How to improve breeding value prediction for feed conversion ratio in the case of incomplete longitudinal body weights[1]

V. H. Huynh Tran,[2] H. Gilbert, and I. David

GenPhySE, INRA, Université de Toulouse, INPT, ENVT, Castanet-Tolosan, France

ABSTRACT: With the development of automatic self-feeders, repeated measurements of feed intake are becoming easier in an increasing number of species. However, the corresponding BW are not always recorded, and these missing values complicate the longitudinal analysis of the feed conversion ratio (FCR). Our aim was to evaluate the impact of missing BW data on estimations of the genetic parameters of FCR and ways to improve the estimations. On the basis of the missing BW profile in French Large White pigs (male pigs weighed weekly, females and castrated males weighed monthly), we compared 2 different ways of predicting missing BW, 1 using a Gompertz model and 1 using a linear interpolation. For the first part of the study, we used 17,398 weekly records of BW and feed intake recorded over 16 consecutive weeks in 1,222 growing male pigs. We performed a simulation study on this data set to mimic missing BW values according to the pattern of weekly proportions of incomplete BW data in females and castrated males. The FCR was then computed for each week using observed data (obser_FCR), data with missing BW (miss_FCR), data with BW predicted using a Gompertz model (Gomp_FCR), and data with BW predicted by linear interpolation (interp_FCR). Heritability (h^2) was estimated, and the EBV was predicted for each repeated FCR using a random regression model. In the second part of the study, the full data set (males with their complete BW records, castrated males and females with missing BW) was analyzed using the same methods (miss_FCR, Gomp_FCR, and interp_FCR). Results of the simulation study showed that h^2 were overestimated in the case of missing BW and that predicting BW using a linear interpolation provided a more accurate estimation of h^2 and of EBV than a Gompertz model. Over 100 simulations, the correlation between obser_EBV and interp_EBV, Gomp_EBV, and miss_EBV was 0.93 ± 0.02, 0.91 ± 0.01, and 0.79 ± 0.04, respectively. The heritabilities obtained with the full data set were quite similar for miss_FCR, Gomp_FCR, and interp_FCR. In conclusion, when the proportion of missing BW is high, genetic parameters of FCR are not well estimated. In French Large White pigs, in the growing period extending from d 65 to 168, prediction of missing BW using a Gompertz growth model slightly improved the estimations, but the linear interpolation improved the estimation to a greater extent. This result is due to the linear rather than sigmoidal increase in BW over the study period.

Key words: feed efficiency, longitudinal data, pig, quantitative genetic

INTRODUCTION

Although genetics and management of pigs have been improved in recent decades, feed still accounts for around two-thirds of the production costs in western countries (Agriculture and Horticulture Development Board, 2016; Patience et al., 2015). In addition, feed efficiency is a trait of importance in several species (Nardone et al., 2010). In practice, feed efficiency is generally expressed as its inverse trait, the feed conversion ratio (**FCR**), which corresponds to the ratio of feed intake (**FI**) to BW gain (Losinger, 1998). Today, with

the development of automatic self-feeders and electronic identification, repeated measurements of FI and BW are available in many species, making it possible to analyze longitudinal FCR. Analysis of the individual profile of FCR over time can improve the genetic evaluation of this trait (Shirali et al., 2012). However, when FI is not recorded at the same time as BW, BW may be missing for substantial parts of the period to be analyzed. For instance, in an experimental French Large White pig population, male pigs are weighed every week during the growing period, whereas females and castrated males are weighed every month, meaning 60% of weekly BW are missing for the females and castrated males. Missing BW records can complicate the analysis of longitudinal FCR. Although mixed-effect regression models are supposed to be quite robust to missing data (Gibbons et al., 2010), estimation of variance components has proved to be erratic when some records are missing (Nobre et al., 2003). Little is known about the impact of missing BW on the estimation of the genetic parameters for FCR. Therefore, on the basis of the missing BW pattern observed in the French Large White pig experiment, the objectives of this study were to evaluate whether missing BW records have an impact on the estimation of genetic parameters for FCR and if the use of a Gompertz model or linear interpolation to predict the missing BW can improve estimation of the genetic parameters for FCR.

MATERIAL AND METHODS

Data

For the current study, data were collected in accordance with the national regulations of animal care in agriculture in France. Body weight records and FI of 2,503 growing French Large White pigs (1,222 males, 594 females, and 687 castrated males) were used in this study. This population is described in detail in Gilbert et al. (2007). Animal management was the following: animals born in a given farrowing batch were gathered at weaning (28 d of age) in the same postweaning unit. At 10 wk of age, 48 pigs were moved to a growing-finishing room with 4 pens per batch equipped with single-place electronic feeders (ACEMA 64, Pontivy, France; Labroue et al., 1997)). Twelve animals of the same sex were allotted to each pen. Animals were provided with an ad libitum pelleted diet based on cereals and soybean meal containing 10 MJ NE/kg and 160 g CP/kg, with a minimum of 0.80 g digestible Lys/MJ NE. The BW and age at the beginning of the test averaged 24.9 ± 3.8 kg and 67 ± 1 d, respectively. The average BW and age at the end of the test were 115.3 ± 10.9 kg and 168 ± 13 d. The pigs were allowed to acclimate to the feeders for

about a week, so the records of the first week of the test period were removed from the data set.

During the 16 consecutive weeks (from wk 2 to 17) of the test period, males were weighed weekly, and the majority of females and castrated males were weighed monthly. This resulted in a weekly proportion of missing BW of up to 60% in the females and castrated males in comparison with males, whose missing BW records were low (6%). The details of the available weekly BW of the females and castrated males are presented in Fig. 1. The individual FI of each animal was recorded automatically each time it used the feeder. Weekly averages of daily feed intake (**WDFI**) were then computed for each animal. The outlier values of WDFI and WDFI for which more than 2 d of records were missing in a given week were removed from the analysis, as reported by David et al. (2015). The final data set comprised 16,301 weekly BW records and 17,398 WDFI for the male pigs, 3,430 weekly BW records and 8,786 WDFI for the females, and 3,766 weekly BW records and 9,561 WDFI for the castrated males.

Analyses

Our aim was to measure the impact of missing BW records on estimations of the genetic parameters of FCR and to explore how to improve these estimations. To this end, we compared the estimations of genetic parameters and breeding values of FCR under 4 scenarios: FCR computed using complete observed BW and WDFI data (**obser_FCR**), FCR computed with missing BW data (**miss_FCR**), and FCR computed using missing BW replaced by predicted values obtained using a "by nearest" linear interpolation (**interp_FCR**) or using a Gompertz model (**Gomp_FCR**). For this purpose, we used the male data as the reference (very low proportion of missing BW records) and simulated randomly a pattern of missing values of BW on this data set by mimicking the same pattern of proportions of BW missing values per week as those observed in castrated males and females. For example, the full male data set contained 100% BW available for wk 5. After simulating the pattern of missing values, only 6.8% remained available for further analyses.

The FCR was then calculated for each animal i and week j as follows:

$$\text{FCR}_{ij} = \frac{\text{WDFI}_{ij}}{\text{ADG}_{ij}},$$

where WDFI_{ij} is the WDFI of animal i in week j and ADG_{ij} is the ADG of animal i at week j ($j \in [4,13]$) calculated over a 4-wk period as follows:

$$\text{ADG}_{ij} = \frac{\text{BW}_{ij+2} - \text{BW}_{ij-2}}{\text{age}_{ij+2} - \text{age}_{ij-2}}.$$
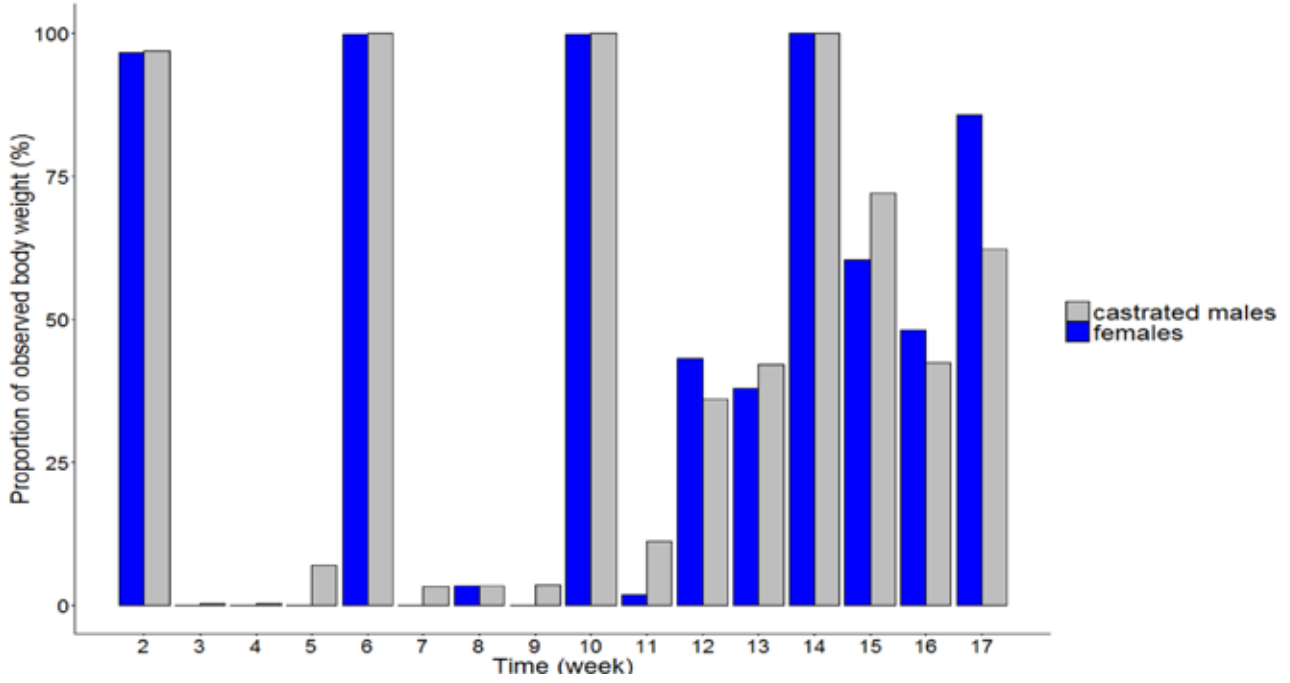
Figure 1. Proportion of BW available for females and castrated males per week from wk 2 (11 wk of age) to wk 17.

The BW used in the last formula differed depending on the scenario. In the first scenario, (obser_FCR), BW_{ij+2} and BW_{ij-2} corresponded to the measured BW. In the second scenario, (miss_FCR), if BW_{ij-2} or BW_{ij+2} was considered to be missing during the simulation of the missing data, then ADG_{ij} and hence miss_FCR_{ij} were not calculated but were considered missing. In the third scenario (interp_FCR), if BW_{ij-2} was missing, then BW_{ij-3} was used to compute ADG_{ij}. If BW_{ij-3} was also missing, then BW_{ij-1} was used to compute ADG_{ij}. If none were available, ADG_{ij} was considered missing. Similarly, missing BW_{ij+2} were replaced primarily by BW_{ij+3} and then by BW_{ij+1} if BW_{ij+3} was missing. If both were missing, then ADG_{ij} was considered missing. This method is equivalent to a linear interpolation except if BW_{ij-1} or $BW_{i,j+1}$ was used. In the following, the method is referred to as the by nearest linear interpolation. In the fourth scenario (Gomp_FCR), missing BW was predicted by a Gompertz model (Porter et al., 2010; Cai et al., 2011). For this purpose, the Gompertz model was fitted to the data with missing BW records using the NLIN procedure of SAS (SAS 9.4; SAS Inst. Inc., Cary, NC). The Gompertz model is given by

$$BW_{ij} = A_i * e^{-C_i * e^{-B_i j}}$$

where A_i is the asymptotic or maximum growth response (mature weight), B_i is the growth rate constant, and C_i is log(mature weight/birth weight). This model was fitted to each individual animal separately to estimate individual parameters A_i, B_i, and C_i. Subsequently, $\hat{A}_i, \hat{B}_i$, and $\hat{C}_i$ were used in the Gompertz formula to predict the missing BW. To reduce the effect of outliers and leverage points, BW was predicted from Gompertz model only when $\hat{A}_i, \hat{B}_i$, and $\hat{C}_i$ were between the 1st and 99th percentiles of distribution of each parameter.

In the genetic analysis, FCR_{ij} less than 0 and greater than 6 were considered outliers and were discarded from the analysis. The goal was to compare miss_EBV, interp_EBV, and Gomp_EBV obtained from miss_FCR, interp_FCR, and Gomp_FCR and see how they were correlated with obser_EBV of obser_FCR. To estimate the genetic parameters, a random regression model using Legendre polynomials (**RR-PL**) was fitted to a repeated FCR.

The RR-PL is given by

$$FCR_{ij} = \mathbf{X}_{ij}\boldsymbol{\beta} + \sum_{k=1}^{m} a_{ik}\varphi_{kj} + \sum_{k=1}^{n} p_{ik}\varphi_{kj} + \varepsilon_{ij}$$

where FCR_{ij} is obser_FCR, miss_FCR, interp_FCR, or Gomp_FCR for individual i at week j; $\boldsymbol{\beta}$ is the vector of fixed effect; a_{ik} and p_{ik} are the kth random regression coefficients for genetic and permanent environmental effects for animal i, respectively, with $\mathbf{a} \sim N(0, \mathbf{G} \otimes \mathbf{A})$ and $\mathbf{p} \sim N(0, \mathbf{P} \otimes \mathbf{I})$, where $\mathbf{A}$ is the known relationship matrix, $\mathbf{I}$ is an identity matrix whose order is equal to the total number of individuals, $\mathbf{G}$ is the (co)variance matrix of the additive random regression coefficients, and $\mathbf{P}$ is the (co)variance matrix of the random permanent environmental regression coefficients; φ_{kj} is the $(k-1)$th Legendre polynomial in week j; and m and n are the orders of regression for the genetic and permanent environmental effects, respectively. The permanent effect reflects the nongenetic individual effects that are correlated across repetitions.

Table 1. Percentage of missing BW and missing feed conversion ratios (FCR) in the simulation study (median across 100 simulation replicates) depending on the scenario

Item	Scenario[1]			
	Observed	Missing	Interpolation	Gompertz
Missing BW,[2] %	5.8	61.5 [60.8–62.1]		7.3 [6.6–7.7]
Missing FCR,[3] %	12.5	77.2 [76.1–78.2]	24.8 [24.1–25.9]	8.8 [7.5–9.6]

[1]Observed = available data; missing = data with a simulated pattern of missing BW; interpolation = ADG calculated using the by nearest interpolation; Gompertz = missing BW predicted using a Gompertz model. The numbers in brackets show the minium to the maximum.

[2]Percentage of missing BW over a period of 14 wk (from wk 2 to 15).

[3]Percentage of missing FCR over a period of 10 wk (from wk 4 to 13).

The covariance components and genetic parameters were estimated using the REML approach with ASReml software (Gilmour et al., 2009). All the fixed effects and 1-way interaction of biological relevance included in the model were selected beforehand in a stepwise manner using nested models that were compared with a likelihood ratio test. The fixed effects retained in the models were the week of observation (10 levels), the pen (96 levels), the batch (32 levels), the age, and BW of the animal at the beginning of the test. Likelihood ratio tests were used to choose the best polynomial orders for genetic and permanent environmental effects on the animal. Legendre polynomials of orders 3 and 2 were retained to model the genetic and permanent environmental effects, respectively. Heritability was computed for each week j as the ratio of the genetic to the total variance:

$$h_j^2 = \frac{\sum_{k=1}^{m} \varphi_{kj}^2 G_{kk}}{\sum_{k=1}^{m} \varphi_{kj}^2 G_{kk} + \sum_{k=1}^{n} \varphi_{kj}^2 P_{kk} + \sigma_{\varepsilon}^2},$$

where σ_{ε}^2 is the residual variance. Standard errors of estimates of genetic parameters were computed in ASReml using the method proposed by Fischer et al. (2004). Pearson correlations were used to compare the breeding values (EBV) for the different FCR: obser_EBV, miss_EBV, Gomp_EBV, and interp_EBV. The simulation of missing BW and the genetic analysis of each FCR were repeated 100 times. The mean and SD of the correlation coefficients and heritability of the 100 simulations were computed.

In the second step of the analysis, we estimated the genetic parameters and EBV for the full data set (males, females, and castrated males, 32,552 BW records) that "naturally" contained missing BW. For this data set, 3 FCR were computed for each animal and week, miss_FCR, Gomp_FCR, and interp_FCR, using the methods described above. As the full data set naturally contained missing values, the previous miss_FCR also corresponded to observed data. As described for the simulations, the EBV and heritability were esti-

mated using the RR-PL model. Gender was added to the models as a fixed effect. The correlation between Gomp_EBV, miss_EBV, or interp_EBV and the heritability of Gomp_FCR, miss_FCR, and interp_FCR were estimated as described above for the simulation study.

RESULTS

Simulation

A detailed description of missing BW data and resulting FCR in the 4 scenarios are given in Table 1. In the initial data set, 11,790 observations of WDFI over the 10-wk period (wk 4 to 13) were available to calculate FCR. The proportion of missing BW over the 14-wk period (wk 2 to 15) used to calculate FCR varied depending on the scenario; the proportion was low in the observed scenario (5.8%), slightly higher in the Gompertz scenario (7.3%), and very high in the missing scenario (61.5%). The percentage of missing BW in the scenario corrected using the by nearest linear interpolation was the same as in the missing scenario since BW is not replaced with this approach. A huge proportion (77.2%) of FCR was missing in the missing scenario. Correction using the by nearest linear interpolation scenario greatly reduced the proportion of missing FCR (median of 24.8%), but it remained higher than for the observed data (12.5%). Finally, the Gompertz scenario had the lowest percentage of missing FCR (median of 8.8%). It should be noted that missing Gomp_FCR values were due to extreme values of $\hat{A}, \hat{B},$ and $\hat{C}$ or to outlier values of Gomp_FCR.

The genetic variances and genetic correlations across the 10 consecutive weeks obtained with the RR-PL model in the different scenarios are listed in Table 2. The genetic variances obtained with obser_FCR, interp_FCR, and Gomp_FCR were quite similar, ranging from 0.01 to 0.09 for obser_FCR, from 0.02 to 0.09 for Gomp_FCR, and from 0.01 to 0.08 for interp_FCR, depending on the week. Higher genetic variances were obtained in the first week (0.04 for obser_FCR and Gomp_FCR, 0.05 for interp_FCR) and

Table 2. Mean and SD over 100 simulations of the additive genetic variance (on the diagonal) and genetic correlations (above the diagonal) of FCR over the 10-wk period in the different scenarios

Week	4	5	6	7	8	9	10	11	12	13
obser_FCR[1]										
4	0.04	0.89	0.70	0.48	0.14	−0.24	−0.48	−0.58	−0.56	−0.40
5		0.03	0.94	0.79	0.44	−0.06	−0.39	−0.51	−0.43	−0.19
6			0.03	0.94	0.67	0.18	−0.18	−0.33	−0.27	−0.06
7				0.03	0.88	0.13	0.13	−0.05	−0.07	0.04
8					0.02	0.84	0.57	0.37	0.23	0.13
9						0.01	0.92	0.76	0.54	0.25
10							0.01	0.95	0.75	0.41
11								0.03	0.91	0.64
12									0.04	0.89
13										0.09
miss_FCR[1]										
4	0.03 ± 0.01	0.26 ± 0.16	0.04 ± 0.15	−0.12 ± 0.12	−0.35 ± 0.08	−0.23 ± 0.14	−0.18 ± 0.14	−0.21 ± 0.14	−0.37 ± 0.11	−0.44 ± 0.17
5		0.10 ± 0.03	0.97 ± 0.02	0.85 ± 0.06	0.03 ± 0.15	−0.75 ± 0.09	−0.87 ± 0.05	−0.90 ± 0.04	−0.77 ± 0.08	0.31 ± 0.24
6			0.13 ± 0.04	0.95 ± 0.02	0.21 ± 0.14	−0.65 ± 0.12	−0.81 ± 0.08	−0.84 ± 0.06	−0.69 ± 0.09	0.39 ± 0.21
7				0.06 ± 0.02	0.49 ± 0.11	−0.40 ± 0.17	−0.60 ± 0.14	−0.66 ± 0.11	−0.54 ± 0.11	0.37 ± 0.20
8					0.02 ± 0.00[2]	0.59 ± 0.13	0.37 ± 0.15	0.29 ± 0.15	0.23 ± 0.12	−0.01 ± 0.16
9						0.09 ± 0.02	0.97 ± 0.01	0.93 ± 0.02	0.76 ± 0.06	−0.32 ± 0.20
10							0.20 ± 0.06	0.99 ± 0.00[2]	0.83 ± 0.05	−0.32 ± 0.21
11								0.23 ± 0.06	0.90 ± 0.03	−0.21 ± 0.22
12									0.13 ± 0.02	0.21 ± 0.19
13										0.20 ± 0.07
Gomp_FCR[1]										
4	0.04 ± 0.01	0.62 ± 0.06	0.26 ± 0.01	0.10 ± 0.10	0.00 ± 0.10	−0.06 ± 0.07	−0.10 ± 0.07	−0.18 ± 0.07	−0.35 ± 0.08	−0.57 ± 0.09
5		0.03 ± 0.00[2]	0.91 ± 0.02	0.78 ± 0.04	0.44 ± 0.08	−0.19 ± 0.07	−0.50 ± 0.05	−0.61 ± 0.04	−0.63 ± 0.05	−0.45 ± 0.08
6			0.03 ± 0.00[2]	0.96 ± 0.01	0.64 ± 0.06	−0.09 ± 0.07	−0.47 ± 0.05	−0.58 ± 0.04	−0.54 ± 0.05	−0.24 ± 0.08
7				0.02 ± 0.00[2]	0.83 ± 0.03	0.16 ± 0.06	−0.24 ± 0.06	−0.37 ± 0.06	−0.34 ± 0.07	−0.08 ± 0.09
8					0.01 ± 0.00[2]	0.69 ± 0.04	0.34 ± 0.08	0.19 ± 0.09	0.15 ± 0.10	−0.18 ± 0.11
9						0.02 ± 0.00[2]	0.91 ± 0.02	0.82 ± 0.04	0.71 ± 0.06	0.43 ± 0.10
10							0.03 ± 0.00[2]	0.98 ± 0.01	0.87 ± 0.03	0.52 ± 0.18
11								0.05 ± 0.01	0.95 ± 0.01	0.64 ± 0.06
12									0.07 ± 0.01	0.84 ± 0.03
13										0.09 ± 0.01
interp_FCR[1]										
4	0.05 ± 0.01	0.93 ± 0.02	0.80 ± 0.05	0.63 ± 0.07	0.36 ± 0.09	0.05 ± 0.10	−0.19 ± 0.10	−0.39 ± 0.09	−0.57 ± 0.09	−0.68 ± 0.11
5		0.03 ± 0.00[2]	0.95 ± 0.01	0.81 ± 0.04	0.49 ± 0.09	0.08 ± 0.10	−0.23 ± 0.09	−0.44 ± 0.07	−0.60 ± 0.06	−0.65 ± 0.12
6			0.02 ± 0.00[2]	0.93 ± 0.02	0.66 ± 0.07	0.24 ± 0.11	−0.09 ± 0.11	−0.33 ± 0.09	−0.49 ± 0.08	−0.54 ± 0.13
7				0.02 ± 0.00[2]	0.87 ± 0.03	0.55 ± 0.09	−0.23 ± 0.12	−0.02 ± 0.12	−0.23 ± 0.10	−0.38 ± 0.13
8					0.01 ± 0.00[2]	0.88 ± 0.03	0.66 ± 0.08	0.44 ± 0.10	0.18 ± 0.10	−0.10 ± 0.11
9						0.02 ± 0.00[2]	0.94 ± 0.02	0.79 ± 0.05	0.56 ± 0.09	0.21 ± 0.12
10							0.03 ± 0.01	0.95 ± 0.01	0.78 ± 0.06	0.45 ± 0.12
11								0.04 ± 0.01	0.93 ± 0.02	0.68 ± 0.08
12									0.06 ± 0.01	0.89 ± 0.03
13										0.08 ± 0.02

[1]Here obser_FCR = feed conversion ratio (FCR) computed using available data; miss_FCR = FCR computed using data with a simulated pattern of missing BW; interp_FCR = FCR computed using ADG calculated with the by nearest interpolation; Gomp_FCR = FCR computed using missing BW predicted by a Gompertz model.

[2]SD < 0.00.

in the last 2 wk (0.04 to 0.09 for obser_FCR, 0.07 to 0.09 for Gomp_FCR, and 0.06 to 0.08 for interp_FCR) of the test period in comparison with the middle of the growing period (wk 5 to 10, ranging from 0.01 to 0.03). Except for wk 4 and 8, the genetic variances obtained for miss_FCR were generally higher (ranging from 0.06 to 0.23) than those obtained in the other scenarios. The same comparison between scenarios and the same pattern of changes in variance over time were observed for the permanent environmental effect (result not shown).
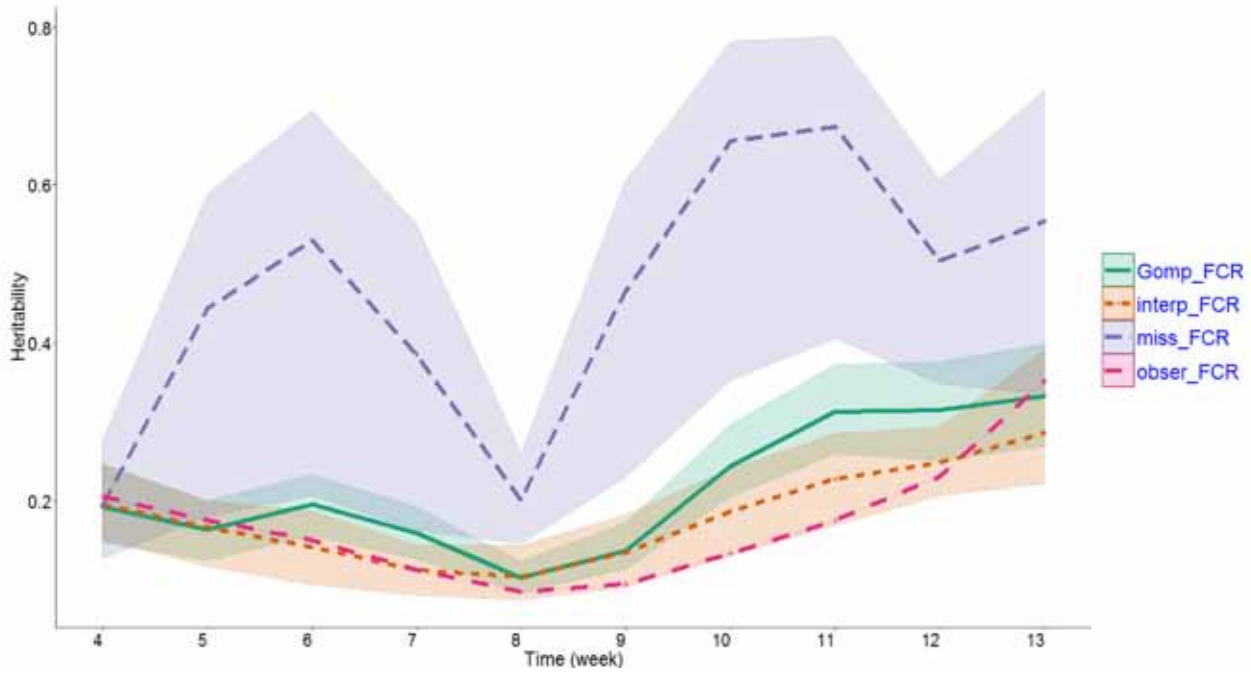
Figure 2. Changes in heritability of feed conversion ratio (FCR) over time in the different missing data scenarios. The shaded area delimits the 2.5 and 97.5 percentiles (100 iterations). Here obser_FCR = FCR computed using available data; miss_FCR = FCR computed using data with a simulated pattern of missing BW; interp_FCR = FCR computed using ADG calculated with the by nearest interpolation; Gomp_FCR = FCR computed using missing BW predicted by a Gompertz model.

The genetic correlations varied depending on the length of the interval between measurements. They ranged from −0.58 to 0.95 for obser_FCR, from −0.90 to 0.99 for miss_FCR, from −0.63 to 0.98 for Gomp_FCR, and from −0.68 to 0.95 for interp_FCR (Table 2). The 1-wk interval correlations were generally high. They were higher than 0.84 for interp_FCR and obser_FCR and ranged from 0.62 to 0.98 for Gomp_FCR. Nonetheless, low genetic correlations between FCR measured in 2 successive weeks were sometimes obtained for miss_FCR (0.26 between wk 4 and 5, 0.21 between wk 12 and 13) but with high SD. In general, the pattern of changes in the genetic correlations with the length of the interval between measurements was similar for obser_FCR, Gomp_FCR, and interp_FCR. The genetic correlation was highly positive for short time intervals, tended to decrease with the length of the interval, and became negative, resulting in an opposite correlation when the interval between the 2 measurement weeks was more than 4 to 5 wk. The genetic correlations for miss_FCR followed a similar pattern with lower genetic correlations for some of the short time intervals and strong negative correlation for others (−0.90 between wk 5 and 11). For 2 given weeks, the SD of the genetic correlation coefficients of miss_FCR was higher than those of Gomp_FCR and interp_FCR. Among interp_FCR and Gomp_FCR, the SD of correlation coefficients of interp_FCR was higher than those of Gomp_FCR from wk 9 to 13. The same patterns of correlation were ob-

served for the permanent environmental effect (result not shown). We also observed that the means of residual variance of interp_FCR and obser_FCR were comparable (0.12, 0.12) and higher than the residual variance of miss_FCR (0.10) and double that of Gomp_FCR (0.06).

In the simulation study, changes in heritability over time for obser_FCR, miss_FCR, interp_FCR, and Gomp_FCR are illustrated in Fig. 2. The pattern of heritability over time was quite similar for interp_FCR and obser_FCR. Heritabilities obtained for Gomp_FCR followed a similar pattern, but estimates were generally higher, except for wk 4, 5, 8, and 13. The 3 curves (heritabilities of obser_FCR, interp_FCR, and Gomp_FCR) tended to decrease up to wk 8 and then to increase and reach a maximum value in wk 13. Compared to heritability of obser_FCR, the heritability of interp_FCR was slightly higher in wk 9, 10, and 11. On the other hand, the heritability estimates obtained for miss_FCR were higher than those obtained with the other scenarios at all time points (except week 4) and reached very high values. The SD of the heritabilities across simulations was much larger for miss_FCR than for Gomp_FCR or interp_FCR.

The mean and SD of correlations among the EBV in the different scenarios with 100 simulations are presented in Table 3. The correlations between obser_EBV and the other EBV were significantly different from 1. We observed a higher average correlation between obser_EBV and interp_EBV (0.93) than between obser_EBV and Gomp_EBV (0.91) and between

Table 3. Pearson correlation ± SD between the EBV obtained for obser_FCR and those obtained for miss_FCR, Gomp_FCR, and interp_FCR in the simulation study of missing BW (100 replicates)

Week	obser_FCR, miss_FCR[1]	obser_FCR, Gomp_FCR[1]	obser_FCR, interp_FCR[1]
4	0.86 ± 0.02	0.86 ± 0.01	0.86 ± 0.01
5	0.49 ± 0.02	0.78 ± 0.02	0.81 ± 0.02
6	0.39 ± 0.02	0.71 ± 0.03	0.79 ± 0.02
7	0.57 ± 0.03	0.80 ± 0.02	0.84 ± 0.02
8	0.85 ± 0.04	0.93 ± 0.01	0.90 ± 0.02
9	0.76 ± 0.04	0.91 ± 0.01	0.90 ± 0.02
10	0.68 ± 0.04	0.83 ± 0.02	0.87 ± 0.02
11	0.69 ± 0.03	0.81 ± 0.02	0.86 ± 0.01
12	0.77 ± 0.02	0.85 ± 0.01	0.88 ± 0.01
13	0.63 ± 0.03	0.84 ± 0.02	0.83 ± 0.02
All weeks	0.79 ± 0.04	0.91 ± 0.01	0.93 ± 0.01

[1]Here obser_FCR = feed conversion ratio (FCR) computed using available data; miss_FCR = FCR computed using data with a simulated pattern of missing BW; interp_FCR = FCR computed using ADG calculated with the by nearest interpolation; Gomp_FCR = FCR computed using missing BW predicted by a Gompertz model.

Table 4. Heritability over time (10 wk) for the full data set using miss_FCR, Gomp_FCR, and interp_FCR

Week	miss_FCR[1] (h^2 ± SE)	Gomp_FCR[1] (h^2 ± SE)	interp_FCR[1] (h^2 ± SE)
4	0.33 ± 0.04	0.33 ± 0.04	0.34 ± 0.04
5	0.30 ± 0.03	0.35 ± 0.03	0.31 ± 0.03
6	0.26 ± 0.03	0.33 ± 0.03	0.25 ± 0.03
7	0.21 ± 0.02	0.25 ± 0.02	0.19 ± 0.02
8	0.16 ± 0.02	0.17 ± 0.02	0.15 ± 0.02
9	0.14 ± 0.02	0.16 ± 0.02	0.17 ± 0.02
10	0.15 ± 0.03	0.20 ± 0.03	0.20 ± 0.03
11	0.18 ± 0.03	0.23 ± 0.03	0.21 ± 0.03
12	0.24 ± 0.04	0.23 ± 0.03	0.24 ± 0.04
13	0.34 ± 0.05	0.31 ± 0.04	0.35 ± 0.05

[1]Here miss_FCR = feed conversion ratio (FCR) computed using observed data with missing BW; interp_FCR = FCR computed using ADG calculated with the by nearest interpolation; Gomp_FCR = FCR computed using missing BW predicted by a Gompertz model.

obser_EBV and miss_EBV (0.79). The correlation of obser_EBV with other predictions varied depending on the week from 0.39 to 0.86 for miss_EBV, from 0.71 to 0.93 for Gomp_EBV, and from 0.79 to 0.90 for interp_EBV. The lowest correlation between EBV was observed in wk 6 in all cases. The correlations between obser_EBV and EBV obtained in the other scenarios were generally the highest in wk 4, 8, and 12.

Full Data Set

The percentage of missing BW in the full data set was 34%, leading to 41.6% missing FCR. Correction using the by nearest interpolation reduced this percentage to 9% and to 0.3% using the Gompertz model to predict missing BW. The genetic variances and correlations obtained for the full data set (results not shown) were in the same range as those obtained for only males (obser_FCR in the simulation study). The heritabilities of miss_FCR, Gomp_FCR, and interp_FCR using the full data set are listed in Table 4. The patterns of heritability over time were similar in the 3 scenarios. Heritability decreased until wk 8 or 9 and increased again until the end of the test. These values ranged from 0.14 to 0.34 (miss_FCR), 0.15 to 0.35 (interp_FCR), and 0.17 to 0.35 (Gomp_FCR), which are higher than those obtained for only males (observed FCR in the simulation study). The heritabilities of Gomp_FCR were slightly higher than those of obser_FCR and miss_FCR from wk 5 to 7. In general, the SE were similar for miss_FCR, interp_FCR, and Gomp_FCR. The correlations between EBV obtained for the different FCR with the full data set are listed in Table 5. The correlations for all the weeks between EBV were high (>0.96). Within weeks, the correlations between EBV were lower but always higher than 0.87.

DISCUSSION

The purpose of this study was to evaluate the impact of missing BW values on the estimation of genetic parameters of longitudinal FCR and to evaluate techniques to improve these estimations. In our experimental pig population, the BW of females and castrated males was recorded only monthly, which complicated the estimation of genetic parameters for weekly FCR. In the current study, we predicted the missing BW to improve the genetic evaluation for FCR. Two methods were tested. The first uses a growth curve model. Several growth models (von Bertalanffy, Richards, logistic, etc.) are proposed in the literature (e.g., Strathe et al., 2010; Coyne et al., 2015), among which we chose the Gompertz model. This growth model has been widely used to study growth curves in pigs (Koivula et al., 2008; Strathe et al., 2010; Cai et al., 2011; Coyne et al., 2015) and in other species (Narinc et al., 2010; Podisi et al., 2013; Goldberg and Ravagnolo, 2015). It is reported to be a suitable approach for data extrapolation (Koivula et al., 2008; Coyne et al., 2015) and requires fewer parameters to obtain the equivalent data fit than corresponding linear models (Archontoulis and Miguez, 2015). Using the Gompertz model to fit the BW over time, we assumed that the pigs developed normally and that their growth followed the classical sigmoidal curve. The second method we tested is a less elaborate approach to predict missing BW. If ADG for week j could not be computed due to missing BW values at week $j + 2$ or $j − 2$, then we used the nearest available BW in the adjacent weeks and modified the time

Table 5. Pearson correlations between the EBV obtained for the full data set using miss_FCR, Gomp_FCR, and interp_FCR

Week	interp_FCR, Gomp_FCR[1]	miss_FCR, Gomp_FCR[1]	miss_FCR, interp_FCR[1]
4	0.92	0.93	0.96
5	0.89	0.89	0.94
6	0.90	0.90	0.93
7	0.92	0.92	0.93
8	0.96	0.95	0.93
9	0.96	0.93	0.92
10	0.93	0.90	0.92
11	0.93	0.91	0.93
12	0.95	0.95	0.93
13	0.92	0.91	0.87
All weeks	0.96	0.94	0.97

[1]Here miss_FCR = feed conversion ratio (FCR) computed using observed data with missing BW; interp_FCR = FCR computed using ADG calculated with the by nearest interpolation; Gomp_FCR = FCR computed using missing BW predicted by a Gompertz model.

interval accordingly to calculate ADG. This is equivalent to a linear interpolation of BW using the 2 nearest BW records, which leads to changes in ladder steps of ADG over time. A slightly different option would have been to perform a "real" linear interpolation of BW before computing ADG (Zumbach et al., 2010).

We used a RR-PL model to study the repeated measurements of FCR. Different approaches are available to account for the correlation between successive measurements for the estimation of genetic parameters (character process model, spline model, structured antedependence model; Jaffrézic et al., 2003; Jaffrézic, 2004; Borquis et al., 2013; Xie and Zimmerman, 2013). However, the RR-PL model is one of the most frequently used approaches in longitudinal genetic studies thanks to its ease of use and speed of convergence (Speidel et al., 2010). Such models have, for instance, been widely used for growth traits in pigs (Zumbach et al., 2010), for milk production in cattle and goats (Silva et al., 2013), for egg production in poultry (Wolc and Szwaczkowski, 2009), for volume of ejaculate in Holstein bulls (Carabaño et al., 2007), and for carcass traits in beef cattle (Englishby et al., 2016).

The moderate heritability obtained for the observed records (obser_FCR) in male pigs is in line with estimates obtained in a previous study in the same population (0.24; Saintilan et al., 2012). The higher heritability values obtained for the full data set (males + females + castrated males) are in line with the higher value of heritability in castrated males than in males reported by Saintilan et al. (2012) for FCR (0.41 vs. 0.24). In accordance with the conclusions of these authors, we assumed that FCR corresponded to the same trait in the 3 genders. For obser_FCR, Gomp_FCR, and interp_FCR, we ob-

served the same pattern of heritability over time, which tended to be higher at the beginning and at the end of the test period. This trend could be due to the "border effect" problem previously reported for RR models (i.e., an increase in variance at the borders of the test space; Sesana et al., 2010; Wolc et al., 2011; David et al., 2015).

Generally, our results show that the genetic correlations estimated between adjacent weeks were high. They decreased with an increase in the interval between weeks and reached high negative values for weeks separated by a longer period, which is unlikely to reflect the true correlations between these long periods. This pattern may reflect a compensatory growth phenomenon (Fabian et al., 2004; Kamalakar et al., 2009). Nonetheless, the phenomenon is generally observed when the animals' feed is restricted at the beginning of the measurement period, which was not the case in our study. Another possible explanation is that RR-PL models provided biased estimates of the correlations, and in fact, RR-PL models cannot handle a correlation pattern that decreases asymptotically to zero (Jaffrézic et al., 2004). In that case, the correlations become negative and subsequently increase again (David et al., 2015), as observed in our case.

In the simulation study, the heritabilities of FCR obtained with a missing-values pattern (miss_FCR) were very different from those obtained with the other FCR (for most weeks the 95% quantile for the heritabilities of miss_FCR and obser_FCR did not overlap), indicating that a high proportion of missing values leads to an overestimation of the genetic parameters. This was related to a combination of decreased residual variance and increased genetic variance compared to interp_FCR and obser_FCR. In addition, the SD of the heritability of miss_FCR was much higher than that of obser_FCR, Gomp_FCR, and interp_FCR, certainly because of the less accurate available measurements. Finally, the EBV estimated for miss_FCR were quite different from those of obser_FCR.

Accurate prediction of the missing BW is thus necessary to obtain accurate estimations and predictions for selection. Results of the simulation study showed that the by nearest linear interpolation provided better estimates of heritabilities and EBV (obser_FCR corresponding to the "true" heritabilities and EBV) than the prediction of missing BW using a Gompertz model, which tended to overestimate them. This result is probably explained by the fact that in the growth period in our particular data set, the increase in BW over time was quasi-linear and not sigmoidal, as assumed in the Gompertz model (Porter et al., 2010). The Gompertz model was therefore not the most appropriate model to fit the missing BW during the period of measurements. Compared to the nearest approach, the Gompertz model

has been cited as a reference to provide a good evaluation of individual growth dynamics (Koivula et al., 2008), suggesting that selection of growth curve parameters can be envisaged. The purpose of our study was different: The growth curve was used as a means to predict missing BW and to use the missing data together with the original available BW in the genetic analysis. We thus conclude that because it smooths individual variability, the Gompertz model is not appropriate in this situation. However, it should be noted that for a longer test period (i.e., including the sigmoidal portion of the growth curve) or when larger proportions of BW are missing in a data set, leading to high proportions of missing FCR with the by nearest linear interpolation, the use of Gompertz models could be appropriate.

The highest correlations between EBV were obtained for wk 4, 8, and 12 because the proportion of missing BW was low in wk 2, 6, 10, and 14, which were used to compute FCR for wk 4, 8, and 12 (the proportions of missing FCR in these weeks were lower: 29%, 26%, and 22%, respectively). It should be noted that the heritabilities obtained for the different FCR were also the closest for these weeks for the same reason. This explains the dips observed in the heritability of miss_FCR in wk 4, 8, and 12.

The proportion of missing FCR in the full data set was 41.6%, which was reduced to 9% with the by nearest linear interpolation and to 0.3% with the Gompertz approach. In the latter, the proportion of missing FCR was negligible because prior to our study, animals for which the Gompertz model showed convergence problems were removed from the analysis. Thus, the proportion of missing Gomp_FCR in the full data set corresponded to only the proportion of FCR values <0 or >6. In contrast to the results with the simulated data, the heritabilities obtained with the full data set with miss_FCR were not much larger than those obtained for Gomp_FCR or interp_FCR. This might be due to the overall lower proportion of missing FCR and, particularly, the absence of weeks with more than 95% of missing values. In fact, the highest proportion of missing FCR values per week was 59% for the full data set, meaning there was sufficient information per week to estimate the parameters of the RR-PL model. Nonetheless, for the sake of simplicity, we assumed the same changes in FCR and heritability over time for the 3 genders in our RR-PL model. These assumptions are questionable. Changes in FCR and heritabilities over time that differ between genders may be more realistic: A genetic correlation close to 1 was estimated by Saintilan et al. (2012) between genders at the test level, but growth dynamics could differ between genders. In that case, the effect on heritability and EBV estimates of missing BW records in a given gender would probably be larger and in the range of those obtained in the simulated study. In such a situation, the prediction of missing BW to calculate weekly FCR is very useful to obtain accurate longitudinal estimates of FCR.

Conclusion

This study showed that 61.5% of missing BW led to a major overestimation in heritability and EBV for longitudinal FCR. Using the Gompertz model to predict the BW reduced this phenomenon. However, in growth periods with a quasi-linear increase in BW over time, the by nearest approach provided better estimations of genetic parameters.

LITERATURE CITED

Agriculture and Horticulture Development Board. 2016. 2014 pig cost of production in selected countries: AHDB market intelligence. http://www.pork.ahdb.org.uk/media/74797/cost-of-production-web-2014.pdf. (Accessed 26 August 2016.)

Archontoulis, S. V., and F. E. Miguez. 2015. Nonlinear regression models and applications in agricultural research. Agron. J. 107:786–798. doi:10.2134/agronj2012.0506

Borquis, R. R. A., F. R. de A. Neto, F. Baldi, N. Hurtado-Lugo, G. M. F. de Camargo, M. Muñoz-Berrocal, and H. Tonhati. 2013. Multiple-trait random regression models for the estimation of genetic parameters for milk, fat, and protein yield in buffaloes. J. Dairy Sci. 96:5923–5932. doi:10.3168/jds.2012-6023

Cai, W., H. Wu, and J. C. M. Dekkers. 2011. Longitudinal analysis of body weight and feed intake in selection lines for residual feed intake in pigs. Asian-Australas. J. Anim. Sci. 24:17–27. doi:10.5713/ajas.2011.10142

Carabaño, M. J., C. Díaz, C. Ugarte, and M. Serrano. 2007. Exploring the use of random regression models with Legendre polynomials to analyze measures of volume of ejaculate in Holstein bulls. J. Dairy Sci. 90:1044–1057. doi:10.3168/jds.S0022-0302(07)71591-6

Coyne, J. M., D. P. Berry, E. A. Mäntysaari, J. Juga, and N. McHugh. 2015. Comparison of fixed effects and mixed model growth functions in modelling and predicting live weight in pigs. Livest. Sci. 177:8–14. doi:10.1016/j.livsci.2015.03.031

David, I., J. Ruesche, L. Drouilhet, H. Garreau, and H. Gilbert. 2015. Genetic modeling of feed intake. J. Anim. Sci. 93:965–977. doi:10.2527/jas.2014-8507

Englishby, T. M., G. Banos, K. L. Moore, M. P. Coffey, R. D. Evans, and D. P. Berry. 2016. Genetic analysis of carcass traits in beef cattle using random regression models. J. Anim. Sci. 94:1354–1364. doi:10.2527/jas.2015-0246

Fabian, J., L. I. Chiba, L. T. Frobish, W. H. McElhenney, D. L. Kuhlers, and K. Nadarajah. 2004. Compensatory growth and nitrogen balance in grower-finisher pigs. J. Anim. Sci. 82:2579–2587. doi:10.2527/2004.8292579x

Fischer, T. M., A. R. Gilmour, and J. H. J. van der Werf. 2004. Computing approximate standard errors for genetic parameters derived from random regression models fitted by average information REML. Genet. Sel. Evol. 36:363–369. doi:10.1186/1297-9686-36-3-363

Gibbons, R. D., D. Hedeker, and S. DuToit. 2010. Advances in analysis of longitudinal data. Annu. Rev. Clin. Psychol. 6:79–107. doi:10.1146/annurev.clinpsy.032408.153550

Gilbert, H., J. P. Bidanel, J. Gruand, J. C. Caritez, Y. Billon, P. Guillouet, H. Lagant, J. Noblet, and P. Sellier. 2007. Genetic parameters for residual feed intake in growing pigs, with emphasis on genetic relationships with carcass and meat quality traits. J. Anim. Sci. 85:3182–3188. doi:10.2527/jas.2006-590

Gilmour, A. R., B. J. Gogel, and B. R. Cullis. 2009. ASReml user guide release 3.0. VSN Int., Hemel Hempstead, UK.

Goldberg, V., and O. Ravagnolo. 2015. Description of the growth curve for Angus pasture-fed cows under extensive systems. J. Anim. Sci. 93:4285–4290. doi:10.2527/jas.2015-9208

Jaffrézic, F. 2004. Multivariate character process models for the analysis of two or more correlated function-valued traits. Genetics 168:477–487. doi:10.1534/genetics.103.019554

Jaffrézic, F., R. Thompson, and W. G. Hill. 2003. Structured antedependence models for genetic analysis of repeated measures on multiple quantitative traits. Genet. Res. 82:55–65. doi:10.1017/S0016672303006281

Jaffrézic, F., E. Venot, D. Laloe, A. Vinet, and G. Renand. 2004. Use of structured antedependence models for the genetic analysis of growth curves. J. Anim. Sci. 82:3465–3473. doi:10.2527/2004.82123465x

Kamalakar, R. B., L. I. Chiba, K. C. Divakala, S. P. Rodning, E. G. Welles, W. G. Bergen, C. R. Kerth, D. L. Kuhlers, and N. K. Nadarajah. 2009. Effect of the degree and duration of early dietary amino acid restrictions on subsequent and overall pig performance and physical and sensory characteristics of pork. J. Anim. Sci. 87:3596–3606. doi:10.2527/jas.2008-1609

Koivula, M., M.-L. Sevón-Aimonen, I. Strandén, K. Matilainen, T. Serenius, K. J. Stalder, and E. A. Mäntysaari. 2008. Genetic (co) variances and breeding value estimation of Gompertz growth curve parameters in Finnish Yorkshire boars, gilts and barrows. J. Anim. Breed. Genet. 125:168–175. doi:10.1111/j.1439-0388.2008.00726.x

Labroue, F., R. Guéblez, and P. Sellier. 1997. Genetic parameters of feeding behaviour and performance traits in group-housed Large White and French Landrace growing pigs. Genet. Sel. Evol. 29:451. doi:10.1186/1297-9686-29-4-451

Losinger, W. C. 1998. Feed-conversion ratio of finisher pigs in the USA. Prev. Vet. Med. 36:287–305. doi:10.1016/S0167-5877(98)00094-4

Nardone, A., B. Ronchi, N. Lacetera, M. S. Ranieri, and U. Bernabucci. 2010. Effects of climate changes on animal production and sustainability of livestock systems. Livest. Sci. 130:57–69. doi:10.1016/j.livsci.2010.02.011

Narinc, D., E. Karaman, M. Z. Firat, and T. Aksoy. 2010. Comparison of non-linear growth models to describe the growth in Japanese quail. J. Anim. Vet. Adv. 9:1961–1966. doi:10.3923/javaa.2010.1961.1966

Nobre, P. R. C., I. Misztal, S. Tsuruta, J. K. Bertrand, L. O. C. Silva, and P. S. Lopes. 2003. Analyses of growth curves of Nellore cattle by multiple-trait and random regression models. J. Anim. Sci. 81:918–926. doi:10.2527/2003.814918x

Patience, J. F., M. C. Rossoni-Serão, and N. A. Gutiérrez. 2015. A review of feed efficiency in swine: Biology and application. J. Anim. Sci. Biotechnol. 6:33. doi:10.1186/s40104-015-0031-2

Podisi, B. K., S. A. Knott, D. W. Burt, and P. M. Hocking. 2013. Comparative analysis of quantitative trait loci for body weight, growth rate and growth curve parameters from 3 to 72 weeks of age in female chickens of a broiler-layer cross. BMC Genet. 14:22. doi:10.1186/1471-2156-14-22

Porter, T., E. Kebreab, H. Darmani Kuhi, S. Lopez, A. B. Strathe, and J. France. 2010. Flexible alternatives to the Gompertz equation for describing growth with age in turkey hens. Poult. Sci. 89:371–378. doi:10.3382/ps.2009-00141

Saintilan, R., P. Sellier, Y. Billon, and H. Gilbert. 2012. Genetic correlations between males, females and castrates for residual feed intake, feed conversion ratio, growth rate and carcass composition traits in Large White growing pigs. J. Anim. Breed. Genet. 129:103–106. doi:10.1111/j.1439-0388.2011.00972.x

Sesana, R. C., A. B. Bignardi, R. R. A. Borquis, L. El Faro, F. Baldi, L. G. Albuquerque, and H. Tonhati. 2010. Random regression models to estimate genetic parameters for test-day milk yield in Brazilian Murrah buffaloes: Milk yield in Brazilian Murrah buffaloes. J. Anim. Breed. Genet. 127:369–376. doi:10.1111/j.1439-0388.2010.00857.x

Shirali, M., A. Doeschl-Wilson, P. W. Knap, C. Duthie, E. Kanis, J. M. van Arendonk, and R. Roehe. 2012. Nitrogen excretion at different stages of growth and its association with production traits in growing pigs. J. Anim. Sci. 90:1756–1765. doi:10.2527/jas.2011-4547

Silva, F. G., R. A. Torres, L. F. Brito, R. F. Euclydes, A. L. P. Melo, N. O. Souza, J. I. Ribeiro Jr., and M. T. Rodrigues. 2013. Random regression models using Legendre orthogonal polynomials to evaluate the milk production of Alpine goats. Genet. Mol. Res. 12:6502–6511. doi:10.4238/2013.December.11.1

Speidel, S. E., R. M. Enns, and D. H. Crews. 2010. Genetic analysis of longitudinal data in beef cattle: A review. Genet. Mol. Res. 9:19–33. doi:10.4238/vol9-1gmr675

Strathe, A. B., A. Danfaer, H. Sorensen, and E. Kebreab. 2010. A multilevel nonlinear mixed-effects approach to model growth in pigs. J. Anim. Sci. 88:638–649. doi:10.2527/jas.2009-1822

Wolc, A., E. Barczak, J. Wójtowski, P. Ślósarz, and T. Szwaczkowski. 2011. Genetic parameters of body weight in sheep estimated via random regression and multi-trait animal models. Small Rumin. Res. 100:15–18. doi:10.1016/j.smallrumres.2011.05.009

Wolc, A., and T. Szwaczkowski. 2009. Estimation of genetic parameters for monthly egg production in laying hens based on random regression models. J. Appl. Genet. 50:41–46. doi:10.1007/BF03195650

Xie, Y., and D. L. Zimmerman. 2013. Antedependence models for nonstationary categorical longitudinal data with ignorable missingness: Likelihood-based inference. Stat. Med. 32:3274–3289. doi:10.1002/sim.5763

Zumbach, B., I. Misztal, C. Y. Chen, S. Tsuruta, M. Łukaszewicz, W. O. Herring, and M. Culbertson. 2010. Use of serial pig body weights for genetic evaluation of daily gain. J. Anim. Breed. Genet. 127:93–99. doi:10.1111/j.1439-0388.2009.00827.x