

Deriving genomic breeding values for residual feed intake from covariance functions of random regression models

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ABSTRACT: Random regression models were used to estimate covariance functions between cumulated feed intake (CFI) and BW in 8424 Danish Duroc pigs. Random regressions on second order Legendre polynomials of age were used to describe genetic and permanent environmental curves in BW and CFI. Based on covariance functions, residual feed intake (RFI) was derived as the conditional genetic variance in feed intake given mid-test breeding value for BW and rate of gain, leading to consistent definition of RFI. The heritability of RFI over the entire period was 0.36, but more interestingly, the genetic variance of RFI was only 6% of the genetic variance in feed intake, revealing that only a minor component of feed intake was genetically independent of maintenance and growth. The heritability of daily RFI ranged from 0.01 to 0.07. The breeding value for 70 test days RFI was defined based on the coefficients of the Legendre polynomials. The accuracy of the estimated breeding values for RFI was further increased by 7 % by adding SNP information in a single-step genomic BLUP model.

Keywords:

Pigs

Feed efficiency

Genomic prediction

Introduction

In most breeding schemes for growing pigs, a large proportion of the selection capacity is allocated to improving feed efficiency (FE). The definition of the trait, expressing FE is not unambiguous; however, it is usually derived from basic records of weight and feed intake and computed prior to the genetic analysis, using multiple regression analysis. A bivariate random regression model for growth and feed intake may simultaneously account for changes in genetic and environmental variance in each of the two traits over time, and further allow genetic and environmental correlations between the two traits to vary over time. Deriving residual feed intake (RFI) directly from the resulting covariance functions lead to a clear expression of FE, as the covariance functions are based on a set of consistent parameters, which are estimated simultaneously (Jensen, 2013). Moreover, breeding values for RFI can be defined on a daily basis or integrated over part or the entire test period (Jensen, 2013). Christensen and Lund (2010) proposed the single-step GBLUP (ssGBLUP) that simultaneously integrates phenotypes, genotypes and pedigree information, which has recently been used for genomic evaluations of FE in pigs (Christensen et al., 2012). Here we extend their model to a bivariate random regression ssGBLUP model for genomic evaluation of FE in pigs with the aim of estimating variance components,

deriving RFI directly from the covariance functions and predicting genomic breeding values (GEBV) for RFI under this framework.

Materials and Methods

Data. A total of 8424 Danish Duroc boars were performance tested at the National test-station from approximately 30 to 120 kg BW, where feed intake is routinely collected using ACMO electronic feeders. These pigs were weighed biweekly (on average 6 times) during the performance test. The daily feed intake records were cumulated to the dates of weight recordings, yielding 51506 records. Additionally, 2 weight records per animal were available on 61693 animals (both females and males) from the herd performance testing scheme, giving a total of 174892 BW records. The additional weight records from the breeding herds were added to account for selection and additional accuracy. Data collected in the period from October 2008 to December 2012 were used for the genetic analysis. The pedigree was traced back to 1st of January 1995 and the file contained 79785 animals in total, where 5935 animals were genotyped with the PorcineSNP60 Illumina iSelect BeadChip. Data quality control prior to genetic analyses was implemented by discarding animals and SNPs with a call rate < 0.95, SNPs deviating from Hardy Weinberg equilibrium ($p < 0.0001$), and SNPs with a minor allele frequency < 0.05. After editing, there were 33302 SNP markers available.

Bivariate random regression model. The BW (\mathbf{y}^W) and CFI (\mathbf{y}^F) traits were modelled as follows:

$$y_{ijklmno\tau}^W = \sum_{q=0}^{q=2} b_{i,q}^W \xi_q(t) + par_j^W + tnb_k^W + \sum_{q=0}^{q=2} s_{l,q}^W \xi_q(t) + pen_m^W + litter_n^W \\ + \sum_{q=0}^{q=2} p_{o,q}^W \xi_q(t) + \sum_{q=0}^{q=2} a_{o,q}^F \xi_q(t) + e_{ijklmno\tau}^W \\ y_{ijklmno\tau}^F = \sum_{q=0}^{q=2} b_{i,q}^F \xi_q(t) + par_j^F + tnb_k^F + pen_m^F + \sum_{q=0}^{q=2} p_{o,q}^F \xi_q(t) \\ + \sum_{q=0}^{q=2} a_{o,q}^F \xi_q(t) + e_{ijklmno\tau}^F$$

The fixed effects were (superscripts denote trait, i.e. **W** for BW and **F** for CFI):

- $b^{W/F}$ = barn-year-replicate coefficients on basis Legendre polynomials of 2nd order ($\xi_q(t)$); t = age in days, ranging from 60 to 169 days and standardized to [-1, 1]. Hence, contemporary group specific growth and feed intake curves were fitted.

- $\text{par}^{\text{W/F}}$ = birth mother parity effect with 4 (1, 2, 3, 4) classes
- $\text{tnb}^{\text{W/F}}$ = total number born in litter of birth with 15 (<3,...,17) classes
- s^{W} = gender coefficients on basis Legendre polynomials of 2nd order and hence, gender specific growth curves were fitted.

The random effects were:

- litter^{W} = common litter effect; $\text{litter}^{\text{W}} \sim N(0, \uparrow_1^2 \mathbf{I})$
- $\text{pen}^{\text{W/F}}$ = pen-year-replicate effect;
 $[\text{pen}^{\text{W}} \text{pen}^{\text{F}}] \sim N(0, \mathbf{P}_1 \otimes \mathbf{I})$ where \mathbf{P}_1 was the covariance matrix for the pen-year-replicate effect
- $\text{p}^{\text{W/F}}$ = permanent environmental coefficients on basis Legendre polynomials of 2nd order;
 $[\text{p}^{\text{W}} \text{p}^{\text{F}}] \sim N(0, \mathbf{P}_2 \otimes \mathbf{I})$ where \mathbf{P}_2 was the covariance matrix for the Legendre polynomials
- $\text{a}^{\text{W/F}}$ = additive animal genetic coefficients on basis Legendre polynomials of 2nd order;
 $[\text{a}^{\text{W}} \text{a}^{\text{F}}] \sim N(0, \mathbf{K} \otimes \mathbf{H})$ where \mathbf{K} was the genetic covariance matrix for the Legendre polynomials and \mathbf{H} was the combined relationship matrix, as described in detail by Christensen et al. (2012).
- $\text{e}^{\text{W/F}}$ residual with
 $[\text{e}^{\text{W}} \text{e}^{\text{F}}] \sim N(0, \mathbf{R} \otimes \mathbf{W}^{-0.5})$; $\mathbf{W} = \text{diag}(\text{age})$ to account for increasing residual variance due to age.

Derivation of RFI. As RFI is defined as the conditional genetic (or phenotypic) variance of feed intake given mid-test BW (maintenance) and rate of gain (production), then

$$\hat{\mathbf{G}}_{012} = \hat{\mathbf{G}}_{011} - \hat{\mathbf{G}}_{012} \hat{\mathbf{G}}_{022}^{-1} \hat{\mathbf{G}}_{021} \text{ where } \hat{\mathbf{G}}_0 = \begin{bmatrix} \hat{\mathbf{G}}_{011} & \hat{\mathbf{G}}_{012} \\ \hat{\mathbf{G}}_{021} & \hat{\mathbf{G}}_{022} \end{bmatrix}; \mathbf{G}_0 = \mathbf{M} \hat{\mathbf{K}} \mathbf{M}'$$

Here $\hat{\mathbf{G}}_{011}$ was the estimated variance component related to feed intake, and $\hat{\mathbf{G}}_{022}$ was the estimated covariance components related to mid-test BW and rate of gain, and $\hat{\mathbf{G}}_{012}$ and $\hat{\mathbf{G}}_{021}$ were the corresponding estimated covariance components. The block-diagonal matrix \mathbf{M} contains the Legendre polynomials for a given age and growth period. For the entire growth period we will consider the period from 84 to 154 days of age where the breeding value for RFI for i 'th animal will be defined as $\hat{a}_i^{\text{RFI}} = \mathbf{Z} \hat{\mathbf{a}}_i^{\text{F}} - \hat{b}_1 \mathbf{X} \hat{\mathbf{a}}_i^{\text{W}} - \hat{b}_2 \mathbf{Z} \hat{\mathbf{a}}_i^{\text{W}}$ where b_1 [cov(feed intake, mid-test BW)/V(mid-test BW)] and b_2 [cov(feed intake, rate of gain)/V(rate of gain)] are partial regression coefficients (derived from \mathbf{G}_0) and $\mathbf{X} = [\{\}_0(119) \ \{\}_1(119) \ \{\}_2(119)]$ and $\mathbf{Z} = [0 \ \{\}_1(154) - \{\}_1(84) \ \{\}_2(154) - \{\}_2(84)]$.

Implementation and analyses. The software DMU was used to estimate variance components and predict the breeding values (Jensen and Madsen, 2012). The predictive abilities of the model were investigated by

splitting the records into a training dataset and a validation dataset by date 1. August 2011. The validation dataset included 2209 pigs with feed intake records. The accuracy of prediction was reflected by the validation correlation, which was defined as the correlation between EBVs from the full dataset and that predicted for validation dataset. Bias was detected by the corresponding regressions being different from unity.

Results and Discussion

Estimates of genetic parameters. The maintenance component b_1 (kg feed/kg BW) decreased throughout the growth period, which was expected because maintenance requirements are considered to be proportional to the BW raised to the power of 0.60 in growing pigs. The partial regression b_2 has a direct biological interpretation as the feed conversion ratio and it can be defined directly from the genetic or phenotypic covariance matrix. Feed conversion ratio increases in a curvilinear fashion from 1.5 at 80 to 2.5 at 160 days of age, reflecting the change in FE as the animal matures.

For selection purposes, a single breeding value for feed intake, efficiency and growth is desired. Genetic parameters were presented in Table 1 for these three quantities. The heritability of feed intake and growth, averaged over the entire period, were 0.35 and 0.41, respectively. The genetic correlation between the two traits was 0.87. The heritability of average daily feed intakes were reported by Schulze et al. (2002) to 0.39 and by Mrode and Kennedy (1993) to 0.45, which was in agreement with the current estimate. The heritability of RFI was 0.36, but more interestingly, the genetic variance of RFI was only 6% of genetic variance in feed intake. This shows that the opportunity for improving the genetic component of feed intake, being independent of production, is reduced. Hence, the genetic covariance to mid-test BW and weight gain explains the majority of the variability in feed intake. Also, this estimate can be considered a minimum as it was derived from the genetic covariance function and thus being genetically independent of production. Do et al. (2013) reported recently the heritability of RFI to 0.34 in Danish Duroc, where RFI trait was derived from phenotypic regression prior to the genetic analysis.

The heritability of both cumulative traits increased from 0.15 to 0.45 at the end of the performance test, while genetic correlation between the two traits increased from 0.60 to 0.95, reflecting that information was gained during the course of time as expected. The genetic correlation between daily feed intake and daily gain increased from 0.75 at 80 to 0.95 at 115 days of age and then decreased to 0.90 at 160 days of age. Genetic correlations between BW and daily feed intake were likewise high and followed similar pattern. As shown in Figure 1, the genetic variance of daily RFI decreased until day 110 of age and then increased for the remainder of the growth period. The heritability of daily RFI was low ranging from 0.01 to 0.07. The curvilinear trend of genetic variance could reflect the genetic determined variability between animals in

partitioning of nutrients for growth and maintenance during growth phase.

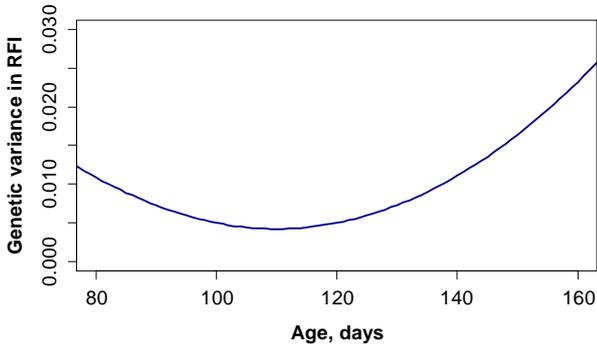


Figure 1. The genetic variance (kg/d)² in daily residual feed intake plotted as a function of the age of the animals.

Prediction of breeding values for RFI. Genomic breeding values for RFI can be predicted on a daily basis or integrated over the entire period (Table 2). Daily GEBVs are presented in Figure 2 for the highest and lowest efficient animals, being the 10th and 90th percentile of the distribution. The time-trend in the daily GEBVs were linear because of the use of second order Legendre polynomials for cumulative traits. The difference in efficiency between the two groups increased during the course of time.

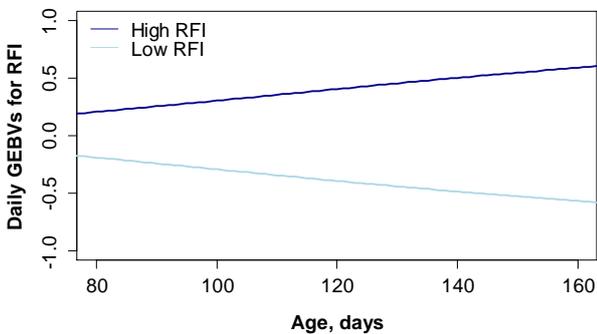


Figure 2. Genomic breeding values (GEBV) for daily residual feed intake for the highest and lowest efficient animals plotted as a function of the age.

The predictive abilities of the model are presented in Table 2 where we observed an increase in the prediction of GEBV for RFI, i.e. 0.481 versus 0.515. All predictions were biased, but ssGBLUP yielded less bias than traditional pedigree based BLUP.

Conclusion

A consistent definition of RFI was presented that was derived from the covariance functions of a bivariate random regression model. The conclusions are: 1) the approach allowed RFI to be defined on a daily basis or integrated over part or the entire test period 2) the heritability of RFI can be misleading as the genetic variance

in feed intake, being independent of rate of gain and mid-test BW, was low, and 3) the method with marker information gave an improvement of prediction compared with the pedigree-based method.

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Table 1. Genetic parameters for weight gain, feed intake and residual feed intake derived from covariance functions and evaluated from 84 to 154 days of age.

	Genetic variance (kg ²)	Heritability
Weight gain	81.35	0.35
Feed intake	424.9	0.41
Residual feed intake	23.94	0.36

Table 2. Predictions of breeding values for residual feed intake evaluated from 84 to 154 days of age, using traditional pedigree-based BLUP (BLUP) or single-step GBLUP (ssGBLUP) methods.

	Cor.	Reg.
All pigs		
BLUP	0.461	0.84
ssGBLUP	0.515	0.89
Genotyped pigs		
BLUP	0.479	0.84
ssGBLUP	0.517	0.86
Non-Genotyped pigs		
BLUP	0.474	0.79
ssGBLUP	0.505	0.90