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Simultaneous Bayesian estimation of genetic parameters for curves of weight, feed intake, and residual feed intake in beef cattle

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Abstract

Rates of gain and feed efficiency are important traits in most breeding programs for growing farm animals. The rate of gain (GAIN) is usually expressed over a certain age period and feed efficiency is often expressed as residual feed intake (RFI), defined as observed feed intake (FI) minus expected feed intake based on live weight (WGT) and GAIN. However, the basic traits recorded are always WGT and FI and other traits are derived from these basic records. The aim of this study was to develop a procedure for simultaneous analysis of the basic records and then derive linear traits related to feed efficiency without retorting to any approximation. A bivariate longitudinal random regression model was employed on 13,791 individual longitudinal records of WGT and FI from 2,827 bulls of six different beef breeds tested for their own performance in the period from 7 to 13 mo of age. Genetic and permanent environmental covariance functions for curves of WGT and FI were estimated using Gibbs sampling. Genetic and permanent covariance functions for curves of GAIN were estimated from the first derivative of the function for WGT and finally the covariance functions were extended to curves for RFI, based on the conditional distribution of FI given WGT and GAIN. Furthermore, the covariance functions were extended to include GAIN and RFI defined over different periods of the performance test. These periods included the whole test period as normally used when predicting breeding values for GAIN and RFI for beef bulls. Based on the presented method, breeding values and genetic parameters for derived traits such as GAIN and RFI defined longitudinally or integrated over (parts of) of the test period can be obtained from a joint analysis of the basic records. The resulting covariance functions for WGT, FI, GAIN, and RFI are usually singular but the method presented here does not suffer from the estimation problems associated with defining these traits individually before the genetic analysis. All the results are thus estimated simultaneously, and the set of parameters is consistent.

Key words: feed intake, gain, growing bulls, random regression, residual feed intake

Introduction

Traditionally breeding programs for beef cattle have focused on output traits such as weight, gain, meat content, and meat quality (Rolf et al., 2012). Increased focus on overall economic efficiency in the production system has increased the interest in input traits such as feed intake since feed comprises 60%–70% of

Abbreviations

ADG	average daily gain
AWGT	average weight
DFI	daily feed intake
FI	feed intake
RFI	residual feed intake
TFI	total feed intake
TRFI	total residual feed intake
WGT	weight

the production costs in a beef operation (Anderson et al., 2005). Selection for output traits such as weight and gain have had a positive effect on feed efficiency due to strong and positive phenotypic and genetic relationships between feed efficiency and these output traits (Arthur et al., 2001). However, this indirect effect on feed efficiency is primarily due to reduced total maintenance requirements (Koch et al., 1963) that follows from faster growth (i.e., shorter time to slaughter weight) but probably only have a limited effect on the metabolic efficiency of growing cattle. Furthermore, selection for growth will lead to increased mature size and thus increased maintenance requirements for the cow herd (Archer et al., 1999).

Recent focus, therefore, has been on improving feed efficiency in growing beef cattle by focusing on the part of feed intake that is independent of weight and gain. This is usually called residual feed intake (RFI), which is defined as the feed intake expressed as a deviation from the expected feed intake based on weight and gain. This term was first introduced by Koch et al. (1963) and by definition it should be phenotypically independent of weight and gain. The trait is centered at zero and animals with lower RFI are the most efficient because their feed intake is lower than expected based on their production requirements. The use of RFI has advantages over the traditional use of feed efficiency as a ratio trait (feed intake over gain or its inverse) because it is a linear trait. Ratio traits are not easy to include in a breeding program due to poor statistical properties. In fact, genetic selection on a ratio trait may only affect one of the two parts of the ratio, and this part may not be constant over animals and time, which would reduce the selection efficiency (Gunsett, 1984; Campo and Rodríguez, 1990).

Several definitions of RFI can be derived as described in detail by Archer et al. (1999), which all are based on the difference between observed feed intake and the expected feed requirements, given the maintenance and production of an animal. Differences in these definitions usually arise from the differences in recording periods and the method used to compute the expected intake. To compute the expected feed intake, either an approach using linear regression on (metabolic) body weight and gain (Koch et al., 1963) is used or the expected feed intake is computed from standard tables of feed requirement of growing cattle. The first approach will ensure that residual feed intake and the production traits body weight and gain is phenotypically independent of residual feed intake, whereas this might not be the case for the latter method because expected feed intake based on standard feeding tables often does not predict intake for individual animals very precisely. RFI is often defined as the residuals of a multiple regression model that accounts for weight and gain (Koch et al., 1963). As shown by Kennedy et al. (1993), joint selection on RFI and its component traits (e.g., weight and gain) based on selection index principles is equivalent to joint selection on feed intake and the component traits. As a result, computation of RFI, in a statistical sense, does not add

extra information since it is a (linear) combination of other traits measured. However, it may lead to expressions of efficiency that are more easily understood and interpreted when comparing animals with different production potentials.

As indicated above, the primary records related to efficiency in growing beef cattle are feed intake (FI) and weight (WGT). From the weight records, average daily gain (ADG) in a period can be computed such that production can be expressed as WGT and ADG over a certain production period. Generally, ADG is defined as a function of WGT at different time points. Most studies on RFI have used a two-step procedure to compute RFI of individual animals. First, a regression procedure has been used to regress feed intake on weight and production (WGT and ADG) and the estimated regression coefficients are used to compute expected RFI as residuals from the regression model used.

In this study, a Bayesian analysis of records on WGT and FI is presented and the aim is to show that inference on derived traits such as ADG and different definitions of RFI can be obtained from analysis of the basic records. This avoids the analysis of derived traits as well as the use of a two-step procedure for computing RFI so that more consistent inference can be made. The method was previously applied for the estimation of genetic parameters for feed efficiency in pigs (Shirali et al., 2018), broiler chickens (Mebratie et al., 2019), and dairy cattle (Islam et al., 2020). Here, we illustrate the method with more theoretical background and apply it on data on growing beef bulls.

Material and Methods

Data

In Denmark, each of the individual beef breeds used to have their own breeding program (i.e., slightly different breeding goals per breed) and a central part of these programs was a common performance test station where potential breeding bulls were tested for growth and feed efficiency performance. Briefly, animals were brought to the test station around 6 mo of age and stayed on the test station until they reached the age of 13 mo. Animals were weighed at arrival to the test station and then weighed with intervals of approximately 28 d. Animals were fed with a total mixed ration and feed intake was measured daily using automatic feeding gates. Feed intake records were averaged over each weighing period so that each individual record consisted of average weight (WGT) and average daily feed intake in a period (DFI). In addition, age and day of test were known for each record. DFI were expressed in Scandinavian feed units (SFU) per day. One SFU is equivalent to the net energy content of 1 kg of barley (85% dry matter). The content of SFU per kg feed dry matter is calculated as

$$SFU = (1.43.DCP + k.DCF + 1.DCFi + 1.DN) \times \left(\frac{V}{0.75} \right)$$

where *DCP* is the digestible crude protein percent of dry matter; *DCF* is the digestible crude fat percent of dry matter; *DCFi* is the digestible crude fiber percent of dry matter; *DN* is the digestible nitrogen-free extract, percent of dry matter, *k* being 2.41, 2.12, and 1.91 for concentrates, grains, and roughages, respectively; and *V* is the value number (Refsgaard Andersen and Foldager, 1980).

Records were distributed on 2,827 animals that originated from six different breeds of beef cattle and were collected over

a period of 20 yr (1998–2017). After pre-processing of the raw dataset, a total of 13,791 periods remained for downstream analyses. On average, each animal had 5.6 periods recorded with a range from 3 for animals with records in progress to 9 for animals having completed the test and no records edited. A summary of the data can be seen in Table 1. A total of 38,005 animals from six different beef breeds were included in the pedigree file, with 12,914 sires and 22,314 dams. Pedigree records were available for up to nine generations.

Statistical models

The longitudinal data were analyzed using bivariate random regression models by the use of the DMU software package (Madsen and Jensen, 2013). The analysis model used for each trait (WGT and DFI) was

$$y_{ijkl} = ys_i + breed_j + b_j(age_k) + l_{q_1}(t)'r_j + l_{q_2}(t)'a_k + l_{q_2}(t)'p_k + e_{ijkl} \tag{1}$$

where y_{ijkl} is a record in period l, from animal k belonging to breed j which arrived to the test station in year-season i, at an age at arrival to the central test station of (age_k). In the model, ys_i is the effect of year season i, $breed_j$ is the effect of breed j, b_j is the linear regression on age at arrival to the test station for $breed_j$, $l_{q_1}(t)$ is a vector-valued function that yields the vector of standardized Legendre polynomial coefficients of order q (i.e., the function returns $q + 1$ elements), r_j is the vector of regression coefficients on Legendre polynomials for breed j, a_k is a vector of order $q_2 + 1$ of random additive genetic effects of animal k, p_k is a vector of length $q_2 + 1$ of random permanent environmental effects of animal k, and e_{ijkl} is a residual measurement error. Covariance parameters to be estimated were as follows: $\mathbf{G}$, a matrix of genetic co-variances with dimension $2(q_2 + 1)$; $\mathbf{C}$, a matrix of permanent environmental co-variances of dimension $2(q_2 + 1)$; and $\mathbf{E}_t$, a 2×2 co-variance matrix of residual measurement error which was assumed to be heterogeneous with a different variance for each month on test resulting in six classes of residual variance. Co-variances between additive genetic effects were considered using the relationship matrix $\mathbf{A}$. In model (1), $l_{q_2}(t)$ was a vector-valued function of Legendre polynomials of order q evaluated at a standardized day of test t. If $q = 0$, the model reduced to a traditional linear repeatability model with no random regressions. A different order of fit was used in different parts of the model as indicated by q_1 and q_2. After initial univariate analysis using REML, q_1 was chosen to be 5 and q_2 was chosen to be 3 based on likelihood ratio tests with the proper degrees of freedom. The same order of fit (q_2) was used for both the random effects of animal additive genetic and permanent environmental effects. All results presented were estimated in bivariate models with a

Bayesian approach using Gibbs sampling. The model assumed flat priors for all dispersion parameters as well as location parameters associated with year-season, breed, and age at arrival to the station and breed-specific Legendre polynomials. The Gibbs sampler was run for 600,000 rounds, with the first 50,000 rounds considered as burn-in and from the remaining, and every 200th sample was saved for posterior analysis. The large number of samples was necessary due to the highly parameterized structure of the model. Convergence of the posterior distributions was assessed and confirmed by several diagnostic tests (e.g., Heidelberger and Welch's convergence diagnostic) implemented in the R package CODA (Plummer et al., 2006).

Derivation of (co)variances for observed and derived traits

Since model (1) is a random regression model, the functions $l_{q_2}(t)$ contain coefficients of Legendre polynomial for the test day t. Let $a_t = \begin{pmatrix} a_{WGT(t)} \\ a_{DFI(t)} \end{pmatrix} = l(t)' \begin{pmatrix} a_{k(WGT)} \\ a_{k(DFI)} \end{pmatrix}$ be a 2×1 vector of breeding values for WGT and DFI on test day t, where $a_{k(WGT)}$ and $a_{k(DFI)}$ are the vectors of additive genetic values for animal k from the sub-models in (1) for the traits WGT and DFI, respectively. Note that $a_{WGT(t)}$ and $a_{DFI(t)}$ are scalars but dependent on t, whereas $a_{k(WGT)}$ and $a_{k(DFI)}$ are vectors of length $(q_2 + 1)$ that are not dependent on t. Then, the final matrix containing the genetic (co)variances of WGT and DFI for the test day t can be obtained as

$$\mathrm{var}(a_t) = l(t)' Gl(t) \tag{2}$$

where $l(t) = \begin{pmatrix} l_{q_2}(t) & 0 \\ 0 & l_{q_2}(t) \end{pmatrix}$ is the covariance function for a_t, which is clearly a function of t. Similarly, the variance due to permanent environmental effects is $\mathrm{var}(p_t) = l(t)'\mathbf{C}l(t)$ and the variances due to measurement errors were $\mathrm{var}(e_t) = \mathbf{E}_t$. The phenotypic variance is thus $\mathrm{var}(y_t) = \mathbf{P}_t = \mathrm{var}(a_t) + \mathrm{var}(p_t) + \mathrm{var}(e_t)$. Standard population parameters such as heritability, repeatability, phenotypic, genetic, and residual correlations can be computed using the covariance functions and all these parameters are of course functions of t.

Based on the covariance functions defined by equation 2, we can derive new functions for other traits or aspects of the curves defined by model (1). Derivations are only shown for additive breeding value but the derivations of the other components of the phenotype (e.g., permanent environmental effect) are similar. The additive genetic value for deviation for gain on test day t can be computed as

Table 1. Summary statistics of the data per breed

Breed	Animals	Periods	WGT[1]			DFI[2]		
			Mean ± SD	Min	Max	Mean ± SD	Min	Max
Simmental	573	3181	571.92 ± 98	292	874	10.33 ± 2.0	2.27	16.10
Angus	246	1367	512.23 ± 90	271	774	9.77 ± 1.8	2.01	13.90
Herford	287	1621	492.00 ± 85	206	745	9.00 ± 1.6	1.95	13.46
Blonde d'Aquitaine	179	1017	520.40 ± 94	267	800	8.40 ± 1.6	1.06	12.45
Charolais	209	1177	542.23 ± 92	300	792	9.00 ± 1.7	2.06	13.60
Limousin	983	5428	487.60 ± 82	266	778	8.23 ± 1.5	2.23	14.40
Total	2477	13791						

[1]Weight records per breed.
[2]Daily feed intake per breed.

$$a_{G[t]} = \frac{\partial l_{q_2}(t)}{\partial t} a_{k(WGT)} \tag{3}$$

Note that the derivative with respect to the measurement error is constant and is unity since the measurement errors in (1) do not depend on t. This means that heritability of **G** is not influenced by the day-specific measurement error variance corresponding to **G** being estimated by a function defined in the same class of residual variance. However, if gain is derived over a period involving different periods of residual variances, then the residuals are not constant.

Alternatively, the derivative expressing additive breeding value for gain on test day t can be approximated as

$$a_{G[t]} \approx \left(l_{q_2}(t+1) - l_{q_2}(t)\right)' a_{k(WGT)} \tag{4}$$

The additive genetic value for average daily gain over a period (e.g., t_1 to t_n) can be computed as

$$a_{ADG[t_1,t_n]} = \frac{1}{(t_n - t_1)}(l_{q_2}(t_n) - l_{q_2}(t_1))' a_{k(WGT)} \tag{5}$$

Again, this is a linear function of model parameters and therefore phenotypic variance and all variance components can easily be computed using equation 2 as a quadratic in the linear form used to compute the additive breeding value. Note that using equation 4 for gain, phenotypic variance depends on the residual variance associated with the time steps considered, while in equation 3 that is not the case.

Residual feed intake was defined as the actual feed intake corrected for expenditure due to maintenance and gain. Following Kennedy et al. (1993), this can be derived from parameters of the model for the basic recorded traits as

$$RFI_t = DFI_t - b_1.WGT_t - b_2.GAIN_t \tag{6}$$

where b_1 and b_2 are partial phenotypic regression coefficients. Based on the derivations above, we can compute the phenotypic covariance matrix $\mathbf{P}_t$ for WGT, FI, and GAIN at time t. Based on this covariance matrix, the partial regression coefficients b_1 and b_2 in equation 6 can be computed using standard multivariate theory as used in equation 2. The regression coefficients in equation 6 therefore also become functions of time and thus can be denoted as $b_1(t)$ and $b_2(t)$.

Additive genetic values for RFI can be computed as $a_{R(t)} = a_{F(t)} - \begin{pmatrix} b_1(t) \\ b_2(t) \end{pmatrix}' \begin{pmatrix} a_{WGT(t)} \\ a_{DFI(t)} \end{pmatrix}$. This is again a linear function of model parameters and thus variance of $a_{k(R)}$ as well as all co-variances with any other model parameter can be computed in the usual way similar to equation 2. Clearly $a_{R(t)}$ is the breeding value for feed intake corrected for additive genetic breeding values for weight and gain.

In the derivation above, RFI was defined on a per day basis. Alternatively, RFI can be defined as total residual feed intake (TRFI) over a longer period of the test period including the whole test period. In this case, the following model will be used:

$$TRFI = TFI - b_1.AWGT - b_2.ADG \tag{7}$$

where TRFI is the residual feed intake, TFI is the total feed intake, AWGT is the average body weight, and ADG is the average daily gain over the chosen test period. This definition depends on the start and end of the chosen test period (e.g., t_1 and t_n), but

these subscripts were dropped from equation 7 for simplicity. The regression coefficients in equation 7 therefore must be computed from the covariance matrix pertaining to the period chosen. Again, a linear function for the elements in equation 7 and the computation of the corresponding covariance matrices are straightforward.

Feed intake was measured as average daily feed intake between consecutive weighing dates. Additive genetic values for total feed intake (TFI) over the test period (e.g., t_1 to t_n) can be computed as

$$a_{TFI[t_1,t_n]} = \sum_{t_1}^{t_n} l_{q_2}(t) a_{k(DFI)} \tag{8}$$

The additive genetic value for average weight (AWGT) in a period can be computed as

$$a_{AWGT[t_1,t_n]} = \frac{1}{2}[l_{q_2}(t_1) + l_{q_2}(t_n)]' a_{k(WGT)}$$

and the gain in a period chosen can be computed using (5).

Based on this, we can compute phenotypic as well as all other covariances for AWGT, ADG, and TFI in a chosen period. Subsequently, we can define RFI for any part of the test period including the total test period in the same way as in equation 2.

In the results section, it is chosen to compute accumulated RFI for all periods starting from $t_1 = 1$ and for each day until end of the test. In this way, TRFI becomes a function of t_1 and final day of the chosen part of the test period. This then includes the whole test period and results accumulated to all possible parts of the test period when each part always starts with $t_1 = 1$.

Results

Observed daily traits

Estimates of heritability for WGT and DFI together with posterior standard deviations (PSDs) are shown in Figure 1. The estimates of heritability for WGT were fairly constant around 0.6 over the test period. For DFI, the heritability was low at around 0.3 early in the test and increased gradually to 0.4 at the middle of the test period. The low heritability of DFI early in the test is probably related to animals adapting to the feed and environment at the test station. The functions for heritability were not continuous due to the heterogeneous residual variance assumed in the model.

The genetic correlation (r_g) between WGT and DFI on the first, middle, and end test days (i.e., 225, 300, and 391 d of age) with all other days on days for the same traits is shown in Figure 2. For weight, estimates of r_g among all days on test were high. This is in part due to the part-whole relationships. As the animal is growing, earlier weight is also part of the weight of animal later in the test period. For DFI, the situation was quite different and the estimates of r_g between DFI at the beginning of test and remaining days quickly dropped to zero and stayed at that level for the rest of the performance test period. This clearly shows that DFI early in the test cannot be used to predict genetic merit for feed intake later in the test period. The estimates of r_g between DFI at the end test day with all other days on test was in opposite direction of trend of test day 1 (age = 225) as expected.

Derived daily traits

Computation of RFI involves the partial regression coefficients on WGT and gain (GAIN) for a particular test day. Gain was
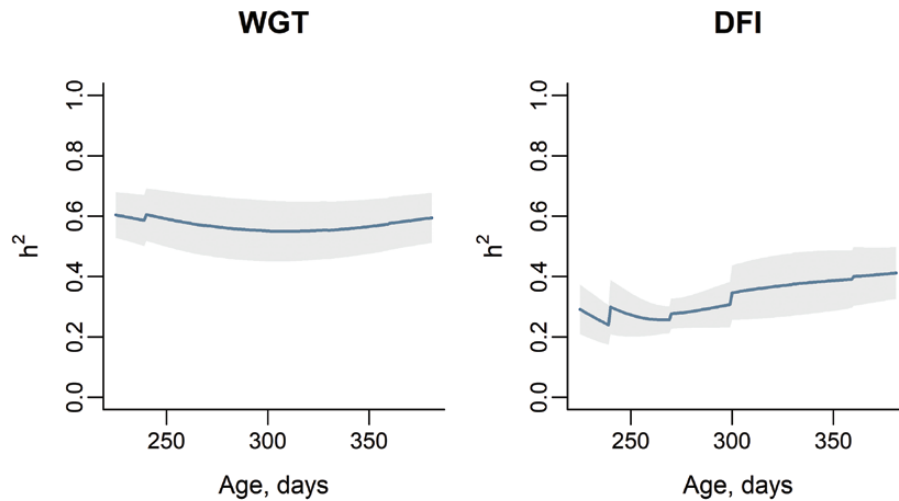
Figure 1. Posterior means (±PSD) of heritabilities (h^2) of weight (WGT, kg) and daily feed intake (DFI, SFU/day) over the test period (225–391 d of age).
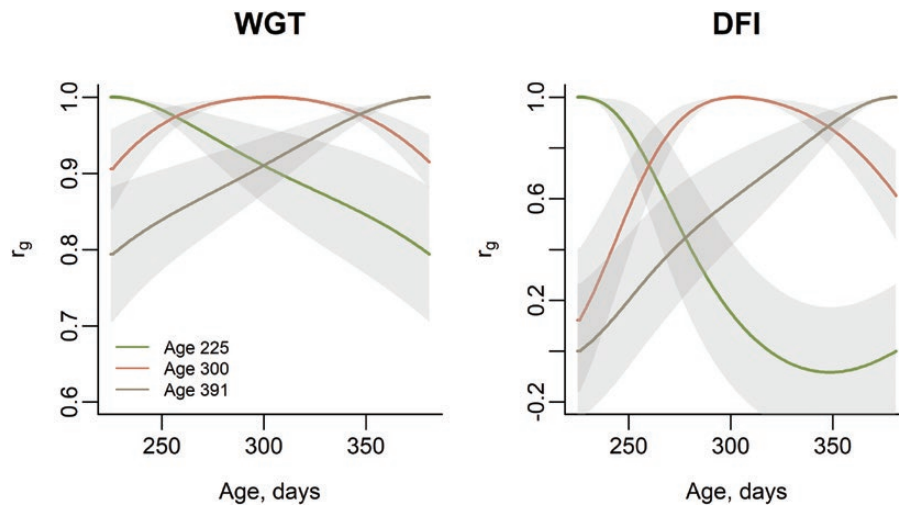

Figure 2. Posterior means (±PSD) of genetic correlations of weight (WGT, kg) and daily feed intake (DFI, SFU/d) at 225, 300, and 391 d of age with all other ages (225–391 d of age).

computed as the first derivative of the regression function for WGT. Based on this derivative, then covariance among WGT, GAIN, and DFI was computed for each test day. This allowed computing the partial regression of DFI on WGT and GAIN. Note that it is possible to obtain both genetic and phenotypic partial regressions depending on which covariance matrix (phenotypic or genetic) is used; as a result, it is possible to compute genetic RFI as defined by Kennedy et al. (1993) or RFI on the phenotypic level defined by Koch et al. (1963). In estimation of breeding values, using genetic partial regressions makes most sense, but in the characterization of the derived traits, phenotypic partial regression coefficients are more relevant. In the results below, for both derived traits (daily and accumulated), phenotypic partial regressions were computed.

In Figure 3a, the phenotypic partial regressions of DFI on WGT and GAIN are shown as a function of age. The partial regression of DFI on WGT which indicates maintenance requirement per kg of body weight was almost constant at 0.012 SFU/kg WGT changes over the whole test period. This figure agrees well with

table values of energy requirement for maintenance of growing bulls (Refsgaard Andersen and Foldager, 1980). Similarly, the partial regression of DFI on GAIN is also shown in Figure 3b. The amount of change in DFI due to 1-kg change in GAIN was low early in the test but increased close to 2 SFU/kg GAIN which gradually decreased for the remainder of the test.

RFI is often defined as the residuals of a multiple regression model that accounts for weight and gain (Koch et al., 1963). From this definition, variation in RFI is the part of variance in DFI that is not explained by variation in WGT and GAIN. Ratio of residual feed intake (RFI, SFU/d) variance to daily feed intake (DFI, SFU/d) variance over the test period (225–391 d of age) is shown in Figure 4. Very early in the test most variance in DFI was independent of variation in WGT and GAIN but after approximately 60 d on test (age of 285 d) about 0.60 of the variance in DFI could be explained by WGT and GAIN, and this level was maintained for the remainder of the test period. The variance not explained by WGT and GAIN is the variance in RFI, and the results clearly show that there is considerable phenotypic variation in RFI, i.e., in efficiency.
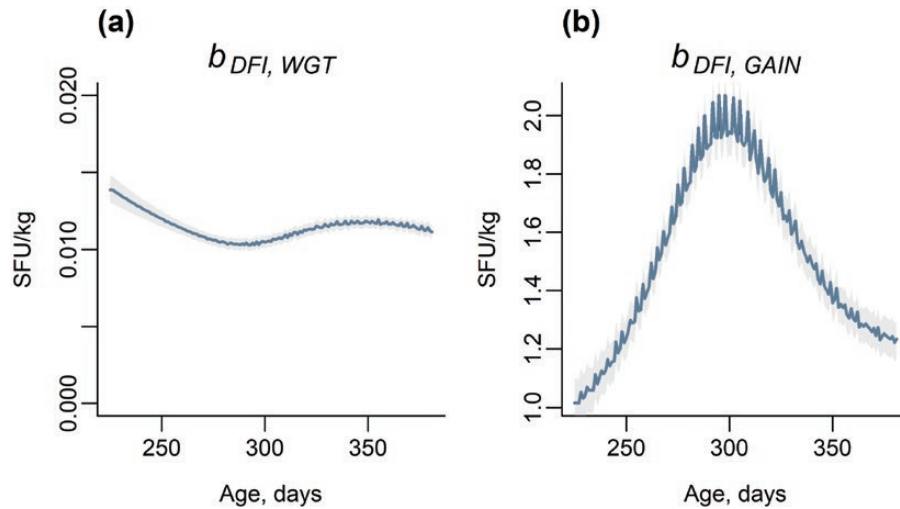
Figure 3. Phenotypic partial regressions of daily feed intake (DFI) in Scandinavian feed unit (SFU) on weight (WGT, kg) and gain (GAIN, kg/d) as a function of age (225–391 d of age).
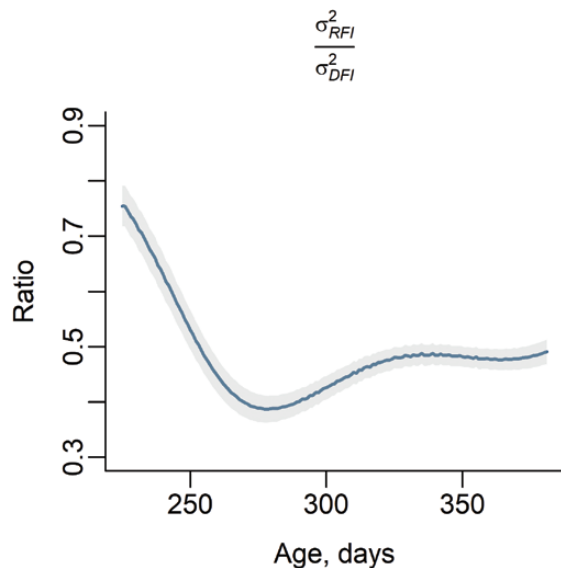

Figure 4. Ratio of residual feed intake (RFI, SFU/d) variance to daily feed intake (DFI, SFU/d) variance over the test period (225–391 d of age).

The genetic parameters for the derived traits GAIN and RFI (Figure 5) were computed based on equation 6 and using phenotypic partial regression coefficients. Heritability for GAIN was around 0.4 early in the test and gradually increased to 0.5 in middle of the test period (age of 300 d). For RFI, the heritability estimates were constant around 0.5 for the whole test period. Note that in this context heritability is for traits expressed on daily basis.

The estimates of r_g between derived traits expressed at start (age = 225 d), middle (age = 300 d), and end of the test (age = 391 d) with all other days on test are shown in Figure 6. For GAIN, the estimates of r_g of the first day of test dropped gradually to below zero at the end of the test period. Genetic correlation of the last day on test was in opposite direction and gradually increased over the test period. For the middle test day (age = 300 d), the genetic correlation was quite high (> 0.8) during the first and

middle test periods and gradually decreases to 0.4 at the end of the test period.

For RFI, the estimate of r_g of the first test day (age = 225 d) with all following days on test dropped to below zero in the middle of the test period and increased back to zero for the remainder of the test. The estimates of r_g of the last test day (age = 391 d) and all other days gradually increased over the test period.

Derived accumulated traits

Based on the estimated covariance functions, many other derived traits can be defined as linear functions of the parameters in model (1). The choice here are the average weight (AWGT, equation 9), total feed intake (TFI, equation 8), average daily gain (ADG, equation 5), and total residual feed intake (TRFI, equation 7) defined from start day on test and computed by using the same principles as for the daily derived traits. Note that derived accumulated traits were computed from start day of the test (age = 225 d) and each subsequent test day up to the end of the test period (age = 391 d). This is different from daily derived traits that were defined on a per day basis. As an example, AWGT is defined as average weight from 225 d of age to the next day of age and up to the end age. For the results below, it was chosen to compute accumulated traits for all periods starting from $t_1 = 1$ and each subsequent test day up to the end of the test.

Heritability of the derived accumulated traits AWGT and TFI is shown in Figure 7a and b. The heritability for AWGT was fairly constant around 0.6 either in short test interval (e.g., $t_1 = 1$ to $t_n = 25$) or extended days on test interval (e.g., $t_1 = 1$ to $t_n = 157$). The same trend was observed for TFI with heritability around 0.4 early in the test and was constant by extending the length of the test interval to the end of the test period. Note that due to the definition of daily and accumulated traits, the starting points for the curves for heritability and genetic correlation are identical because an accumulated period of 1 d is the same as the first daily trait.

The estimates of r_g between AWGT and TFI at the start, middle, and end days on test and all other days on test are shown in Figure 7c and d. For AWGT, the estimates of r_g at the start and following days in the test period were very high and close to unity. For the middle and end test days, the estimate of
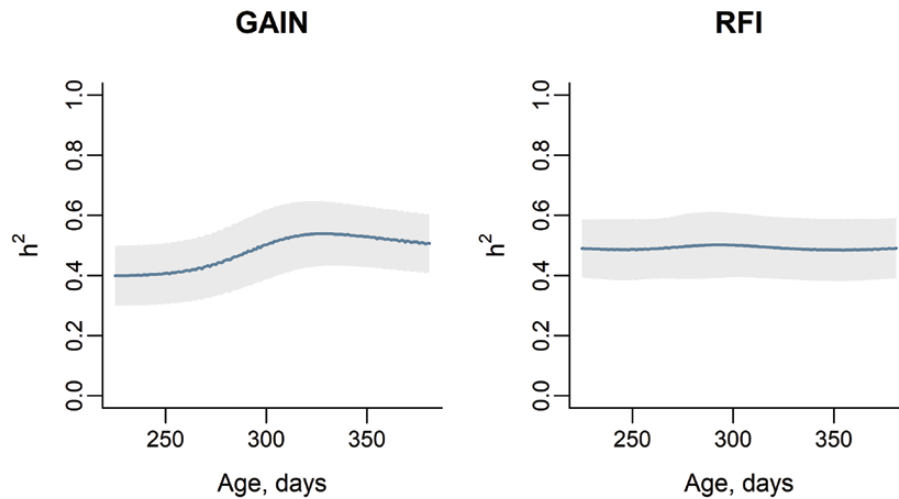
Figure 5. Posterior means (±PSD) of heritabilities (h^2) of gain (GAIN, kg/d) and residual feed intake (RFI, SFU/d) over the test period (225–391 d of age).
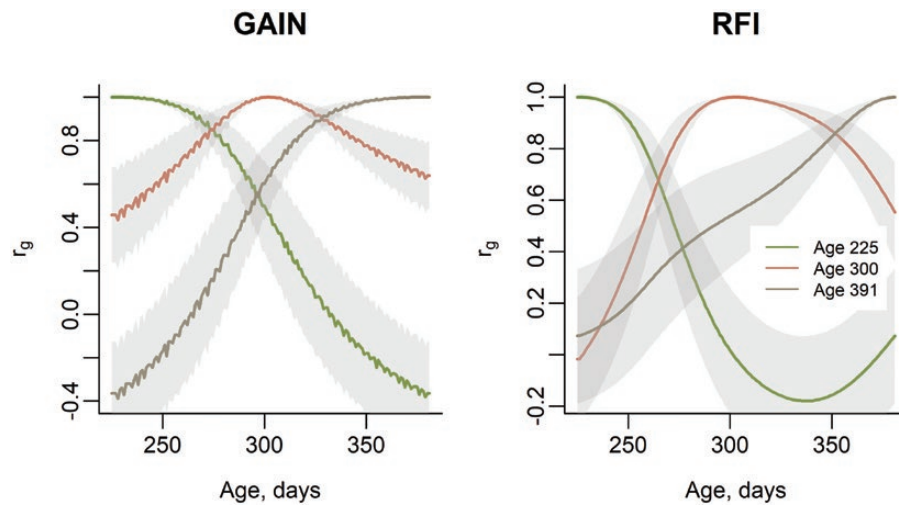

Figure 6. The posterior means (±PSD) of genetic correlations of gain (GAIN, kg/d) and residual feed intake (RFI, SFU/d) at 225, 300, and 391 d of age with all other ages (225–391 d of age).

r_g of AWGT and all other days on test were also quite high. The estimates of r_g for TFI of the first test day and following days decreased gradually during the test period and the estimate of r_g was around 0.4 at the end of the test.

The selected population parameters for derived accumulated traits of ADG and TRFI are shown in Figure 8. Heritability for ADG is around 0.4 in the whole period with a slight increase at the end of the test period. Similar to RFI in daily basis, the heritability estimates for TRFI were around 0.5 in the early part of the test period and when the test period was increased until 1 yr of age.

The estimates of r_g between ADG and TRFI at the start, middle, and end test days and all other days on the test are shown in Figure 8c and d. The estimate of r_g between ADG early in the test and ADG in increasingly long test periods was high but gradually dropped around 0.4 considering cumulative all test period. For TRFI, the r_g between the first test day and following days steadily dropped over the test period to an estimate of r_g of 0.4 between very short test periods and the full length of the test period used.

Discussion

Feed represents the largest input cost in beef production. Several studies have confirmed that feed intake is a heritable and considerable genetic variation that exists in feed efficiency both within and across breeds of beef cattle (Fan et al., 1995; Herd and Bishop, 2000; Arthur et al., 2001; Schenkel et al., 2004; Nkrumah et al., 2007; Rolfe et al., 2011; Retallick et al., 2017). All these studies have estimated the heritability of feed intake in the growing animal and estimates are in a moderate range of 0.25 and 0.44. Heritability estimates for feed intake vary between studies depending upon breed, method used for measuring feed intake, population, and other environmental factors. In the current study, observed traits for FI (DFI) had lower heritabilities at early ages and moderate to high heritabilities in later ages, with a range from 0.28 to 0.41 (Figure 1). For derived traits of FI including RFI, TFI, and TRFI, the estimates of heritability were high (0.4–0.5) over the test period and the trend of heritability changes was similar for both derived daily and accumulated FI traits.
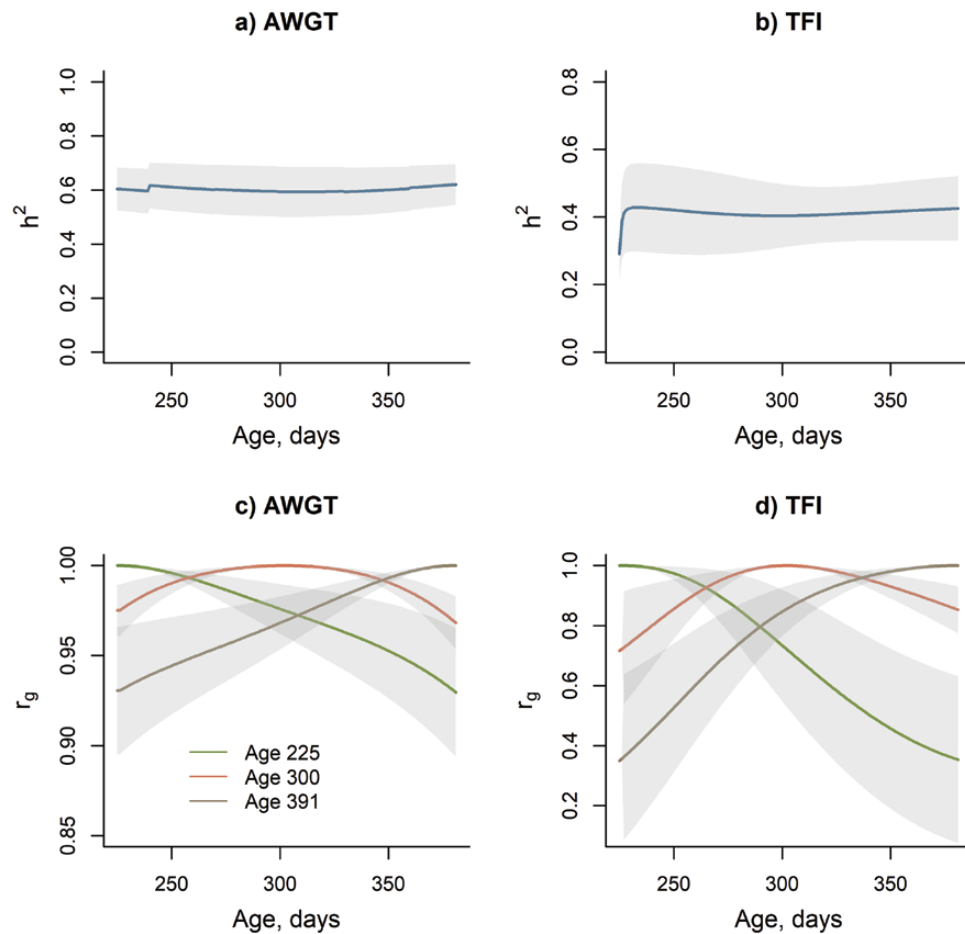
Figure 7. Posterior means (±PSD) of heritabilities for accumulated observed traits (AWGT, kg/d; TFI, SFU/d) over the test period (225–391 d of age) (a and b). Posterior means (±PSD) of genetic correlations for accumulated observed traits (AWGT, TFI) at 225, 300, and 391 d of age with all other ages (c and d). AWGT, average weight; TFI, total feed intake.

In this study, WGT was the basic record from which related derived traits such as GAIN, ADG, and AWGT could be obtained. Among weight traits, weight gain (e.g., GAIN and ADG) is of great interest owing to its economic importance which not only influences productive efficiency of desirable beef but also affects feed requirements in growing animals (Koch et al., 1963). Like feed intake, numerous studies have reported that growth is also a heritable trait in both dairy and beef cattle (Jensen et al., 1992; Archer et al., 1999; Herd and Bishop, 2000; Albuquerque and Meyer, 2001; Arango et al., 2004; Meyer, 2005; Bouquet et al., 2010; Rolfe et al., 2011; Baldi et al., 2012). Our estimates for trends of changing in heritability of WGT, ADG, and AWGT were all similar and in a range of 0.4–0.6 over the test period. These estimates are in agreement with the reported values of 0.26 and 0.62 by Rolfe et al. (2011) and Baldi et al. (2012), respectively.

Generally, the r_g between weight traits early in the test and end of the test period was high in a range of 0.8–1. This positive and close to unity estimate of r_g for weight traits at different ages suggests that animals with high body weight at early ages also tend to have higher than average body weight at the end of the growth trajectory. Similar results in terms of magnitude of genetic correlations have been reported in other studies (e.g., Nobre et al., 2003; Englishby et al., 2016).

Contrary to weight and growth traits, feed efficiency traits had a wide range of estimates of r_g (−0.2–1.0) over the test period and the genetic correlations consistently decreased with increasing age intervals. From the breeding perspective, this clearly shows that DFI or RFI early in the test cannot be used to predict genetic merit for feed intake later in the test period. Furthermore, the estimate of r_g between RFI in the middle of the test period (age = 300 d) with the start and end of the test was also moderate, indicating that decreasing length of the test period is not beneficial. Derived cumulative traits for feed efficiency (i.e., TFI and TRFI) also had a decreasing trend in estimates of r_g between early and late test periods. However, for these traits, the estimates of r_g between 300 d of age (middle test) with other ages were relatively high, and the selection of animals based on the breeding value of cumulative feed intake traits up to this age may not render the overall genetic gain.

In the results section, the estimates of r_g among days on test within each trait are presented. However, based on the covariance matrix and the partial regression coefficients in equations 6 and 7, obtaining the genetic correlations among observed and derived traits (e.g., r_g between RFI and GAIN for different or same days on test) is straightforward. The r_g among feed efficiency and production traits are among important genetic parameters being estimated in the literature (see review by Berry and Crowley, 2013; Kenny et al., 2018).

Since the proposal of RFI as a prominent trait of interest for assessment of feed efficiency by Koch et al. (1963), several studies have further developed the methodology of RFI or the relationships between its components. The conventional
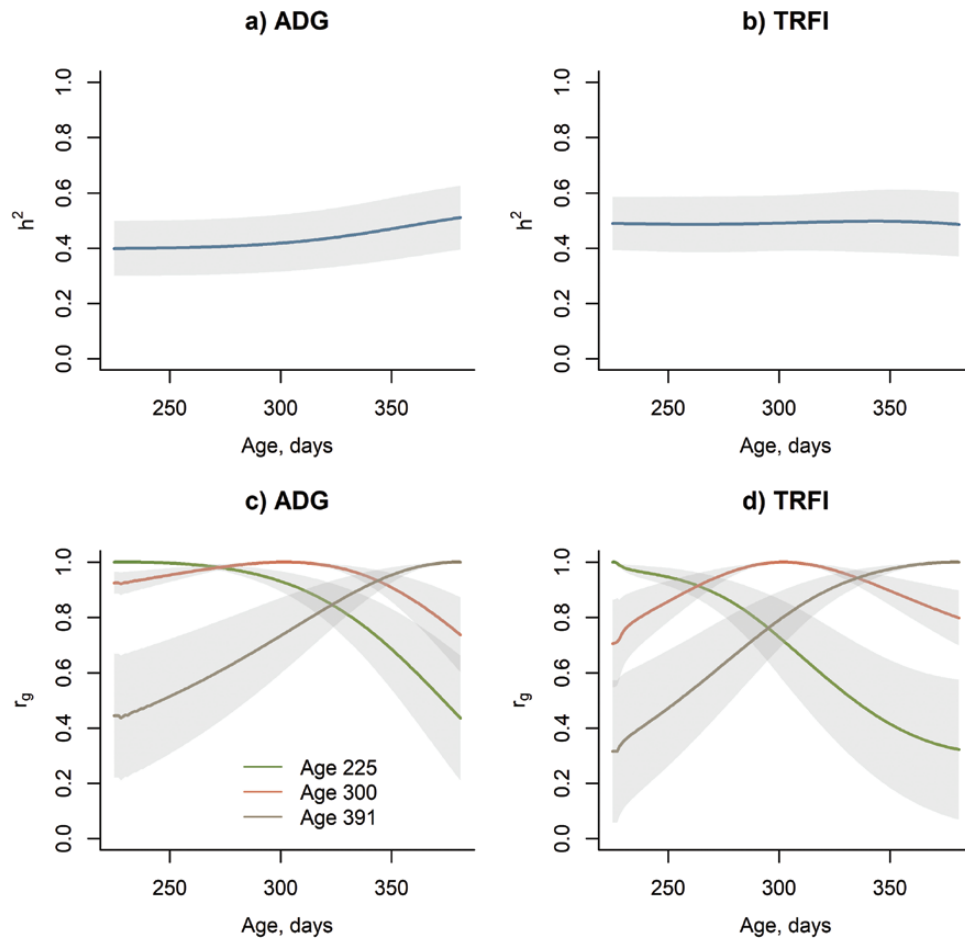
Figure 8. Posterior means (±PSD) of heritabilities for derived accumulated traits (ADG, kg/d; TRFI, SFU/d) over the test period (225–391 d of age) (a and b). Posterior means (±PSD) of genetic correlations for derived accumulated traits (ADG, TRFI) at 225, 300, and 391 d of age with all other ages (c and d). ADG, average daily gain; TRFI, total residual feed intake.

method for the calculation of RFI faces some limitations. For instance, the calculation methods are based on linear regression, which may not account for all environmental factors affecting RFI. Moreover, RFI are calculated based on summarized energy sink traits (e.g., ADG), which cannot explain the possible variances of calculated RFI over time periods. As a result, it has been suggested to analyze RFI as a longitudinal trait in the context of random regression models which have the advantages such as better definition of contemporary groups and better adjustment for environmental effects (Jensen, 2001). The first applications of this model for feed intake and growth were made by Andersen and Pedersen (1996). They used polynomial models with random regression coefficients to describe cumulated feed intake and gain as a function of number of days on test for gilts and castrated male pigs. More recently, Strathe et al. (2014) proposed a RFI derived from a bivariate random regression model for body weight and cumulative feed intake in pigs. Lu et al. (2015) used a multi-trait modeling strategy that exploits a Cholesky decomposition to provide a potentially more robust measure of feed efficiency when data on some of the feed efficiency component traits are missing. Shirali et al. (2017) presented a Horizontal model for multi-trait random regression analysis of longitudinal traits (feed intake) with single recorded traits of average daily gain and lean meat percentage. The one-step method presented here is an additional step on the way to

improve modeling of feed efficiency in different livestock species.

In this study, a Bayesian analysis of records on WGT and DFI was presented, and the aim was to show that inference on derived traits such as ADG and different definitions of RFI can be obtained from analysis of the basic records. This avoids the analysis of derived traits and avoids the use of a two-step procedure for computing derived traits such as RFI so that more consistent inference can be made. In the classical two-step procedure, first feed intake and production traits (or any other energy sink trait) are analyzed in a multiple linear regression analysis and regression coefficients are obtained before genetic analysis of the derived RFI. In the next step, RFI for each animal is computed using regression coefficients from the first step and then genetic analysis is performed together with production or body composition traits. In these procedures, the resulting covariance functions of RFI and production traits are usually singular because RFI is defined before genetic analysis as a linear combination of the other traits. However, in the proposed one-step procedure, the partial phenotypic and genetic regression coefficients are estimated from co(variance) matrices of feed intake and production traits in a multi-trait analysis, and then derived traits (e.g., phenotypic and genetic RFI) could be derived within the model simultaneously. In addition, the one-step approach properly accounts for errors in the estimation of regression coefficients as compared to

the classical two-step approach of Kennedy et al. (1993), which assumes co(variance) matrices of component traits of RFI to be known without error and that of Koch et al. (1963). Also, the one-step procedure in the Bayesian analysis avoids singularity of the co(variance) matrices by simultaneously estimating the co(variance) functions of RFI based on the conditional distribution of feed intake, given the production and other energy sink traits. Furthermore, estimation of the parameters in the regression analysis by the proposed one-step procedure is not biased by including fixed effects in the model, or by effects due to genetic trends for component traits in the population under investigation.

The method presented here has been applied for the estimation of genetic parameters and prediction of response to selection for linear or ratio expressions of feed efficiency in pigs by Shirali et al. (2018). Mebratie et al. (2019) used this approach for the simultaneous estimation of genetic parameters for production and feed efficiency traits for male and female broiler chickens using a multi-trait Bayesian analysis. In dairy cattle, Islam et al. (2020) used a Bayesian multivariate random regression to analyze dry matter intake, energy-corrected milk, body weight, and body condition score and derived a genetic RFI from it.

Conclusions

A one-step method for the simultaneous analysis of the basic records and derived traits related to weight and feed intake in growing bulls was presented. We showed that breeding values and genetic parameters for derived traits (e.g., RFI) defined either longitudinally or integrated over (parts of) of the test period can be obtained from a joint analysis of the basic records using a Bayesian framework. The method avoids the use of a two-step procedure to obtain the regression coefficients needed for computing RFI so that more consistent inference can be made. For the beef dataset analyzed, estimates of heritabilities for both weight and feed efficiency traits indicated ample potential for improvement by selecting bulls that are genetically superior.

Acknowledgments

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