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Towards an improved estimation of the biological components of residual feed intake in growing cattle

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LIST OF ABBREVIATIONS

(In order of appearance)

RFI	-	Residual feed intake	**CH**	-	Charolais
FI	-	Feed intake	**HE**	-	Hereford
BW	-	Body weight	**LI**	-	Limousin
MW	-	Mid-test weight	**SI**	-	Simmental
EB	-	Energy balance	**ADG**	-	Average daily gain
BCS	-	Body condition score	**MTW**	-	Mid-test metabolic body weight
CI	-	Concentrate intake	**FAT**	-	Fat depth
AN	-	Angus	**AIC**	-	Akaike Information Criteria

SUMMARY

Residual feed intake (**RFI**) is the difference between observed and predicted feed intake (**FI**). It is represented as the residuals from a multiple regression model of FI on the various energy-sinks (e.g., maintenance, growth, activity). Residual feed intake is often cited to be indicative of feed efficiency differences among animals. Explaining a large proportion of the (phenotypic and genetic) inter-animal variation in RFI has, in large, remained elusive. Here we first describe a biological framework for RFI dwelling on analogies between RFI and energy balance. Alternative phenotypic and genetic statistical models are subsequently applied to a dataset of 1,963 growing bulls of alternative breeds. A novel aspect of this study was the characterisation of heritable inter-animal variation in deviations from the energy coefficients on the energy sinks, quantified using a mixed model. The variation in RFI declined as the number of energy sinks in the statistical model to estimate RFI increased. The variation in RFI reduced considerably when the significant genetic variation in animal deviations from the population average energy coefficient of maintenance was considered in the model. No significant genetic variation in deviations from the population average energy cost for growth or body fat levels existed in this study population. The presence of genetic variation in the energy coefficient of maintenance suggests either difference among animals in their partial efficiency of maintenance or that this term could simply be detecting inter-animal genetic variation in correlated energy sinks not included in the model. Estimated breeding values for the random regression coefficient could be useful phenotypes in themselves for studies wishing to elucidate the underlying mechanisms governing differences among animals in RFI.

INTRODUCTION

Improving animal feed efficiency is of great interest for increasing profitability in the Agri-Food industry as well as reducing the environmental footprint of animal production systems. Many alternative definitions of feed efficiency exist, each with their advantages and disadvantages (Berry and Crowley, 2013). Residual feed intake (**RFI**) is increasing in popularity as a measure of animal-level feed efficiency (Berry, 2008). Originally proposed by Byerly (1941) in poultry and later developed by Koch et al. (1963) in growing cattle, RFI is the difference between actual feed intake (**FI**) and the expected FI based on observed performance and the associated energy coefficients. These coefficients are usually estimated by least squares regression of FI on selected energy sinks.

Irrespective of the definition, the estimate of feed efficiency used should account for different functions involved in resource usage. For instance, two animals with a similar intake could have different growth rates because of differences in their maintenance and/or activity level. If all functions are considered, if the coefficients can be precisely estimated, and if all measurements are error free, then the residual must equal zero across all animals. Such a model is however unlikely for three reasons: 1) the measurement of traits will always contain some error, 2) it is difficult to directly measure and thus include all functions, 3) the precise estimation of coefficients relies upon a clear separation of functions according to their energy costs; growth is for example comprised of both protein and lipid deposition which have different energy costs (Pullar and Webster, 1977), and 4) individual animal energy coefficients may deviate from the population mean reflecting differences in the efficiency of energy conversion into bodily functions. Speculation on individual animal differences in the efficiencies of conversion of feed to different bodily functions exist (Meyer and Garret, 1967; Johnson et al., 2003; Van Milgen and Noblet, 2003). These differences represent individual animal deviations from a population average conversion efficiency; we hypothesis that such inter-animal variation could be quantified in a mixed model framework modelling both the (fixed) population average conversion efficiency and (random) animal deviations from this population average.

The objective of this study was to evaluate alternative models for assessing efficiency in growing animals and in particular quantify if any genetic variation in individual

animal deviations from the fixed regression coefficients of feed intake on the energy sinks exist.

BIOLOGICAL FRAMEWORK FOR FEED EFFICIENCY

In growing animals feed efficiency over a given time period was traditionally represented by feed conversion rate:

Feed conversion rate (%) = Body weight (**BW**) gain (kg) / FI (kg) **[1]**

This measure however presents the limitation of not accounting for individual differences in maintenance costs, and if the efficiency of feed conversion is considered independently of type, size, and stage of maturity, some control of composition of gain is necessary (Guilbert and Gregory, 1944). For this reason Guilbert and Gregory (1944) defined the feed conversion rate corrected for maintenance as partial feed efficiency:

Partial efficiency (%) = BW gain (kg) / [Total feed (kg) - Maintenance feed (kg)] **[2]**

In a similar approach Koch et al. (1963) accounted for maintenance costs regressing FI (adjusted for the mid-test weight, **MW**) on BW gain (kg / d):

$$\text{FI (kg / d)} = \mu + b_0 \cdot \text{MW} + b_1 \cdot \text{MW}^2 + b_3 \cdot \text{BW gain} + b_4 \cdot (\text{BW gain})^2 + e \qquad \textbf{[3]}$$

The advantage of the model proposed by Koch et al. (1963) is that after accounting for the maintenance cost, and for the FI required for a given rate of gain, the residual is expect to represent, among random noise; individual differences in feed efficiency. For this reason, the regression of FI on performance has been extensively used to compute the residuals and subsequently considering these residuals as a measure of feed efficiency (Berry, 2008; Berry and Crowley, 2013).

It is worth noting that the regression of FI on production (i.e., RFI equation) is, in principle, the same as the equation for energy balance (**EB**):

EB (kJ / d) = Feed energy content · FI (kJ / d) - Energy for maintenance · $\text{BW}^{0.75}$ (kJ / d) + Energy for gain · BW gain (kJ / d) **[4]**

This is useful because research on separating biological components of performance according to their energy costs has mainly been undertaken in the context of energy balance and predicting energy requirements (Emmans, 1994; 1997). Apart from the re-arrangement of the EB equation to isolate the FI term, the RFI approach differs in two ways. Firstly, the purpose of the RFI equation is to generate the residuals, and secondly to achieve this without bias; the energy coefficients are estimated in the regression for the local conditions of the data rather than being assumed to be universal, as in the case for EB.

During the animal growth period, the feed net energy content (i.e., after accounting to individual differences in the digestibility process) is used, in the broad sense, for the maintenance, growth, and activity. Maintenance is related to protein and lipid turnover, immune system, thermoregulation, response to stress, nutrient recycling, skin and hair growth, among other biological functions. It has been long known that the major factor influencing maintenance energy requirements is $BW^{0.75}$ (Kleiber, 1947). It should be noted that this ignores that maintenance costs may differ between animals of the same size with different protein and fat content. Differences in energy requirements for different body composition exist because there is substantial turn-over of protein but little, if any, turn-over of lipid (Kirkland et al., 2002). Pullar and Webster (1977), for example, estimated a higher heat increment of heat production per kJ of protein (1.25 kJ / d) than per kJ of fat (0.36 kJ / d) deposited. Thus, the energy requirements for maintenance should be a function of BW adjusted to constant body fatness (Emmans, 1997). In practice, attempts have been made to make this correction by including an (ultrasound) measure of body fat in the RFI equation (Basarab et al., 2003). However, such an approach does not properly account for the energy demand because of the multiplicative effect between body size and body fat content (Friggens et al., 2007). This phenomenon can be appropriately accounted for by including an interaction between body size and fat depth (i.e., fat mass) in the RFI equation or by adjusting BW prior to inclusion in the RFI equation. Zygoyiannis et al. (1997) documented a generalized method to estimate kilograms mass per unit of body condition score (**BCS**) adjusted for mature size of sheep, extended to cattle data. Other methods exist (NRC, 2000; Thorup et al., 2012).

Growth can be defined as the accretion of ash, protein and lipid plus water retained in the body within a defined period. There is a very strong allometry between ash, water and protein (Moulton, 1923) and thus the vast majority of variation in composition of growth is between protein and lipid; protein and lipid are also the only two energy depots in growth.

The energy cost of depositing protein is almost 1.64 times greater than the cost of depositing fat (Pullar and Webster, 1977); thus it is important to describe the energy demand for growth in terms of protein growth, and separately the deposition of fat. Thorup et al. (2012) developed this argument, based on the fact that body lipid content can be estimated from BCS (Wright and Russel, 1984). Given this, empty BW, body lipid and body protein masses can be estimated (details in Thorup et al. 2012).

Depending on the energy system used, activity is sometimes implicitly assumed within the definition of maintenance (i.e., the energy used when both protein and lipid changes are zero; Emmans, 1994). The inclusion of activity as a maintenance cost is based on some arbitrary and constant level of activity (Emmans, 1997). However, animals show considerable differences in activity levels (Ramseyer et al., 2009), especially in grazing production systems (Wesley et al., 2012). The development of accelerometer and global positioning system based technologies for individual monitoring offer the opportunity to reliably measure activity (Moreau et al., 2009). The energy cost for activity relates not only to the distance moved but also to the mass being moved (i.e. BW) and thus the interaction between BW and activity should be considered in the model.

Gut fill content is expected to be a function of FI and the individual degradability rate of that feed. Thorup et al. (2012) argues that in vivo measures of gut fill can be obtained from the residual gut fill; an estimable measure proportional to FI (Martin and Sauvant, 2010). It may thus be reasonable to assume that the effects of gutfill are effectively absorbed into coefficients translating the energy content of feed. Another issue is the effect of intake level on the energy value of the feed. This effect, related to the rate of passage of the feed through the digestive tract, challenges the implicit assumption of linearity in most RFI equations.

Any factor contributing to the individual variability in FI not included in the model, or assumed to be constant among individuals, will contribute to inaccurate feed efficiency estimations. This is also a shortcoming of the model proposed in the present study. However, the novelty of the approach proposed here lays in the fact of considering the individual deviation from the population average of factors included in the RFI equation.

In the following, within the limits of the dataset available, we attempt to incorporate these considerations, derived from the biological assumptions made primarily in the construction of the EB equation, into the development of a multiple regression model to estimate expected FI, and subsequently interpret RFI.

MATERIAL AND METHODS

Data editing

Performance data from 3,724 purebred beef bulls tested at the national bull performance centre at Tully, Kildare, Ireland between September 1983 and September 2011 were available. Details of the test station practices, the criteria used to select bulls, and the feed composition during the performance test program was described in detail by Crowley et al. (2010). Over the years, the feed offered was composed of forage (1.5 kg / animal per d) and *ad libitum* concentrate. In the present study the concentrate intake (**CI**, kg / d) was used as the measure of feed intake; between the years 1983 and 1991, available CI records were averages across a 14 d period. Between the years 1992 and 2005, available CI records were averages across a 21 d period, and from the year 2005 onwards, CI records was available on a weekly basis. Animal BW was measured every 14 d, 21 d, and 7 d between the years 1983 - 1991, 1992 - 2005, and 2005 - 2011, respectively.

From the original data, 161 bulls with less than four BW and CI records during the test period (last 70 d on test) were discarded. Bulls enter the performance station in batches, with up to 3 batches per year. The 3,563 bulls represented 106 different batches (i.e., contemporary groups) and 5 breeds (Angus; **AN** = 263, Charolais; **CH** = 880, Hereford; **HE** = 164, Limousin; **LM** = 1,311, and Simmental, **SI** = 945).

Performance traits

Average daily gain (**ADG**, kg / d) was calculated for each animal by regressing BW on days in test, considering all the BW records available for each animal within 96 d before the end of the test as described by Crowley et al., (2010). Bulls where the linear regression explained less than 95 % of the BW variability (n = 303) during the 96 d test period were discarded. Mid-test metabolic BW (**MTW**, $kg^{0.75}$) was calculated from the intercept and regression coefficient estimated by a linear regression of $BW^{0.75}$ on days in test. Mean CI was calculated as the arithmetic mean of the CI records from the last 70 d on test. Fat depth (**FAT**, cm) measurements were available on 2,008 bulls. A total of 45 bulls (AN = 5, CH = 16, HE = 0, LM = 18, and SI = 6) with a fat depth greater than 3 standard deviation from the breed group mean were considered as outliers and excluded. Only 1,963 bulls (AN = 183, CH =

485, HE = 100, LM = 821, and SI = 374) belonging to 69 contemporary groups with information on CI, MTW, ADG and FAT were retained.

Phenotypic regression models

Alternative multiple regression models for feed efficiency were progressively built up following the biological framework presented previously. All analyses were performed using the GLM procedure of SAS (SAS Inst. Inc., Cary, NC). All phenotypic models included contemporary group (69 levels) and breed (5 levels) as fixed effects. The phenotypic models investigated were:

$$CI = b_0 \cdot MTW + e \qquad \textbf{[P1]}$$

$$CI = b_0 \cdot MTW + b_1 \cdot ADG + e \qquad \textbf{[P2]}$$

$$CI = b_0 \cdot MTW + b_1 \cdot ADG + b_2 \cdot FAT + e \qquad \textbf{[P3]}$$

$$CI = b_0 \cdot MTW + b_1 \cdot ADG + b_2 \cdot FAT + b_3 \cdot MTW \times ADG + e \qquad \textbf{[P4]}$$

$$CI = b_0 \cdot MTW + b_1 \cdot ADG + b_2 \cdot FAT + b_3 \cdot MTW \times FAT + e \qquad \textbf{[P5]}$$

$$CI = b_0 \cdot MTW + b_1 \cdot ADG + b_2 \cdot FAT + b_3 \cdot ADG \times FAT + e \qquad \textbf{[P6]}$$

Where, b_0, b_1, and b_2 represent the partial regression coefficients of CI on mid-test metabolic body weight, average daily gain, and fat depth, respectively, and b_3 represents the partial regression coefficient for the different two-way interactions between MTW, ADG and FAT. The goodness of fit (R^2, adjusted-R^2, and Akaike Information Criteria; **AIC**) and the CI predicted by different models were used to compare models. An additional series of analyses tested the significance of the interactions between breed and the regressor variables.

Genetic regression models

Variance components were estimated using model P3 described previously, but fitting alternative random components. All models were fit using mixed model methodology in ASREML (Gilmour et al., 2009) and included contemporary group and breed as fixed effects. In all instances, relationships among animals were considered by tracing the pedigree of each animal back to founder animals. The genetic models fitted were:

$$CI = b_0 \cdot MTW + b_1 \cdot ADG + b_2 \cdot FAT + Animal + e \qquad \textbf{[G1]}$$

$$CI = (b_0 + b_{0A}) \cdot MTW + b_1 \cdot ADG + b_2 \cdot FAT + Animal + e \qquad \textbf{[G2]}$$

$$CI = b_0 \cdot MTW + (b_1 + b_{1A}) \cdot ADG + b_2 \cdot FAT + Animal + e \qquad \textbf{[G3]}$$

$$CI = b_0 \cdot MTW + b_1 \cdot ADG + (b_2 + b_{2A}) \cdot FAT + Animal + e \qquad \textbf{[G4]}$$

$$CI = (b_0 + b_{0A}) \cdot MTW + (b_1 + b_{1A}) \cdot ADG + b_2 \cdot FAT + Animal + e \qquad \textbf{[G5]}$$

$$CI = (b_0 + b_{0A}) \cdot MTW + b_1 \cdot ADG + (b_2 + b_{2A}) \cdot FAT + Animal + e \qquad \textbf{[G6]}$$

$$CI = b_0 \cdot MTW + (b_1 + b_{1A}) \cdot ADG + (b_2 + b_{2A}) \cdot FAT + Animal + e \qquad \textbf{[G7]}$$

$$CI = (b_0 + b_{0A}) \cdot MTW + (b_1 + b_{1A}) \cdot ADG + (b_2 + b_{2A}) \cdot FAT + Animal + e \qquad \textbf{[G8]}$$

Where b_0, b_1, and b_2 represents the fixed (i.e., population average) partial regression coefficients of CI on MTW, ADG, and FAT, respectively, and b_{0A}, b_{1A}, and b_{2A} represent the random (i.e., individual animal) partial regression coefficients for MTW, ADG, and FAT, respectively. The covariances between the random intercept and random regression coefficients were also estimated. In a separate analysis, the heritability of the residuals from model P3 (i.e., RFI as traditionally defined) was estimated using a mixed model that included breed as a fixed effect and animal as a random effect as undertaken by Crowley et al. (2010).

RESULTS

Data description

Summary statistics for initial and final age, as well as performance measures for the 1,963 beef bulls included in the study are in Table 1. No breed differences existed for either initial or final age. Charolais and Simmental bulls were heavier than the other breeds both at the start and end of test. Charolais and Limousin bulls had the lowest CI (11.38 and 10.19 kg / d) and fat depth (0.256 and 0.249 cm). Hereford, Simmental and Charolais bulls grew fastest (1.74, 1.74 and 1.75 kg / d, respectively). Angus and Simmental bulls were ranked as high RFI (0.332 kg / d and 0.443 kg / d, respectively) and Limousin as low RFI (-0.205 kg / d).

Table 1 Overall mean and least square means for initial and final age, initial and final body weight (BW), concentrate intake (CI), mid-test metabolic body weight (MTW), average daily gain (ADG), fat depth (FAT), and residual feed intake (RFI) across breeds

Trait	Mean, $n = 1,963$	Breeds[1]					Pooled SEM	*P*-value for breed effect
		AN, $n = 183$	CH, $n = 485$	HE, $n = 100$	LM, $n = 821$	SI, $n = 374$		
Initial age, d	314	334	320	307	306	305	31	0.4551
Final age, d	399	418	404	392	390	390	29	0.3857
Initial BW, kg	456.3	436.0[a]	487.2[b]	427.9[a]	437.1[a]	493.1[b]	9.12	<0.0001
Final BW, kg	599.2	574.1[a]	635.5[b]	574.5[a]	572.2[a]	640.0[b]	9.62	<0.0001
CI, kg / d	10.94	11.71[c]	11.38[b]	11.56[bc]	10.19[a]	12.24[d]	0.19	<0.0001
MTW, $kg^{0.75}$	113.2	108.4[a]	117.2[b]	107.8[a]	108.3[a]	118.1[b]	1.42	<0.0001
ADG, kg / d	1.70	1.63[a]	1.75[b]	1.74[b]	1.60[a]	1.74[b]	0.04	<0.0001
FAT, cm	0.309	0.552[c]	0.256[a]	0.559[c]	0.249[a]	0.316[b]	0.015	<0.0001
RFI[2], kg / d	0	0.332[c]	-0.124[ab]	0.025[b]	-0.205[a]	0.443[c]	0.12	<0.0001

[a-d] Least square means within a row with different superscripts differ (*P* < 0.05).

[1] Breeds: AN = Angus; CH = Charolais; HE = Hereford; LM = Limousin; SI = Simmental.

[2] RFI: residuals from the multiple regressions of CI, corrected for contemporary group, on MTW, ADG and FAT.

Phenotypic models

The partial regression coefficients of CI on MTW, ADG, FAT and their interactions (all corrected for the systematic effects of both contemporary group and breed) for the different models evaluated are in Table 2. The partial regression coefficient of CI on MTW (i.e., an approximation for animal size) ranged from 0.080 to 0.093 (kg / d) / $kg^{0.75}$ of MTW when no interaction term was included in the model. Mid-test metabolic BW (corrected by contemporary group and breed) alone explained 69 % of the total variability in CI. Average daily gain explained an additional seven percentage units of CI over and above that explained by MTW. The partial regression coefficients of CI on ADG ranged from 1.808 to 1.900 (kg / d) / (kg / d) of ADG when no interaction term was included in the model. Including FAT with both MTW and ADG in the model increased the R^2 and the adjusted-R^2 by 0.004 and 0.005 units, respectively. The partial regression coefficient of CI on FAT was 1.132 (kg / d) / cm of FAT when both MWT and ADG were also in the model. Mid-test metabolic BW, ADG and FAT together explained an additional 34.3 % of the variance in CI, after accounting for the

systematic effect of both contemporary group and breed (18.8 % and 23.3 % of total variance, respectively).

None of the interactions between the continuous regressor variables improved the fit to the data with the exception of the interaction between MTW and ADG. This term explained an additional 0.15 % of the variability for CI. The correlation between residuals of model P3 (i.e., no interaction term in the model) and P4 (i.e., interaction between MTW and ADG in the model) was 0.998.

Table 2 Partial regression coefficients of concentrate intake (CI) on mid-test metabolic body weight (MTW), average daily gain (ADG), fat depth (FAT), and their interactions

Model[1]	MTW	ADG	FAT	Interactions			R^2	Adj. $R^{2\dagger}$	AIC[2]
				MTW×ADG	MTW×FAT	ADG×FAT			
P1	0.093	.	.	.	.	.	0.691	0.679	-497.3
P2	0.081	1.887	.	.	.	.	0.760	0.750	-991.0
P3	0.080	1.899	1.132	.	.	.	0.764	0.755	-1026.5
P4	0.104	3.471	1.167	-0.014	.	.	0.765	0.756	-1034.2
P5	0.080	1.900	1.254[NS]	.	-0.001[NS]	.	0.764	0.755	-1024.5
P6	0.080	1.831	0.758[NS]	.	.	0.213[NS]	0.764	0.755	-1025.0

[1] Models included the contemporary group ($n = 69$) and breed ($n = 5$) as systematic effects.

[2] AIC: Akaike Information Criterion $= n \cdot \ln (SSE / n) + 2 \cdot k$; where SSE is the error sum of squares, and k is the number of independent variables. Lower is the best.

[†] Adjusted-$R^2 = 1 - (SSE \cdot (n - 1)) / (SST \cdot (n - v))$; where SST is the total sum of squares, SSE is the error sums of squares, n is the number of individuals, and v is the residual degrees of freedom.

[NS] Regression coefficients followed by superscript do not differ from zero at $P < 0.05$.

Only the association between CI and MTW was non-linear ($P = 0.005$). The linear and quadratic regression coefficient of CI on MTW was 0.140 (kg / d) / $kg^{0.75}$ of MTW and -0.0003 (kg / d) / $(kg^{0.75})^2$ of MTW, respectively. However only an additional 0.10 % of the variance in CI was explained by the quadratic term and the correlation between the residuals from a model with just a linear term for MTW or with both a linear and quadratic term for MTW was 0.998; hence the quadratic effect was not further considered. The correlation between the residuals of models P1 to P6 ranged from 0.87 to 1.00. In all instances, the residuals from model P1 had a correlation with the residuals from the other models lower than 0.882. The correlations among the residuals of models P2 to P6 were greater than 0.988.

In a separate analysis, with only contemporary group included as a fixed effect, the association between MTW and CI differed ($P = 0.016$) by breed. When however ADG was also included in the model the interaction between breed and MTW was no longer significant. No significant interaction with breed existed for either ADG ($P = 0.760$) or FAT ($P = 0.781$).

Genetic models

Variance components for the alternative random effects in the genetic models are in Table 3. When the residuals from P3 (i.e., RFI as traditionally defined) was fit as the dependent variable, the heritability was 0.41 ± 0.08. The genetic and residual variance for the simplest model (i.e., G1) with a random animal intercept term was 0.317 (kg / d)^2 and 0.315 (kg / d)^2, respectively; the heritability was 0.50 ± 0.08. The fixed and random terms in both models were identical except that, for the former model, a two-step approach was taken (i.e., RFI was first calculated using a phenotypic model and then the genetic parameters estimated for RFI) while the latter model estimated the systematic environmental effects and genetic effects simultaneously. The correlation between the estimated breeding values for RFI from the single- and two-step approach was 0.991.

When individual animal deviations in the regression of CI on MTW were included as a random effect, the residual variance reduced to 0.178 (kg / d)^2; no genetic variance in the random intercept term existed. Using the phenotypic variance of CI from the base model (i.e., G1) and the residual variances estimated in each of the tested models, a pseudo-heritability was calculated; the pseudo-heritability of the RFI model that included a random animal deviation in the regression coefficient of CI on MTW was 0.72. Using exactly the same random terms in a model without FAT gave a pseudo-heritability of 0.74. The pseudo-heritability obtained from this model, but using the original larger dataset (3,260 bulls) was 0.57.

Relative to the base model (i.e., G1) with just a random animal intercept term, small reductions in the residual variance of the model was observed when random regression terms on both ADG and FAT were separately considered. The residual variance of the model was lowest when individual animal deviations from the fixed regression on both MTW and FAT were included in the model. The AIC of this model however indicated that it was not superior to the model with just random deviations from the fixed regression on MTW (i.e., G2).

The correlation between the animal intercept term and the individual animal deviation in regression coefficient for MTW in model G2 was -0.96 ± 0.02. The new variance components were 2.012 (kg / d)^2, 0.0003 (kg / d) / (kg$^{0.75}$)^2, and 0.239 (kg / d)^2 for the animal

intercept, the animal slope on MTW, and the residual, respectively. The pseudo-heritability was 0.62; including the covariance between intercept and the random regression on MTW improved the AIC from 1137.3 to 1121.5. Therefore the most parsimonious model, as determined by the AIC, was that containing a random intercept, a random deviation from fixed regression on MTW and a covariance between them.

Table 3 Additive genetic variance for animal-specific random regression on the intercept, mid-test metabolic body weight (MTW), average daily gain (ADG), and fat depth (FAT) as well as the residual variance, heritability (h^2) and model fit statistics

Model[1]	Additive genetic variance				Residual variance,	$h^{2\dagger}$	Log (*Likelihood*)	AIC[2]
	Intercept, $(kg / d)^2$	MTW, $(\times 10^{-4} kg^{0.75})^2$	ADG, $(kg / d)^2$	FAT, $(cm)^2$	$(kg / d)^2$			
G1	0.317	.	.	.	0.315	0.50	-581.30	1174.6
G2	0	0.4	.	.	0.178	0.72	-561.63	1137.3
G3	0.222	.	0.035	.	0.306	0.52	-579.41	1172.8
G4	0.299	.	.	0.212	0.308	0.51	-580.59	1175.2
G5	0	0.4	0	.	0.178	0.72	-561.63	1139.3
G6	0	0.4	.	0.173	0.170	0.73	-561.03	1138.1
G7	0.218	.	0.032	0.137	0.302	0.52	-579.11	1174.2
G8	0	0.4	0	0.173	0.170	0.73	-561.03	1140.1

[1] All models included the contemporary group and breed as systematic effects.

[2] AIC: Akaike Information Criteria = -2 · Log (*Likelihood*) + 2 · *k*; where *k* is the number of parameters in the model. Lower is the best.

[†] Heritability for models G2 to G8 were calculated using the phenotypic variance from model G1 and the residual variance from the tested models.

DISCUSSION

Several studies have used RFI as the basis for attempting to identify biological predictors (Herd et al., 2004; Richardson and Herd, 2004; Herd and Arthur, 2009), genomic variation (Nkrumah et al., 2004; Barendse et al., 2007; Sherman et al., 2008), or gene expression patterns (Chen et al., 2011) contributing to differences in feed efficiency among animals. However, the success of such approaches depends heavily on the components included in equation used to obtain RFI. For example, if the RFI model only includes MTW then individual animal differences in ADG will contribute to differences in RFI, and any biological or genomic markers detected to predict these differences in RFI will, to a large extent, simply reflect growth rate rather than differences in true efficiency. Further, if growth is included but modelled incorrectly, i.e. not taking into account the different energy-using components (lipid and protein), then the problem remains; the quantification of the true efficiency phenotype is biased. One aim of this study was to explore the issue of how to extend the RFI equation to minimise this problem.

If relevant energy sinks are included in the equation to obtain RFI (e.g., maintenance, lean growth) it is pertinent to ask the question whether there is individual variation in the partial efficiencies (i.e., the energy coefficients) associated with these components. One way to detect (heritable) differences in these partial efficiencies would be to allow individual animal (random) deviations from the fixed regression coefficients. Thus, the second aim of this study was to investigate if animal differences in the partial efficiencies exist. These, in themselves would be useful phenotypes for further, in-depth, analysis for the detection of biological predictors or understanding the underlying biological mechanisms or genomic variation. The two aims of this study are interrelated because the interpretation of animal differences for specific energy sinks (explored using the genetic models) depends on which energy components are considered in the model (explored using the phenotypic models).

Phenotypic models

The proposed phenotypic models explained more than 69 % of the phenotypic variance in CI, resulting in residual variances (i.e., RFI) lower than 31 %. The partial contribution of ADG to the phenotypic variance of CI was 6.9 % when the model already included MTW, contemporary group, and breed and is at the lower end of the documented 7

and 16 % in other populations (Nieuwhof et al., 1992; Arthur et al., 2001; Robinson and Oddy, 2004; Hoque et al., 2006; Kelly et al., 2010). In the present study, when fat depth, a measure of body lipid content, was added to the multiple regression model already containing MTW and ADG, the residual variability was reduced by only 0.4 % which is less than documented in most other populations of growing animals (up to 7 % as reviewed by Berry and Crowley, 2013). Hoque et al. (2006) reported an even greater marginal contribution of fat measures (13 %) to differences in feed intake in Japanese Black cattle, a breed genetically predisposed for intense fat marbling.

Several studies have described a direct relationship between maintenance requirements and body composition (i.e., body mass of fat and protein; Moe et al., 1971; Noblet et al., 1999; Kirkland et al., 2002). There is good evidence that protein and fat mass have very different maintenance requirements (Webster, 1981; Birnie et al., 2000), and that there is a multiplicative effect between maintenance and body composition (Van Milgen and Noblet, 2003). In other words, maintenance requirements are related to protein mass which means adjusting body weight for fat mass, i.e. body fat content (approximated by subcutaneous fat depth) × body weight. The interaction between MTW (a proxy for body size) and FAT was not, however, significant in the present study. We also considered the interaction between ADG and FAT because, in addition to effects on maintenance, the energy costs of synthesizing protein and lipid differs (Pullar and Webster, 1977). In the present study this interaction was also not significant. The non-significance of these two interaction terms probably reflects the limitations of the FAT measure available, and also the fact that the animals were in the linear phase of growth, a period where relatively little changes in the proportion of protein and fat are observed (Owens et al., 1995). We suggest that the inclusion of these effects would be more important in the calculation of RFI on animals at ages close to maturity (i.e., greater variation in body composition; Owens et al., 1995). These effects should also be considered when defining long-term feed efficiency in mature animals frequently subjected to body condition changes (e.g., mature cows present great changes in BCS during their productive life; Veerkamp et al., 1995).

In the present study, the interaction between MTW and ADG was significant, increasing the model accuracy but only by 0.15 %. This unexpected interaction indicated heavier faster growing animals ate less than predicted by MTW, ADG and FAT alone. Conversely, but to a lesser extent, lighter faster growing animals ate more than predicted. In biological terms these contrasting effects are difficult to explain. However, this interaction

should be interpreted with caution because including this interaction term in the model considerably affected the coefficients of both MWT and ADG suggesting probably an over-parameterised model.

Genetic models

Genetic differences in RFI are normally quantified in a two-step approach: 1) retain the residuals from a regression of intake on the various energy-using components (e.g., maintenance, growth, activity), and 2) estimate the additive genetic variance of these residuals. In the present study a single-step approach was used, the animal (random) effect was included in the multiple regression of FI on MTW, ADG and FAT, after accounting for contemporary group and breed effects. Although the breeding values estimated using either the single- or the two-step approach were strong correlated (r = 0.991), the single-step approach had the advantage of simultaneously estimating all parameters. The heritability for RFI using the single-step approach (0.50 ± 0.08) was not different to the heritability estimated using the two step approach (0.41 ± 0.08) and was within the range of heritability estimates for RFI in growing animals (0.07 to 0.68) reported in the literature (Berry and Crowley, 2013). Although not substantial, the heritability of RFI reduced when FAT was included in the multiple regression model along with MTW and ADG; the small decrease in heritability is likely due to the weak marginal relationship observed in the present study between FAT and CI (adjusted for the other effects in the model). This decrease in heritability nonetheless does suggest that as the multiple regression equation to derive RFI becomes more complete (i.e., more energy sinks are included in model) what remains in the residual term is more residual noise which is likely to not be heritable. However, the residual component may still contain heritable differences in conversion efficiencies for different biological functions (if they exist).

In the present study, the genetic analysis was extended to investigate if animal differences in the partial efficiencies of the energy sinks exist. This approach was intended to provide further information on which components of the efficiency complex (e.g., maintenance, protein deposition) exhibit heritable variation. Accordingly, individual (random regression) deviations to the partial regression coefficients were sequentially included in the models. The existence of significant genetic variation in the random regression coefficients on MTW suggest that (heritable) differences in the partial efficiency of maintenance may indeed exist. This result should nonetheless be interpreted in the context of the available data

and RFI equation used. For example, when FAT was omitted from the mixed model, the random genetic variance on the partial regression coefficient of CI on MTW increased by 6 % because MTW and FAT are to some extent correlated; a meta-analysis of 5 studies indicated a genetic correlation of 0.21 between FAT and MWT (Berry and Crowley, 2013). Thus, the inter-animal variation on the energy coefficient of CI on MTW partly reflected differences in body composition.

Pathway analysis of structural genomic variations (Nkrumah et al., 2004; Barendse et al., 2007; Sherman et al., 2008) and differences in gene expression patterns (Chen et al., 2011) in animals divergently selected for RFI suggest that a large proportion of the variation in RFI among animals can be attributable to maintenance. This hypothesis has been substantiated by physiological evidence (Richardson and Herd, 2004; Herd and Arthur, 2009). The existence, in the present study, of individual (heritable) deviations from the partial regression coefficient of CI on MTW, a proxy for maintenance, supports this hypothesis. The breeding values for these random regression coefficients generated in the present study may help molecular geneticists to focus on the biological mechanisms contributing to the additive variation in maintenance requirements. Elucidation of the underlying biological mechanisms may also aid in deciding what energy sinks (or alternative statistical modelling) should be used to reduce further the variation in RFI providing a more direct strategy to improve feed efficiency. If the inter-animal variation in energy coefficients truly reflect differences in energetic efficiencies they may actually be less prone to genotype by environment (e.g., feed system, age) influences which are known to exist for RFI (Berry and Crowley, 2013).

The lack of significant genetic variance in the intercept of the model is somewhat unexpected since it is likely to contain genetic variation in other energy sinks (e.g., activity) not accounted for through correlations with the terms already in model. No genetic variance existed when the analysis was also applied to the larger dataset (without FAT in the model since it was not available for all animals). Significant genetic variance in the intercept term did however exist once a covariance between the intercept and random regression on MWT was considered in the model. The correlation between both terms was very strong (-0.96); the correlation was -0.98 when applied to the larger dataset.

Understanding the genetic or physiological components contributing to variation in complex phenotypes such as feed intake or efficiency can be best achieved by decomposing the phenotype into its likely contributing components. Here we propose that if studies

attempting to understand contributing factors to RFI are to be successful, the variation in contributing factors to RFI should be removed in the RFI equation thereby reducing the complexity of the RFI phenotype. Moreover, such an approach facilitates selection on the individual components of FI. Here we employed an alternative approach by quantifying the extent of heritable genetic variation in animal deviations from the population average energy coefficients on the energy sinks. As well as reducing the variation (and therefore probably the complexity) of RFI, breeding values for the random regression coefficients themselves could be very useful to help elucidate the relative importance of the various components that are likely to contribute to inter-animal variation in maintenance efficiency or the factors correlated which maintenance which should be included in the RFI equation.

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