Modelling multiplicativity in feed efficiency by regression on expected feed intake

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Abstract

Factors involved in feed efficiency (FE) have multiplicative effect which should be accounted for in genetic evaluation models. We present the conceptual difference between regression on expected feed intake and residual feed intake applying both models on estimation of variance components using simulated and real FE data. Our results showed, when FE is simulated with multiplicative effects, that applying a residual feed intake model underestimates additive genetic variance. Results of the real data analyses were in line with those of the simulated data, which indicates that the regression on expected feed intake approach may be suitable and is preferred for genetic evaluation of FE in dairy cattle.

Introduction

Presently, FE traits are included into dairy cattle breeding programmes and measuring of feed intake on commercial farms is expected to increase. This will require that models for FE traits can account for the nutritional quality of the different diets. It is known that with same amount of dry matter intake (DMI), a cow's production may drop or raise due to the quality of the feed. Feed quality, for instance digestibility, has a multiplicative effect on production, i.e., the effect is less pronounced at low intake level and more pronounced at high intake level. Furthermore, in situations where intake is measured by its volume (Lassen et al., 2018), metabolizable energy (ME) content per intake unit may change considerably across farms. Cow-specific efficiency factors like the individual metabolic efficiency (Martin et al., 2021) have also a multiplicative effect. However, modelling FE by residual feed intake (RFI) (Koch et al., 1963) offers no ways to account for it. Therefore, we present a modelling approach (Lidauer et al., 2021) that is based on regression on expected feed intake (ReFI). The aim of this study was to describe the conceptual difference between ReFI and RFI and to highlight its implications with simulated and real data.

Materials & Methods

For developing simple ReFI and RFI models, we assumed that there are FE records that have been collected repeatedly from cows that performed during different feed years and that the quality of diet differs across feed years.

The regression on expected feed intake approach. Under the assumption that FE factors have a multiplicative effect, it is appropriate to model FE by a random regression model where DMI is regressed on expected DMI (eDMI), which for the assumed FE records could be described as:

$$DMI_{ijk} = \beta_i \times eDMI_{ijk} + \psi_j \times eDMI_{ijk} + \alpha_j \times eDMI_{ijk} + \varepsilon_{ijk}, \quad (1)$$

where DMI_{ijk} is a DMI observation k recorded in the year i for the cow j; β_i is the fixed regression coefficient for the feed year i; ψ_j is the random regression coefficient for the permanent environmental effect of cow j [$\boldsymbol{\psi} \sim N(\mathbf{0}, \mathbf{I}\sigma^2_{\psi})$]; α_j is the random regression coefficient for the additive genetic effect of cow j [$\boldsymbol{\alpha}$~N($\mathbf{0}$,$\mathbf{A}\sigma^2_\alpha$), where $\mathbf{A}$ is the relationship matrix]; ε_{ijk} is the random residual [$\boldsymbol{\varepsilon}$~N($\mathbf{0}$,$\mathbf{I}\sigma^2_\varepsilon$)]; and $eDMI_{ijk}$ for record k is calculated based on energy requirements (ER) and realized production. The $eDMI_{ijk}$ covariable can be calculated by applying ER recommendations and an average ME content of the diets, which was assumed to be 11.0 MJ ME / kg DMI. Applying the Finnish ER values (Luke, 2021) results:

$eDMI_{ijk} = 1.0/11.0\times(5.15\times ECM_{ijk}+0.515\times MBW_{ijk}+28.0\times BW\text{-}loss_{ijk}+34.0\times BW\text{-}gain_{ijk})$, (2)

where the coefficients represent the expected amount of ME needed to produce 1 kg of energy corrected milk (ECM), maintain 1 $kg^{0.75}$ metabolic body weight (MBW), gain 1 kg of body weight (BW), as well as the ME that becomes available by mobilizing 1 kg body tissue.

The residual feed intake approach. On the contrary, when assuming FE factors have an additive effect, it is reasonable to model RFI observations by a classical repeatability model:

$RFI_{ijk} = C_i + p_j + a_j + e_{ijk}$, (3)

where a RFI observation for record k, $RFI_{ijk} = DMI_{ijk} - eDMI_{ijk}$, is calculated by applying equation (2); C_i is a fixed contemporary group effect of feed year i; p_j is the random permanent environmental effect of cow j [$\mathbf{p}$~N($\mathbf{0}$,$\mathbf{I}\sigma^2_p$)]; a_j is the random additive genetic effect of cow j [$\mathbf{a}$~N($\mathbf{0}$,$\mathbf{A}\sigma^2_a$)]; and e_{ijk} is the random residual [$\mathbf{e}$~N($\mathbf{0}$,$\mathbf{I}\sigma^2_e$)].

Conceptual difference between the approaches. The conceptual difference between the ReFI and RFI approaches can be demonstrated by assuming four FE records from four cows (A, B, C, D) that have been made in two contemporary groups, and that cows are equally efficient. Further, cow A is the dam of cow C and both have a daily DMI capability of 10 kg, and cow B is the dam of cow D and both have a daily DMI capability of 20 kg. Cows A and B are contemporaries and get a diet with 10% lower digestibility (L), and cows C and D are contemporaries and get a diet with 10% higher digestibility (H) compared to average diet digestibility. Consequently, under the assumption that digestibility has a multiplicative effect, the differences in the diets will cause cows A and C to have proportionally lower and cows B and D to have proportionally higher production. In the ReFI approach the effect of the diet is accounted by the fixed regression (β_i) on eDMI nested within contemporary groups, which results for these four records β_L=1.11 and β_H=0.91. In the RFI approach the effect of the diet is accounted by a fixed contemporary group effect (C_i), which results C_L=1.5 and C_H=-1.5. Then, the ReFI approach will yield no differences among the corrected observations whereas the RFI approach will yield differences within dam-cow pairs as shown in Table 1.

Table 1. Conceptual differences in correcting for the diet effect.

			Regression on expected feed intake		Residual feed intake	
Cow	CG[1]	$eDMI_k$	DMI_k	$DMI_k-\beta_i\times eDMI_i$	$RFI_k=DMI_k-eDMI_k$	RFI_k-C_i
A	L	9.0	10.0	0.0	1.0	-0.5
B	L	18.0	20.0	0.0	2.0	0.5
C	H	11.0	10.0	0.0	-1.0	0.5
D	H	22.0	20.0	0.0	-2.0	-0.5

[1] Contemporary group with low (L) and high (H) digestible diet; eDMI = expected dry matter intake, DMI = dry matter intake; β_i = fixed regression coefficient effect; C_i = fixed contemporary group effect

Simulation study. The demonstrated example shows that ReFI would be an appropriate approach if FE factors have a multiplicative effect. On the contrary, RFI would result inappropriate fit, which may cause an underestimation of additive genetic variance. To test this hypothesis, we performed a simulation study where DMI observations were simulated for

realized productions that were recorded in FE trials. Therefore, from the Finnish FE research data a suitable data set was extracted that included 5,236 FE records from the lactation period $100 \leq$ days in milk ≤ 200 of 537 primiparous Nordic Red cattle dairy cows that were recorded during a period of 13 years at three research herds. The pedigree of the cows included 3,540 animals. A record consists of a DMI, ECM, MBW and BW change observation.
In a first step, for each record the eDMI was calculated applying equation (2). In a second step, for model (1), when fitted to the data set, simulated values were generated for the model effects from normal distributions with standard deviations (SD) of the effects in FE percent units of 10% for the fixed feed year effects, 5% for the permanent environmental effects, and 3% for additive genetic effects. Thus, the fixed regression coefficients β_i were generated with an expectation of 1.0 and a SD of 0.1. The random regression coefficients for the permanent environmental and additive genetic effects were sampled by $\boldsymbol{\psi} \sim N(\mathbf{0},\mathbf{I}\times 0.0025)$ and $\boldsymbol{\alpha} \sim N(\mathbf{0},\mathbf{A}\times 0.0009)$ where a Cholesky decomposition of $\mathbf{A}$ was used for generating $\boldsymbol{\alpha}$, and the residuals were sampled by $\boldsymbol{\varepsilon} \sim N(\mathbf{0},\mathbf{I}\times 1.0)$. The simulated heritability (h^2) was 0.155 and the simulated repeatability (r) was 0.586 and can be calculated as: $h^2=\varphi\sigma^2_\alpha/(\varphi\sigma^2_\psi+\varphi\sigma^2_\alpha+\sigma^2_\varepsilon)$ and $r=(\varphi\sigma^2_\psi+\varphi\sigma^2_\alpha)/(\varphi\sigma^2_\psi+\varphi\sigma^2_\alpha+\sigma^2_\varepsilon)$ with $\varphi=(\mathbf{d}'\mathbf{d})/N$, where $\mathbf{d}$ is a vector of size N=5,236 that contains all eDMI covariables. For the used data φ was 416.3. In a final step, simulated effects and model (1) were used to calculated simulated DMI and RFI ($RFI_{ijk} = DMI_{ijk} - eDMI_{ijk}$) observations. Ten independent data replicates were simulated. Each data set was used to estimate the variance components by applying the ReFI model (1) and the RFI model (3).

Estimating variance components from real data. To get an indication of whether the ReFI approach is more appropriate for real data, the originally extracted data was used to estimate variance components by applying the ReFI model (1) and the RFI model (3). The data was recorded at three herds and therefore the feed year classification for the fixed effects in model (1) and (3) was replaced by a herd × feed year classification which comprised 20 classes.

Results

Simulation study. On average, same variance components, heritability, and repeatability as applied for the simulation were obtained (Table 2) when the simulated data sets were analysed with the ReFI model (1). However, when applying the RFI model (3), then this was only the case for the residual variance and the repeatability, but the estimated permanent environmental variance was on average larger and the estimated additive genetic variance was on average smaller compared to those used for the simulation. Thus, this resulted for the RFI model on average 20% lower heritability estimates. Furthermore, the SD of the r and h^2 estimates were larger when the RFI model was applied.

Real data. The estimated variance components when applying the ReFI model were 0.00364 ± 0.00056 and 0.00112 ± 0.00059 for the permanent environmental and additive genetic regression coefficients, respectively, and 1.695 ± 0.03 for the residual effect. Thus, the estimated permanent environmental and additive genetic variation of FE were 6.0% and 3.3%. The estimated heritability and repeatability were 0.13 ± 0.065 and 0.54 ± 0.019. When applying the RFI model estimated variance components were 1.658 ± 0.21, 0.246 ± 0.21 and 1.668 ± 0.04 for the permanent environmental, additive genetic and residual effects, respectively, which resulted a heritability and repeatability of 0.07 ± 0.057 and 0.53 ± 0.018. The estimated β_i fixed regression coefficients by model (1) for the herd × feed year classes had a mean of 1.01 and a SD of 3.9%, and the estimated C_i fixed effects of model (3) had a mean of 0.26 kg and a SD of 0.81 kg.

Table 2. Estimated variance components[1] from ten simulated data sets by two models.

Data	Regression on expected feed intake					Residual feed intake				
sample	σ^2_ψ	σ^2_α	σ^2_ε	r	h^2	σ^2_p	σ^2_a	σ^2_e	r	h^2
1	0.00239	0.00090	0.97	0.584	0.160	1.04	0.37	0.99	0.588	0.155
2	0.00287	0.00065	1.01	0.592	0.109	1.41	0.06	1.02	0.589	0.024
3	0.00230	0.00083	1.00	0.565	0.151	1.11	0.17	1.01	0.559	0.075
4	0.00260	0.00096	0.98	0.602	0.163	1.03	0.47	0.99	0.602	0.190
5	0.00255	0.00091	1.00	0.591	0.156	1.07	0.38	1.01	0.591	0.155
6	0.00181	0.00162	1.04	0.577	0.273	0.81	0.58	1.06	0.567	0.237
7	0.00262	0.00082	1.02	0.585	0.139	1.25	0.19	1.02	0.583	0.076
8	0.00225	0.00074	1.05	0.543	0.135	1.03	0.18	1.06	0.533	0.080
9	0.00262	0.00097	0.99	0.601	0.162	1.10	0.45	1.00	0.606	0.175
10	0.00240	0.00056	0.96	0.563	0.107	1.10	0.15	0.97	0.565	0.069
Mean	0.00244	0.00090	1.00	0.580	0.155	1.09	0.30	1.01	0.578	0.124
SD	0.00029	0.00029	0.03	0.019	0.046	0.15	0.17	0.03	0.022	0.068

[1] Estimated variance components, repeatability (r) and heritability (h^2) for regression on expect feed intake model (1) and residual feed intake model (3) and mean and standard deviation (SD) of estimates across samples

Discussion

We elaborated the conceptual difference between the ReFI and RFI approaches. The results of the simulation study indicate that ReFI fits better the data than RFI when FE factors have multiplicative effects. Both models were able to estimate the simulated repeatability. This was most likely because of seasonal calving and therefore having most of the repeated observations nested within same fixed effect classes. Referring to the explanation of the example in Table 2, it can be expected that both models will adjust the feed year effect similarly for average observations but not for observations deviating from the average. For the simulated data this causes reranking of cows within contemporary groups when RFI is applied, which might be the reason that RFI underestimated the additive genetic variance.

The findings from the simulation study were supported by the estimates from the real data analyses. With both models we estimated almost same repeatability for the real data, but the estimated heritability was clearly lower when applying RFI. When studying the fixed effect estimates it showed that for an average observation (eDMI=20.3kg, RFI=0.35kg) both models adjusted almost equally for the herd × feed year effect, i.e., the SD of the differences between the effects of both models was only 0.04 kg, whereas for observations with eDMI of 30 kg the SD of the differences increased to 0.37 kg, which caused reranking of cows. If it is valid that more precise ranking of cows will result higher heritability estimates, then this would give an indication that the multiplicative ReFI model was better suitable for the analysed FE data.

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