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1 **A new method to estimate Residual Feed Intake in dairy cattle using time-**  
2 **series data**

3

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15

16

17 **Abstract**

18

19 In dairy, the usual way to measure feed efficiency is through the residual feed intake  
20 (RFI) method. However, this method is, in its classical form, a linear regression,  
21 which, by construction, does not take into account the evolution of the RFI  
22 components across time, inducing approximations in the results. We present here a  
23 new approach that incorporates the dynamic dimension of the data. Using a multi-  
24 trait random regression model, the correlations between milk, live weight, dry matter  
25 intake (DMI) and body condition score (BCS) were investigated across the lactation.

26 In addition, at each time point, by a matrix regression on the variance-covariance  
27 matrix and on the animal effects from the three predictor traits, a predicted animal  
28 effect for intake was estimated, which, by difference with the actual animal effect for  
29 intake, gave a RFI estimation. This model was tested on historical data from the  
30 Aarhus University experimental farm (1 469 lactations out of 740 cows). Correlations  
31 between animal effects were positive and high for milk and DMI and for weight and  
32 DMI, with a maximum mid-lactation, stable across time at around 0.4 for weight and  
33 BCS, and slowly decreasing along the lactation for milk and weight, DMI and BCS,  
34 and milk and BCS. At the Legendre polynomial coefficient scale, the correlations  
35 were estimated with a high accuracy (averaged standard error of 0.04, min=0.02,  
36 max=0.05). The predicted animal effect for intake was always extremely highly  
37 correlated with the milk production and highly correlated with body weight for the  
38 most part of the lactation, but only slightly correlated with BCS, with the correlation  
39 becoming negative in the second half of the lactation. The estimated RFI possessed  
40 all the characteristics of a classical RFI, with a mean at zero at each time point and a  
41 phenotypic independence from its predictors. The correlation between the averaged  
42 RFI over the lactation and RFI at each time point was always positive and above 0.5,  
43 and maximum mid lactation (>0.9). The model performed reasonably well in the  
44 presence of missing data. This approach allows a dynamic estimation of the traits,  
45 free from all time-related issues inherent to the traditional RFI methodology, and can  
46 easily be adapted and used in a genetic or genomic selection context.

47

48 **Keywords:** feed efficiency, multitrait random regression, dynamic approach,  
49 correlations, lactation parameters.

50

51

## 52 **Implications**

53 This paper proposes a new methodology to estimate feed efficiency in a continuous  
54 manner across the lactation. The efficiency is evaluated from a Residual Feed Intake  
55 derived from a multi-trait random regression model, which allows the coefficients to  
56 vary over time. This approach allows a dynamic estimation of the traits and their  
57 correlations, free from all time-related issues inherent to the traditional methodology  
58 and can easily be adapted and used in a genetic or genomic selection context.

59

## 60 **Introduction**

61 With feed costs representing above 50% of the total costs of dairy production  
62 (European Commission, 2018), the issue of feed efficiency has become a priority for  
63 the sector. The notion of feed efficiency refers to improving the balance between  
64 output (production) and input (feed intake). The most common way to determine feed  
65 efficiency in dairy cattle is through residual feed intake (**RFI**). First proposed by Koch  
66 et al. (1963), RFI is the difference between the actual feed intake of an animal and its  
67 predicted feed intake based on its performance, i.e. the intake necessary to cover the  
68 demands of the different energy sinks, estimated by regression. By construction, this  
69 method benefits from the RFI being phenotypically independent (or genetically in  
70 case of genetic regression) from its predictors, which theoretically allows RFI to  
71 reflect digestive and metabolic variabilities (Archer et al., 2002; Berry and Crowley,  
72 2013).

73 Although this definition of RFI is widely used in dairy cattle (Connor, 2015), some  
74 issues remain with this approach. First of all, the time influence on RFI is a key  
75 question. RFI is usually measured between two given days. If the trial duration is too

76 short, the number of measures will be low and the results of the prediction will not be  
77 accurate. On the other hand, different biological processes are involved at the different  
78 lactation stages, in particular body reserve mobilisation in early lactation and  
79 reserves accretion associated with pregnancy. Therefore, regression coefficients  
80 associated with the different predictors are likely to vary when taken at different  
81 lactation stages, leading to a biased assessment of RFI when estimated from point  
82 measures over the whole lactation (Li et al., 2017). Moreover, with the advent of  
83 precision farming technologies, high-frequency time-series measures are becoming  
84 available, and thereby increasingly offer the opportunity to track efficiency. Key  
85 questions in this context are how to deal with changes over time, when to measure  
86 RFI and for how long. A second issue comes from the nature of RFI itself. Being a  
87 residual, in addition to the actual animal efficiency, it contains all the modeling and  
88 measurement errors. Within this context, Fischer et al. (2018) used random  
89 regression on the individual level to isolate the cow-specific part of RFI. However,  
90 they faced some difficulties due to strong correlations between their predictors  
91 (correlations that changed over time during the lactation), which, combined with a  
92 limited dataset size, restricted their modeling and conclusions.

93 With the aim of solving these two issues, we investigate in this paper the relationship  
94 between intake and its predictors across the lactation using a multi-trait random  
95 regression model on experimental data. With such a model, based on the variance-  
96 covariance functions, it is possible to predict intake from the other traits and to  
97 compare this prediction with actual intake. This leads to a consistent definition of RFI,  
98 with regression coefficients free to vary over time.

99

100

101 **Material and methods**

102

103 ***Population resources and feeding management***

104 Data were collected between 2002 and 2016 at the Danish Cattle Research Centre  
105 (Foulum, Denmark) and shared as part of the GenTORE project  
106 (<https://www.gentore.eu>). Animals were Holstein cows with lactation rank ranging  
107 from first to third lactation. Cows were housed in a freestall barn with cubicles and  
108 slatted floor and milked in an automatic milking system (**AMS**; DeLaval, Tumba,  
109 Sweden) allowing free cow traffic. Data were collected during various trial periods  
110 and cows were not nested within trial. They had ad libitum access to a partial mixed  
111 ration (**PMR**) varying in nutritional content in accordance with the particular trial in  
112 which the cows were involved. The PMR diets used during this period contained the  
113 following ingredients (typical g/kg DM): rapeseed meal (106), barley (135), dried  
114 sugerbeet pulp (51), grass silage (264), maize silage (422), urea (7), and minerals  
115 (18). The corresponding chemical composition was (typical g/kg dry matter): crude  
116 protein (158), neutral-detergent fibre (340), starch (195), sugar (46), crude fat (39),  
117 ash (74), with a Net Energy of Lactation (**NEL**) of 6.9 MJ/kg DM. Across the different  
118 feeding trials carried out during this period, diet differences did not exceed +8% of  
119 the average value for crude protein and likewise +15% for NEL. The nutritional  
120 values of the PMR were all within the range of typically recommended requirements,  
121 formulated to support the milk yield level of the herd, and allocated in amounts  
122 allowing approximately 10%orts to ensure ad libitum intake. In addition, cows were  
123 supplemented daily with a maximum of 3 kg of concentrate to ensure voluntary  
124 access to the AMS. These feeding data were already described in previous studies  
125 (e.g. Li et al., 2016; Byskov et al., 2017).

126

127 ***Phenotypes and data editing***

128 Data from 1 469 lactations of 740 cows were collected. A weekly measurement of  
129 average daily milk yield per cow was obtained from the average of daily milk yield  
130 records per cow in each week. Milk samples were taken weekly for analyses of fat  
131 and protein. On the same basis, the dry matter contents in PMR and concentrates  
132 were analyzed regularly and the compositions were aligned and merged with feed  
133 intake records to obtain weekly dry matter intake (**DMI**) values for individual cows.  
134 Animals were also automatically weighed at each milking so that BW records were  
135 averaged to obtain a weekly record of body weight (**BW**) per cow in each week. Body  
136 Condition Score (**BCS**) was evaluated every two weeks and scored on a scale from 1  
137 to 5.

138 A corrected milk (**cmilk**) trait was created following the FAO formula which defines as  
139 a standard a milk with 4.0% fat and 3.3% protein (FAO, 2010):

140 Corrected milk (kg) = raw milk (kg) \* (0.337 + 0.116 \* Fat content (%) + 0.06 \* Protein  
141 content (%))

142 To avoid nonsensical performances, a filter was used to discard records that differed  
143 too much from the previous record registered in the same lactation for that animal.  
144 Therefore, records implying differences between two consecutive records higher than  
145 12 L for cmilk, 50 kg for the liveweight, 7 kg for the daily dry matter intake and one  
146 unit of BCS were discarded. These threshold values were defined after studying a  
147 previous dataset with similar performance level. Less than 2% of the data were  
148 discarded for cmilk and BCS and about 4% for weight and DMI. A second step of  
149 filtering was made on the duration of data collection for each lactation independently:  
150 only animals that had been recorded for a minimum duration of 200 days during their

151 lactation were kept. This dataset, that was used to conduct the main analyses,  
152 contains 40 619 records of cmilk, 40 662 records of weight, 42 177 records of DMI  
153 and 19 661 records of BCS, which represents about 73% of the overall records.  
154 Additionally, the overall records were used to assess the robustness of our model in  
155 case of missing data and the details of this analysis are presented in **supplementary**  
156 **material S1**.

157

158

### 159 ***Statistical analysis***

160 *Multi-trait random regression model.*

161 To analyze the relationship of the four traits along the lactation, a multi-trait random  
162 regression analysis was performed using the Wombat software (Meyer, 2007). The  
163 model used was as follow:

164

$$165 \quad y_{ilmr} = c_i + \sum_{n=0}^3 \beta_{ln} \varphi_{nr}(t) + \sum_{n=0}^2 \alpha_{mn} \varphi_{nr}(t) + e_{ilmr}$$

166

167 Where  $y_{ilmr}$  is the observation of the r-th trait,  $c_i$  is the fixed effect of the i-th month-  
168 year combination corresponding to the record date,  $\beta_{ln}$  is the n-th fixed regression  
169 coefficient specific to parity class l,  $\alpha_{mn}$  is the n-th random regression coefficient of  
170 the animal m,  $\varphi_{nr}(t)$  is the n-th coefficient of Legendre polynomial of degree (d = 2  
171 for the animal effect and d= 3 for the parity class), evaluated at day in milk (DIM) t,  
172 and  $e_{ilmr}$  is the random residual effect. Residual effects were assumed to have a  
173 homogenous residual variance. Successive lactations of the same animal were



174 considered separately, as if they were from different animals, implicitly ignoring any  
 175 permanent environmental effect across lactations.

176 From the random part of the equation, we get as outputs the three coefficients of the  
 177 Legendre polynomial at each time point, as well as the animal solutions. For each  
 178 trait, we can then obtain at each time and for each cow an estimated animal effect.

179 These animal effects will be denoted  $a_{cmilk}(t)$ ,  $a_{weight}(t)$ ,  $a_{DMI}(t)$  and  $a_{BCS}(t)$  in the  
 180 article.

181 Variance-covariance components of the random regression were obtained and  
 182 gathered into a 12 by 12 matrix, corresponding to the four traits with three Legendre  
 183 coefficients each. Variances ( $V_{trait1}(t)$ ) and covariances ( $C_{trait1,trait2}(t)$ ) for each  
 184 time point were estimated by pre- and post-multiplying the variance-covariance  
 185 matrix by the corresponding time coefficients of the Legendre polynomials using the  
 186 following formulas:

$$187 \quad V_{trait1}(t) = [l_0(t) \quad l_1(t) \quad l_2(t)] \begin{bmatrix} \sigma_{a_0}^2 & \sigma_{a_0 a_1} & \sigma_{a_0 a_2} \\ \sigma_{a_0 a_1} & \sigma_{a_1}^2 & \sigma_{a_1 a_2} \\ \sigma_{a_0 a_2} & \sigma_{a_1 a_2} & \sigma_{a_2}^2 \end{bmatrix} \begin{bmatrix} l_0(t) \\ l_1(t) \\ l_2(t) \end{bmatrix}$$

$$188 \quad C_{trait1,trait2}(t) =$$

$$189 \quad [l_0(t) \quad l_1(t) \quad l_2(t)] \begin{bmatrix} \sigma_{a_0 a_0, trait1, trait2} & \sigma_{a_0 a_1, trait1, trait2} & \sigma_{a_0 a_2, trait1, trait2} \\ \sigma_{a_0 a_1, trait1, trait2} & \sigma_{a_1 a_1, trait1, trait2} & \sigma_{a_1 a_2, trait1, trait2} \\ \sigma_{a_0 a_2, trait1, trait2} & \sigma_{a_1 a_2, trait1, trait2} & \sigma_{a_2 a_2, trait1, trait2} \end{bmatrix} \begin{bmatrix} l_0(t) \\ l_1(t) \\ l_2(t) \end{bmatrix}$$

190

191 These variance-covariance components were then used to calculate correlations  
 192 between traits across the lactation.

193

194 *Derivation of Residual Feed Intake.*

195 Using elements from the 12 by 12 variance-covariance matrix and the animal effects  
 196 for cmilk, weight and BCS, it is possible to estimate a predicted intake from the other  
 197 variables by a matrix regression. If we use the following notation for the variance-  
 198 covariance matrix at a given time:

199

$$200 \begin{bmatrix} V_{DMI} \\ C_{DMI,cmilk} \\ C_{DMI,weight} \\ C_{DMI,BCS} \end{bmatrix} \begin{bmatrix} [C_{DMI,cmilk} & C_{DMI,weight} & C_{DMI,BCS}] \\ V_{cmilk} & C_{cmilk,weight} & C_{cmilk,BCS} \\ C_{cmilk,weight} & V_{weight} & C_{weight,BCS} \\ C_{cmilk,BCS} & C_{weight,BCS} & V_{BCS} \end{bmatrix} = \begin{bmatrix} \mathbf{B}_{11} & \mathbf{B}_{21} \\ \mathbf{B}_{12} & \mathbf{B}_{22} \end{bmatrix}$$

201

202 then a predicted animal effect for DMI can be calculated from a regression similarly to  
 203 what was proposed by Kennedy et al. (1993), but in its matrix form with:

204

$$205 \hat{a}_{eDMI}^*(t) = \mathbf{B}_{12}(t) * \mathbf{B}_{22}^{-1}(t) * \begin{bmatrix} a_{cmilk}(t) \\ a_{weight}(t) \\ a_{BCS}(t) \end{bmatrix}$$

206

207 Where  $\hat{a}_{eDMI}^*$  is the predicted animal effect for DMI at time t. Finally, we can construct  
 208 a RFI estimate which is the difference between the actual animal effect for DMI and  
 209 the one predicted from the three other variables:

$$210 RFI(t) = a_{DMI}(t) - \hat{a}_{eDMI}^*(t)$$

211

212 As this RFI is dependent on time, we also defined  $RFI_{tot}$  as the averaged RFI of each  
 213 animal over the whole lactation.

214

215 *Use of the outputs to study changes between times.*

216 One could also consider that changes of BCS are more important than BCS itself in  
 217 the estimation of RFI. To examine this point, we also estimated  $RFI_{\Delta BCS}(t)$  where all

218 the occurrences of BCS-related variables are replaced by  $\Delta$ BCS-related variables.  
 219  $\Delta$ BCS(t) is defined as the difference of BCS between two consecutive time points. In  
 220 the above formulas, it translates as a difference of Legendre polynomial coefficients  
 221 as follows for the animal effects, the variances and covariances, respectively:

$$222 \quad a_{\Delta BCS}(t) = [l_0(t) - l_0(t_{-1})] * \hat{a}_{c0\_BCS} + [l_1(t) - l_1(t_{-1})] * \hat{a}_{c1\_BCS} + [l_2(t) - l_2(t_{-1})] * \hat{a}_{c2\_BCS}$$

223

$$224 \quad V_{\Delta BCS}(t)$$

$$225 \quad = [l_0(t) - l_0(t_{-1}) \quad l_1(t) - l_1(t_{-1}) \quad l_2(t) - l_2(t_{-1})] \begin{bmatrix} \sigma_{a_0 BCS}^2 & \sigma_{a_0 a_1 BCS} & \sigma_{a_0 a_2 BCS} \\ \sigma_{a_0 a_1 BCS} & \sigma_{a_1 BCS}^2 & \sigma_{a_1 a_2 BCS} \\ \sigma_{a_0 a_2 BCS} & \sigma_{a_1 a_2 BCS} & \sigma_{a_2 BCS}^2 \end{bmatrix} \begin{bmatrix} l_0(t) - l_0(t_{-1}) \\ l_1(t) - l_1(t_{-1}) \\ l_2(t) - l_2(t_{-1}) \end{bmatrix}$$

226

$$227 \quad C_{\Delta BCS, trait2}(t) =$$

$$228 \quad [l_0(t) \quad l_1(t) \quad l_2(t)] \begin{bmatrix} \sigma_{a_0 a_0 \Delta BCS, trait2} & \sigma_{a_0 a_1 \Delta BCS, trait2} & \sigma_{a_0 a_2 \Delta BCS, trait2} \\ \sigma_{a_1 a_0 \Delta BCS, trait2} & \sigma_{a_1 a_1 \Delta BCS, trait2} & \sigma_{a_1 a_2 \Delta BCS, trait2} \\ \sigma_{a_2 a_0 \Delta BCS, trait2} & \sigma_{a_2 a_1 \Delta BCS, trait2} & \sigma_{a_2 a_2 \Delta BCS, trait2} \end{bmatrix} \begin{bmatrix} l_0(t) - l_0(t_{-1}) \\ l_1(t) - l_1(t_{-1}) \\ l_2(t) - l_2(t_{-1}) \end{bmatrix}$$

229

230 And therefore, the predicted animal effect for DMI is calculated from:

$$231 \quad \hat{a}_{eDMI}^*(t) = \mathbf{B}_{12}(t) * \mathbf{B}_{22}^{-1}(t) * \begin{bmatrix} a_{cmilk}(t) \\ a_{weight}(t) \\ a_{\Delta BCS}(t) \end{bmatrix}$$

232 where the B matrix contains the  $\Delta$ BCS-related variances and covariances.

233 The same transformation was also performed on changes of BW.

234

235

## 236 **Results**

237

### 238 ***Descriptive statistics***

239 Descriptive statistics, averaged over the lactation, are reported in **Table 1** for the raw  
 240 data of the four estimated traits, the four animal effects and the RFI. The four traits

241 are variable, with a large range of values. Some values are especially low (for  
242 example 3.06 kg/d of cmilk or 6.02 kg/d of dry matter) but they are unlikely  
243 measurement errors because first, data were averaged on a weekly basis and  
244 second, they are relatively close to the previous value for the same animal (due to  
245 the filtering step). These extreme values are possibly due to health issues.

246 The second half of the table presents the animal effects for the four traits estimated  
247 from the model and RFI. The animal effect corresponds to the deviation of this animal  
248 from the curve fitted to describe the time-course of the performance of an average  
249 animal for a given trait x parity group, after correction for the other fixed effects. The  
250 fixed effects curves are presented in **Supplementary Figure S1**. For the four traits,  
251 the averages of the animal effects obtained from the model are exactly zero, at each  
252 time and overall. The statistics presented in Table 1 were obtained only from animal  
253 effects for which corresponding raw data existed. By construction, the model can  
254 extrapolate and estimate animal effects for each animal at time-points beyond the  
255 range of data for that animal, even though there was no corresponding raw data. As  
256 these extrapolations were discarded to compute these statistics, it is expected that  
257 the means in Table 1 are not exactly zero. The exact same phenomenon occurs for  
258 the RFI estimates, with a mean of 0.04.

259

### 260 ***Correlations between animal effects across time***

261 The correlations between the animal effects for the four traits across the lactation are  
262 presented in **Figure 1**. The curves of correlation between DMI and cmilk and  
263 between DMI and weight showed an increase in early lactation and a decrease in  
264 late lactation. The correlations between DMI and cmilk were always higher by 0.1 or  
265 0.2. However, the correlation between cmilk and weight steadily decreased along the

266 lactation up to a point where it became slightly negative at the extreme end of  
267 lactation. Animals that produce more milk than average in early lactation are heavier  
268 than average, benefiting from a higher intake capacity, but these higher producing  
269 animals are less persistent. The correlation between cmilk and BCS was negative  
270 throughout the lactation, meaning that those who produce more milk always have a  
271 lower BCS than average, and more so in late lactation (they may lose more in early  
272 lactation and then, have difficulty to rebuild body reserves at the end). The correlation  
273 between weight and BCS remained stable over time at around 0.4, reflecting the  
274 weight equivalent of a unit BCS (animals having more reserves are heavier at every  
275 time point). Finally, the correlation between DMI and BCS started around zero and  
276 slowly decreased down to -0.2 in late lactation. At the Legendre polynomial  
277 coefficient scale, the correlations are estimated with a high accuracy (averaged  
278 standard error of 0.04, min=0.02, max=0.05), which correspond to variance  
279 estimation errors (averaged on the lactation) of below 5% for milk, 1% for body  
280 weight, 7% for intake and 4% for BCS.

281 Correlations between animal effects at different time points within each trait are  
282 presented in **Supplementary Figure S2**. The pattern is the same for the four traits  
283 with only positive correlations and with higher correlations between animal effects  
284 that are close in time. Correlations were always high for weight (>0.8), which is a  
285 cumulative trait, while they were a little more variable for the three other traits  
286 (correlations >0.4). The largest changes were mostly at the beginning or end of the  
287 lactation and the middle part was very stable (correlations >0.8). These correlations  
288 are very accurate with sampling errors being below 4% for intake, 2% for milk and  
289 BCS and 1% for body weight.

290

291 ***Correlations between the predicted animal effect of Dry Matter Intake and the***  
292 ***other traits***

293 Correlations between the predicted animal effect for intake ( $\hat{a}_{eDMI}^*$ ) and the four  
294 original animal effects were calculated at each time and are presented in **Figure 2**.  
295 Among the predictors,  $\hat{a}_{eDMI}^*$  was very highly correlated with the animal effect for  
296 cmilk, the correlation being always above 0.8 and almost 1 at the beginning of  
297 lactation. The second largest correlations were with the animal effect for weight,  
298 which starts at 0.7 and slowly decreases down to 0.4 along the lactation. Finally, the  
299 correlation with the animal effect for BCS was always very low, starting positive but  
300 below 0.2 in early lactation and decreasing down to -0.4 at the end of lactation. The  
301 correlation between  $\hat{a}_{eDMI}^*$  and  $a_{DMI}$  was between 0.6 and 0.8 in early lactation and  
302 then remained above 0.8 after 50 days of lactation.

303 Correlations of the animal effects for all the traits with RFI were also calculated. As  
304 expected, by construction, correlations between RFI and the three predictors, as well  
305 as with the predicted intake, were zero all along the lactation. The correlation  
306 between RFI and  $a_{DMI}$  started at almost 0.8 and decreased down to 0.5 during the  
307 first third of lactation and then remained stable until 250 DIM where it slightly  
308 increased to 0.6 at the end of lactation.

309

310 ***Evolution of Residual Feed Intake across the lactation***

311 Various individual profiles of RFI across lactation were observed, with some animals  
312 being efficient/non-efficient during the whole lactation while others were efficient in  
313 early lactation and non-efficient at the end or the opposite. In order to evaluate the  
314 possibility to measure only a part of the lactation and predict the overall RFI, we  
315 calculated correlations between RFI at each time and the RFI averaged over the

316 entire lactation ( $RFI_{tot}$ ). Results are presented in **Figure 3**. The correlation starts at  
317 0.45, increases up to 0.9 at 92 DIM where it remains stable until 197 DIM, decreasing  
318 down to 0.6 afterwards. These results suggests that RFI in the middle of lactation is a  
319 good predictor of the mean RFI over the whole lactation.

320

### 321 ***Using changes rather than the trait itself***

322 Correlations over time points between RFI and  $RFI_{\Delta BCS}$  and between RFI and  $RFI_{\Delta BW}$ ,  
323 are presented in **Figure 4**. Between RFI and  $RFI_{\Delta BCS}$ , the correlations were high  
324 ( $>0.87$ ), reaching 0.99 both at the beginning and the end of the lactation, indicating  
325 that RFI and  $RFI_{\Delta BCS}$  are almost the same trait. Between RFI and  $RFI_{\Delta BW}$ , the  
326 correlations are also always high ( $>0.7$ ), especially in early lactation. This suggests  
327 that changes are already taken into account by the use of the three Legendre  
328 polynomial coefficients (the changes being the derivatives of the trait). The  
329 dramatically high correlation at the beginning (and end of the lactation for BCS) could  
330 also indicate that, during these lactation stages, changes are more important than the  
331 trait itself, as we do not lose information when considering only changes as predictor.  
332 However, this is not true in the middle of lactation where changes are less important  
333 and where the traits bring additional values per se.

334

335

## 336 **Discussion**

337

### 338 ***Contribution of the proposed model to the current methodology***

339 In this study, we proposed a modeling strategy which allows the integration of time-  
340 series data to compute RFI, not only as repeated differences between the end and

341 the beginning of arbitrary periods, but by considering all traits dynamically. The  
342 traditional way of defining RFI - by linear regression – is not appropriate to jointly  
343 describe a dairy cow's non-linear trajectories of relevant traits during her entire  
344 lactation (Li et al., 2017). Indeed, the allocation of energy varies among the different  
345 energy sinks across the lactation, leading to changes in regression coefficients over  
346 time. As a result, feed efficiency in dairy cows is usually computed over short time  
347 periods (Prendiville et al., 2011; Fischer et al., 2018). This implies that results are  
348 based on a small number of data points and therefore are highly sensitive to  
349 measurement errors or one-time events (e.g., mastitis). In addition, even on short  
350 time periods, RFI estimates may still be subject to approximations due to fixed  
351 regression coefficients not being able to reflect biological changes, for instance a  
352 switch between loss and gain of body reserves. With the approach presented here,  
353 the number of measurements included in the system limits its sensitivity to one-time  
354 errors or disturbance. Moreover, it allows a permanent readjustment of the relevant  
355 coefficients over time, leading to estimations of RFI that avoid the biases inherent to  
356 the traditional RFI estimation methodology. As the model accounts for changes in  
357 variance for each trait over time, it also enables the correlations between traits to  
358 change over time, giving us a better overview of the relationships between the four  
359 traits across lactation.

360 Various studies already tried to explore further the methodology of RFI or the  
361 relationships between its components. For example, a multi-trait random regression  
362 model was previously developed by Manzanilla Pech et al. (2014) to investigate the  
363 relationship between DMI, milk and live weight over time but RFI was not estimated.  
364 Lu et al. (2015) used a modified Cholesky decomposition from a multi-trait linear  
365 model that allowed greater accuracy in genetic merit prediction in case of partially



366 missing data. Strathe et al. (2014) proposed a RFI derived from a bivariate random  
367 regression model for body weight and cumulative feed intake in pigs. More recently,  
368 Islam et al. (2020) used a Bayesian multivariate random regression to analyse DMI,  
369 energy corrected milk, BW and BCS and derived a genetic RFI from it. The approach  
370 presented here is an additional step on the way to improving the modeling of feed  
371 efficiency.

372

### 373 ***Evolution of the correlations between traits across the lactation***

374 The approach used here gives us an overview of the evolution of correlations  
375 between traits over the lactation. Such results are still rarely available in the literature  
376 where most studies calculated correlations on specific time-points, on a fixed period  
377 of the lactation, and not in a continuous, dynamic way. The work of Veerkamp and  
378 Thompson (1999), Spurlock et al. (2012), Liinamo et al. (2012) and Manzanilla Pech  
379 et al. (2014) are some of the rare exceptions. In addition, most of the studies  
380 describing correlations include pedigree information and therefore are able to split  
381 the animal effect between a genetic component and a permanent environmental  
382 effect, which was not our case. Even though the animal effects studied here are not  
383 exactly the same as additive genetic effects, some similar patterns with genetic  
384 correlations reported in the literature can be observed.

385 Similarly to what was found here, Manzanilla-Pech et al. (2014) reported that genetic  
386 correlations within traits across the lactation were generally positive and maximum  
387 during mid-lactation, and that correlations taken between times further apart were  
388 smaller. The very high positive correlations were also in accordance with previous  
389 studies (Koenen and Veerkamp, 1998; Veerkamp and Thompson, 1999 and Liinamo  
390 et al., 2012 for live weight; Tetens et al., 2014 for DMI; and Veerkamp and

391 Thompson, 1999 and Hüttmann et al., 2009 for milk production). However,  
392 Manzanilla-Pech et al. (2014) reported slightly negative genetic correlations (-0.2)  
393 between milk in early lactation and milk during the rest of the lactation and similarly  
394 for DMI, while our correlations between animal effects were always positive.

395 Correlations observed here for animal effects of the four traits at the same time point  
396 were also in general accordance with the literature. High positive genetic correlations  
397 were reported by Veerkamp and Thompson (1999) and Spurlock et al. (2012)  
398 between DMI and weight. Hüttmann et al. (2009) found that the genetic correlation  
399 between these two traits was changing over time with an almost null correlation  
400 between 31 to 60 DIM and a correlation of 0.4 between 121 and 180 DIM, while  
401 Manzanilla Pech et al. (2014) reported the correlation to be maximum at 34 DIM  
402 (0.56) and minimum at 153 DIM (0.29). Our results are showing a pattern similar to  
403 what Hüttmann et al. (2009) found but our correlations are always higher and closer  
404 to the values proposed by the other studies. In the literature, general positive genetic  
405 correlations ( $r_g$ ) were also reported between milk and DMI (van Elzakker and van  
406 Arendonk, 1993:  $r_g=0.46$ ; Veerkamp and Brotherstone, 1997:  $r_g=0.34$  ; Vallimont et  
407 al., 2010:  $r_g=0.52$ ). However, Manzanilla Pech et al. (2014) found a negative  
408 correlation between milk and DMI in early lactation that become positive and high  
409 ( $>0.7$ ) only after 38 DIM and reached a maximum at 195 DIM ( $r_g=0.91$ ). Our results  
410 are essentially different at the onset of the lactation and similar after. It may be due to  
411 differences in animal management around calving or to genetic differences between  
412 the datasets. Our evolution of the correlation between milk and weight over time is  
413 also very different to what was reported by Manzanilla-Pech et al. (2014). These  
414 authors found a slightly negative correlation (-0.1) both at the beginning and the end  
415 of lactation and a positive correlation of about 0.3 in mid-lactation. In contrast, our

416 results were similar to what those reported by Karacaören et al. (2006) with a  
417 correlation decreasing with time and becoming negative at the end of lactation.  
418 Body condition score is usually not among the traits considered in these kind of  
419 studies and therefore, estimated correlations are scarce. It is expected that cows  
420 mobilize body reserves in early lactation, while being in a situation of negative energy  
421 balance (Tamminga et al., 1997; Grummer, 2007). In the present study, the negative  
422 correlation between animal effects on milk and BCS is in accordance with this as  
423 higher than average milk production is associated with lower than average BCS. The  
424 stable correlation between weight and BCS supports the suggestion made in  
425 previous studies that live weight change can be a good indicator of body reserve  
426 mobilization (Thorup et al., 2013; Manzanilla Pech et al., 2014).

427

#### 428 ***Use of the Residual Feed Intake***

429 With the methodology proposed in this paper, we obtain a RFI changing through time  
430 for every single animal. This affords new possibilities. First, we identified that the  
431 averaged RFI over the lactation is highly correlated with RFI measured in mid-  
432 lactation, in accordance with Prendiville et al. (2011) and Connor et al. (2012). If the  
433 objective is to identify animals which are on average the most efficient, then the  
434 costly measure of intake could be done only during a few weeks during mid-lactation  
435 (ideally between 115 and 175 dim based on our results) with only a small loss of  
436 information, rather than during the entire lactation.

437 However, the question of what type of animal is desirable to select for is still valid.  
438 Efficient animals on average are also the ones that are more efficient in mid-lactation  
439 because this is the longest stable period of the lactation without dramatic changes.  
440 But because energy sinks and their relative importance are changing over the

441 lactation, efficient animals in mid lactation are not necessarily the ones which are the  
442 most efficient in early or late lactation. It clearly appears that during the lactation, the  
443 first 5 to 7 weeks are the most challenging period for the cows, during which they  
444 have to face a huge increase of milk production associated with a pronounced  
445 mobilization of their body reserves. This pronounced negative energy balance  
446 increases the risk of health issues and reduces fertility (Esposito et al., 2014) and it is  
447 particularly important not to increase the occurrence of health and fertility issues.  
448 Therefore, it is critical to make sure that animals we are selecting for do not have a  
449 deep body reserve mobilization in early lactation. Because BCS (and/or its changes)  
450 was included in the RFI model, the two traits are phenotypically independent but this  
451 may not be the case genetically. In addition, the influence of some health events may  
452 have been discarded in the analyses with the data filtering, or because animals with  
453 dramatic health or reproductive issues were culled. Therefore, the importance of BCS  
454 in the overall efficiency (including from an economic point of view) may have been  
455 underestimated in the model. The relationship between efficiency and resilience or  
456 robustness needs to be further investigated in order to make better choices in  
457 selection.

458 Furthermore, we now get individual trajectories of RFI which are highly variable from  
459 one animal to another. An obvious next step would be to perform a cluster analysis to  
460 see if we could identify specific types of animals. This could help scientists and  
461 breeding companies to determine what is the most suitable type of animals overall.

462

### 463 ***Other issues and future improvement***

464 If this approach and the associated results are very promising, numerous questions  
465 are still to be explored. First, the adaptability of the model in more general situations

466 needs to be tested. For instance, the model should be able to perform well when  
467 mixing data from different farms, or when animals are subject to diet changes during  
468 the lactation. The diet is indeed a major component of interest when studying feed  
469 efficiency, because individual digestive efficiency varies with diet composition. This  
470 influence of the diet was observed, for example, by Tempelman et al. (2015) and Lu  
471 et al. (2017), who determined substantial variability in partial regression coefficients  
472 between different rations. Several studies have already addressed this question.  
473 Durunna et al. (2011a) and Cassady et al. (2016) found moderate phenotypic  
474 correlations of 0.33 and 0.40 respectively between RFI of young beef cattle  
475 determined under both growing and finishing diets. Manafiazar et al. (2015) reported  
476 a correlation of 0.30 for RFI between dry-lot conditions and pasture. Estimate of  
477 genetic correlations between RFI of the same animals in different situations are rare.  
478 They generally give higher values than phenotypic correlations (0.50 in Durunna et  
479 al., 2011b; 0.83 in Martin et al., 2019). These results suggest the existence of a  
480 genotype-by-environment interaction, both in the case of diet changes and variable  
481 systems of production, as discussed by Berry and Crowley (2013) in their review. A  
482 test of the ability of the present model to take different diets, or situations, into  
483 account is therefore of primary interest.

484 Then, the mathematical modeling itself could be improved and adapted to situations  
485 and datasets. For instance, one could use splines instead of Legendre polynomials  
486 for the random regression or a heterogeneous variance for the residual effects.

487 A main point is also how animals with records for more than one lactation should be  
488 taken into account. In its present form, the model considers two lactations from the  
489 same animal as being independent, which may have slightly influenced the figures,  
490 but without changing any conclusion. As the first aim of this work was to present the

491 method, the focus was not on the RFI of individuals. When the interest is on ranking  
492 animals, one can incorporate a between-lactation (permanent environment) animal  
493 effect. Moreover, to be more accurate, all relationships among animals should be  
494 taken into account when pedigree or genomic information is available, which was not  
495 the case here. In addition, pedigree data or genotypes are particularly interesting as  
496 it would allow to split the animal effect into a genetic part and a permanent  
497 environmental part, as showed by Manzanilla-Pech et al. (2014) in a model close to  
498 ours. It is important to note that this new way of computing RFI could indeed be used  
499 in genetic or genomic evaluations.

500

### 501 ***Conclusion***

502 We have shown that it is possible to derive RFI from a multi-trait random regression  
503 model applied to DMI and its predictors, allowing for a dynamic estimation of the  
504 traits, free from all time-related issues inherent to the traditional RFI methodology.  
505 The model allows a better understanding of the correlations between the predictors  
506 during the lactation and it can be adapted and used in a genetic or genomic selection  
507 context.

508

509

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516

517 **Declaration of interest**

518 The authors declare no conflicts of interest.

519

520 **Ethics Approval**

521 During the experiment, all animals were kept indoors and handled with care, in line  
522 with Aarhus University's ethics policy in compliance with the European Union  
523 legislation for the protection of animals used for scientific purposes.

524

525 **Data and model availability statement**

526 None of the data were deposited in an official repository.

527

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530

531 **Author contributions**

532 P. Martin: Conceptualization, Formal analysis, Writing – Original Draft.

533 V. Ducrocq: Conceptualization, Methodology, Writing- review & editing.

534 D.G.M. Gordo: Resources, Writing- review & editing.

535 N.C. Friggens: Conceptualization, Writing- review & editing, Project administration,

536 Funding acquisition.

537

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542

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674 **Table**

675

676 **Table 1:** Means, Standard Deviations (SD), minima (Min.), maxima (Max.) and 5%  
677 and 95% centiles for the raw data of the four considered traits of dairy cattle, animal  
678 effects ( $a_{\text{trait}}$ ) and RFI

679

Type of data	Trait	Mean	SD	Min.	Max.	5% centile	95% centile
<b>Raw data</b>	Milk (kg of corrected milk)	33.4	7.8	3.1	68.9	21.1	46.9
	Weight (10kg)*	64.3	7.5	39.9	98.3	52.7	77.2
	DMI (kg)	21.7	3.4	6.0	38.7	16.3	27.4
	BCS (scale of 10 to 50)*	31.3	3.40	15.0	47.5	25.0	37.5
<b>Computed data</b>	$a_{\text{milk}}$	0.20	5.89	-28.61	24.05	-9.12	10.27
	$a_{\text{weight}}$	-0.11	6.75	-22.02	29.91	-10.27	11.65
	$a_{\text{DMI}}$	0.08	2.74	-14.72	12.61	-4.16	4.69
	$a_{\text{BCS}}$	-0.03	2.43	-10.88	13.48	-3.78	3.88
	RFI	0.04	1.37	-18.26	7.16	-1.99	2.21

680 \*The original scale was divided (for Weight) or multiplied (for BCS) by 10 in order to  
681 have raw data in the multiple trait analysis with similar orders of magnitude for the 4  
682 traits.

683 RFI: Residual Feed Intake

684 DMI: Dry Matter Intake

685 BCS: Body Condition Score

686

687

688

689 **Figure captions**

690

691 **Figure 1:** Time trends of the correlations between the animal effects (i.e. the animal  
692 differences from the average at any given time-point, across the lactation of dairy  
693 cattle) of the corrected milk (cmilk), the body weight, the dry matter intake (DMI) and  
694 the body condition score (BCS).

695

696 **Figure 2:** Correlations between the predicted animal effect for intake ( $\hat{a}_{eDMI}^*$ ) and the  
697 four original animal effects (corrected milk (cmilk), weight, dry matter intake (DMI)  
698 and body condition score (BCS)) in the considered dairy herd.

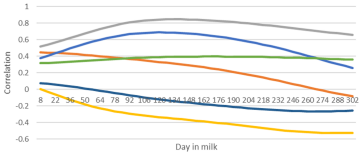
699

700 **Figure 3:** Correlation between the averaged residual feed intake (RFI) over the  
701 whole lactation and the RFI calculated at any given time-point in the considered dairy  
702 herd.

703

704 **Figure 4:** Correlation between the Residual feed intake (RFI) calculated using the  
705 trait as a predictor and the RFI calculated using changes of this trait as a predictor,  
706 for both Weight and Body Condition Score (BCS) in the considered dairy herd.

707



cmilk-weight    cmilk-dmi    cmilk-BCS  
weight-dmi    weight-bcs    dmi-bcs

