted as DMI phenotypically adjusted for energy sinks. Co-variance components involving this RFI can be obtained as:

$$\begin{aligned} \mathbf{G}^* &= \mathbf{\Lambda} \mathbf{G} \mathbf{\Lambda}', \\ \mathbf{E}^* &= \mathbf{\Lambda} \mathbf{E} \mathbf{\Lambda}', \\ \mathbf{R}^* &= \mathbf{\Lambda} \mathbf{R} \mathbf{\Lambda}', \text{ and} \\ \mathbf{P}^* &= \mathbf{G}^* + \mathbf{E}^* + \mathbf{R}^*. \end{aligned}$$

The re-parameterization described above can also be derived using a recursive model approach (Jamrozik et al., 2017). Let Y_1 , Y_2 , and Y_3 refer to phenotypes for ECM, MBW and DMI, respectively, and let recursive equations for DMI in this model be:

$$\begin{aligned} Y_1 &= \text{fixed}_1 + \text{random}_1 + e_1 \\ Y_2 &= \text{fixed}_2 + \text{random}_2 + e_2 \\ Y_3 &= L_{31}^* Y_1 + L_{32}^* Y_2 + \text{fixed}_3 + \text{random}_3 + e_3, \end{aligned}$$

with L_{jk} denoting a recursive coefficient parameter for the effect of change in trait j caused by the phenotype of trait k . The mixed linear recursive model associated with the i -th record for ECM, MBW and DMI can be written as:

$$\mathbf{\Lambda} \mathbf{y}_i = \mathbf{X} \mathbf{b}^* + \mathbf{a}_i^* + \mathbf{p}_i^* + \mathbf{e}_i^*, \text{ with}$$

$$v(\mathbf{a}_i^*) = \mathbf{G}^*, v(\mathbf{p}_i^*) = \mathbf{E}^*, v(\mathbf{e}_i^*) = \mathbf{R}^*, \text{ and } \mathbf{P}^* = \mathbf{G}^* + \mathbf{E}^* + \mathbf{R}^*.$$

Imposing restrictions on phenotypic co-variances i.e. setting $p_{13}^* = p_{23}^* = 0$ of the phenotypic co-variance matrix \mathbf{P}^* of the recursive model will yield the same $\mathbf{\Lambda}$ and expressions of co-variance components and EBVs on a recursive scale for RFI, as presented earlier using a simple re-parametrization of the EBVs to compute EBVs for RFI. Additionally, the recursive model parameters \mathbf{G}^* , \mathbf{E}^* , and \mathbf{R}^* can be interpreted as system co-variances.

Given the estimates of partial regression coefficients and the known co-variance structure of the model, EBV for RFI can be derived using estimates of EBV for DMI and sinks from a regular multiple-trait model for these traits, due to the equivalency between recursive and multiple-trait models (Jamrozik et al., 2017). In addition, the EBVs for RFI can be interpreted as parameters of the recursive model from sinks to DMI, under the assumption of known recursive regression coefficients.

Alternative RFI definitions

So far, RFI has been discussed on the phenotypic level (**pRFI**), as feed intake phenotypically adjusted for, or independent of, energy sinks. In other words, we looked at RFI as feed intake on the same phenotypic level of ECM and MBW. This can be extended to other random variables affecting DMI, like genetic or permanent environment effects, which would lead to different interpretations with different definitions for RFI. Genetic RFI (**gRFI**) can be defined as feed intake genetically independent of energy sinks. Similarly, PE RFI (**eRFI**) can describe feed intake adjusted for (or independent of) systematic environmental effects on repeated measurements for an animal over time (e.g. affecting all daily or weekly DMI measurements throughout a lactation). Finally, residual RFI (**rRFI**) will refer to feed intake adjusted for all effects in the model or independent of all residual effects on the energy sink observations. For derivation of regression coefficients on any given sources of variation we can use the corresponding co-variance matrix of interest to compute L_{jk} , either as shown in the previous paragraph for a pair of energy sinks, or using the more generalized equation below, which accommodates any number of sinks.

Let vector \mathbf{L} with order $(n-1)$ be the vector of multi-variate regressions of variable n on variables 1 through $(n-1)$. Partition the covariance matrix \mathbf{V} of interest for recursions

(e.g. genetic, phenotypic, etc.) to separate the n^{th} row and column from all previous rows and columns, and \mathbf{L} is then defined as follows:

$$\mathbf{V} = \begin{bmatrix} \mathbf{A} & \mathbf{C} \\ \mathbf{C}' & \mathbf{B} \end{bmatrix}$$

$$\mathbf{L} = \mathbf{A}^{-1}\mathbf{C}$$

$$\mathbf{L}' = [L_{n(1)} \quad \dots \quad L_{n(n-1)}]$$

It is easily verified that the general equation above yields the same values for L_{31} and L_{32} as shown in the earlier example for phenotypic RFI with two energy sinks, where $\mathbf{V}=\mathbf{P}$, and the generalization by Kennedy et al. (1993) for genetic RFI, where $\mathbf{V}=\mathbf{G}$.

In the scope of recursive modelling, phenotypic restrictions on covariances (i.e. zeroing phenotypic co-variances between traits) are replaced by restrictions related to the definition of RFI.

An example of application

A first lactation feed efficiency model applied to Canadian Holsteins was used to illustrate the concepts presented above. The data and model descriptions, from Jamrozik et al. (2021), are as follows.

Traits

The model defined all traits in two periods of first lactation: 5-60 days and 61-305 days in milk (DIM). Traits were:

- MBW, calculated as $(\text{body weight})^{0.75}$;
- ECM, calculated as $0.25*\text{Milk} + 12.2*\text{Fat} + 7.7*\text{Protein}$; and
- DMI.

All traits were weekly averages expressed in kg/day (ECM and DMI) or $\text{kg}^{0.75}$ (MBW).

Data

The feed efficiency data available at Lactanet included data from seven herds in five countries within the EDGP project plus eight more US herds outside of EDGP.

The final data (after edits) for co-variance component estimation consisted of 99,713 weekly records on 4,952 first lactation cows from 1,101 sires. Pedigrees of cows with

phenotypes were traced back four generations, for a total of 18,085 animals included in the estimation. More details on the data can be found in Jamrozik et al. (2021).

Model

The linear animal model used for co-variance components estimation was the same for each of the 6 feed efficiency traits (ECM, MBW and DMI, in 2 DIM intervals). Fixed effects in the model were: Age at calving, Lactation week, Year-Season of calving, and Herd-Year of calving. Random effects included Additive genetic, Permanent Environmental (PE), and Residual effects.

The multiple-trait model for 6 traits can be written as:

$$\mathbf{y} = \mathbf{X}\mathbf{b} + \mathbf{Z}_1\mathbf{a} + \mathbf{Z}_2\mathbf{p} + \mathbf{e}, \text{ where}$$

\mathbf{y} is a vector of observations (traits within cows within DIM interval), \mathbf{b} is a vector of all fixed effects, \mathbf{a} is a vector of animal additive genetic effects, \mathbf{p} is a vector of PE effects, \mathbf{e} is a vector of residuals, \mathbf{X} and \mathbf{Z}_i ($i=1, 2$) are respective incidence matrices.

Assumptions were that:

$v(\mathbf{a}) = \mathbf{A} \otimes \mathbf{G}$, \mathbf{A} is additive genetic relationship matrix, \mathbf{G} is the additive genetic covariance (6x6) matrix;

$v(\mathbf{p}) = \mathbf{I} \otimes \mathbf{E}$, \mathbf{E} is the covariance (6x6) matrix for the PE effects;

$v(\mathbf{e}) = \sum_{i=1}^N + \sum_{i=1}^N + \mathbf{R}_i$, \mathbf{R}_i is a residual covariance

matrix (3x3) for either first or second DIM interval, N is the total number of weekly records. Residuals for traits collected in the same week of lactation were assumed correlated, and uncorrelated otherwise.

Co-variance components of the model were estimated with the Monte Carlo - Expectation Maximization - Restricted Maximum Likelihood (MC-EM-REML) algorithm (Matilainen et al., 2012) implemented in the MiX99 software package (MiX99 Development Team, 2017).

Recursive model matrix for the six-trait model $\mathbf{\Lambda}$ was defined as $\sum^+ \mathbf{\Lambda}_i$, where $\mathbf{\Lambda}_i$ ($i =$

1, 2) corresponds to the i -th DIM interval of lactation.

Genomic evaluation

The Single-Step method was used to fit the multiple-trait linear animal model for 6 traits (ECM, MBW and DMI, in 2 DIM intervals) with genotypic information via MiX99 software. The same model as presented for covariance component estimations was used for genomic evaluation, with **A** replaced by **H** (combined pedigree/genotypes relationship matrix).

The data included 111,857 weekly records on 5,325 cows (4,585 cows with DMI; 4,313 genotyped cows with data). There were 1,160 sires of those cows with data (934 genotyped sires). In total, there were 19,137 animals in pedigree, and the genomic reference population included 8,375 genotyped animals.

GEBVs for different expressions of RFI were derived as presented earlier. Sire evaluation for all traits was defined as ‘Official’ when the bull had at least 5 daughters with DMI data and a minimum reliability for GEBV for RFI of 50%. There were 298 Holstein sires with an official status.

Results & Discussion

Genetic RFI calculated in 61 – 305 DIM is the principal selection criterion for feed efficiency in Canadian Holsteins. Therefore, and also for illustration purposes of the proposed methods, only results pertaining to traits (including different expressions of RFI) defined in this part of lactation will further be presented and discussed in this paper. In addition, the most emphasis will be put on comparisons between gRFI and pRFI, as the most popular expressions of RFI.

Genetic parameters

Estimates of regressions coefficients of DMI on energy sinks for different definitions of RFI are in Table 1.

Table 1. Estimates of regression coefficients and relative impact (%) of energy sinks on DMI

		gRFI	pRFI	eRFI	rRFI
Regression coefficient	ECM	0.48	0.31	0.28	0.19
	MBW	0.14	0.13	0.11	0.15
Relative impact	ECM	63	62	63	62
	MBW	37	38	37	38

Regression coefficients differed among different RFI definitions, especially for ECM. Relative impact of energy sinks on RFI remained approximately the same (60:40) for different RFI, with a larger emphasis on ECM.

Estimates of heritability for ECM, MBW and DMI in 61 – 305 DIM were 0.29, 0.50 and 0.27, respectively. Corresponding repeatabilities were 0.67, 0.91 and 0.57. Estimates of heritability and repeatability for different definitions of RFI are in Table 2.

Table 2. Estimates of heritability and repeatability (x100) for different RFI expressions

	gRFI	pRFI	eRFI	rRFI
Heritability	5	9	11	15
Repeatability	38	40	42	45

Heritability of RFI ranged from 5% (gRFI) to 25% (eRFI). Estimates of repeatability were more similar across RFI definitions (38 – 45%), with the same pattern of changes between different RFIs as observed for heritability.

Estimates of genetic and phenotypic correlations between each definition of RFI and the other traits in the model (sinks and DMI) are in Table 3.

By definition, genetic correlations between gRFI and energy sinks were equal to zero. Similarly, pRFI and energy sinks were phenotypically independent. The same patterns applied to eRFI and rRFI, they were independent of energy sinks on PE and R scale, respectively (results not shown).

Table 3. Estimates of genetic and phenotypic correlations (x100) between RFI versus energy sinks and DMI, for different expressions of RFI

Correlation		gRFI	pRFI	eRFI	rRFI
Genetic	ECM	0	62	67	80
	MBW	0	4	11	-11
	DMI	37	82	88	83
Phenotypic	ECM	-33	0	6	23
	MBW	-4	0	3	-6
	DMI	59	81	85	88

Phenotypic RFI was strongly genetically correlated with ECM. It was also genetically and phenotypically more similar to DMI than was the case for gRFI.

Genetic correlations among different RFI expressions were on average smaller than corresponding phenotypic correlations (Table 4). Genetic correlation of 0.84 between pRFI and gRFI would suggest that phenotypic and genetic RFIs are genetically not the same traits.

Table 4. Genetic (above diagonal) and phenotypic (below diagonal) correlations (x100) between different expressions of RFI

	gRFI	pRFI	eRFI	rRFI
gRFI	-	84	72	68
pRFI	94	-	92	99
eRFI	84	92	-	92
rRFI	84	98	91	-

Genomic evaluation

Correlations between GEBVs for gRFI and other definitions of RFI were significantly smaller than 1 for a set of ‘Official’ bulls (Table 5).

Table 5. Correlations (x100) between GEBV of RFI for ‘Official’ sires (N = 298)

	gRFI	pRFI	eRFI	rRFI
gRFI	-	64	58	46
pRFI	-	-	99	96
eRFI	-	-	-	96

Significant re-ranking of animals can therefore be expected between genetic versus phenotypic RFI.

Correlations in Table 6 show that relative to gRFI ranking, pRFI ranking was more similar to ECM and DMI. Selecting for pRFI is to some degree like selecting for ECM.

Table 6. Correlations (x100) between GEBV of RFI and other traits for ‘Official’ sires (N = 298)

	ECM	MBW	DMI
gRFI	-1	-8	21
pRFI	75	14	83
eRFI	80	23	89
rRFI	88	1	82

General remarks

Using recursive modelling as operational tools (re-parameterization of multiple-trait model parameters) allowed for definition, derivation and interpretation of different expressions of RFI in dairy cattle.

No causal links between traits were imposed in the context of structural equation models discussed above. Recursive parameterizations served solely as operational tools, enabling inferences for traits (e.g. RFI) defined as linear combinations of correlated variables (ECM, MBW and DMI), and given certain assumption regarding correlations (i.e. imposing restriction on system parameters).

The presented RFI derivations, based on either the multiple-trait co-variance matrix or the recursive model machinery, can be easily extended for additional energy sinks, for example body weight change.

Similarly, we may contemplate other definitions of RFI. ‘Producing Ability’ RFI, derived from $\mathbf{G} + \mathbf{PE}$ co-variance components, can serve as another management tool. We may also have ‘Herd’ RFI, derived from random ‘herd’ (if considered in the model) parameters. These again will have different, and possibly not always straightforward, interpretations.

Generalizations can also include an expansion of the model for multiple recursive traits of interest. For example, with lifetime feed efficiency being of interest, the first lactation RFI model was extended to a

multiple-lactations RFI model, with DMI and energy sinks all treated as different traits in first versus second lactation for genomic evaluation of Canadian Holsteins (Jamrozik et al., 2022). Finally, heterogeneity of RFI between and across lactations can be modeled using random regressions for DMI and energy sinks (Houlahan et al., 2024)

Recursive model approach to attain genetic independence between trait and energy sinks/sources has recently been applied to derive residual methane production that is genetically independent of milk production traits, for methane efficiency of Canadian Holsteins (Oliveira et al., 2023). Another application could be for functional herd life in dairy cattle, derived as length of productive life independent of production levels.

A similar approach can be used for analysis of traits expressed as ratios (Jamrozik et al., 2017). This relates, in particular, to possible application of this method for methane yield (g/kg DMI) or methane efficiency (g/kg milk).

Conclusions

Results indicate substantial differences among definitions of RFI, for estimates of genetic parameters and genomic evaluations of animals. It should be emphasized, that this could have serious consequences of using genetic vs. phenotypic RFI for genetic/genomic selection in dairy cattle. Phenotypic RFI is commonly used across the world for genetic evaluation of feed efficiency in dairy cattle. An exception is Canada, where gRFI is the genomic selection criterion in Holsteins.

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