1 **Longitudinal modelling of performance and feed efficiency traits in growing Duroc pigs**

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10 **Abstract**

11 In this study we used the phenotypic information of 1,499 Duroc pigs, recorded longitudinally in the

12 age period from 110 to 200 days of age for individual daily feed intake (DFI), backfat thickness (BF)

13 and live body weight (BW). Our aim was to estimate the genetic parameters for production and feed

14 efficiency traits during the fattening period, with the objective to define, based on these parameters,

15 the optimal moment for recording the phenotypes in order to maximize the expected response in a

16 selection program to improve feed efficiency. Additionally to the aforementioned traits, two other

17 traits were derived: average daily gain (ADG) and residual feed intake (RFI). The variance components

18 for these traits were estimated through Bayesian procedures and using a multi-trait random regression

19 animal model fitting Legendre polynomials of degree one. The estimated heritability patterns along

20 the fattening were fairly flat, around 0.15(0.04), 0.37(0.05) and 0.34(0.09) for DFI, BF and DWG,

21 respectively. RFI was the trait with the lowest heritability estimate, below 0.05 from 140d onwards.

22 The only trait that showed relevant variation in the heritability estimate along the fattening period was

23 BW, from 0.18(0.05) to 0.32(0.10). The correlations between performance at different moments of the

24 fattening period and those at 120 days, was not always high. For the case of DFI and RFI these

25 correlations reached values as low as 0.27(0.18) and -0.26(0.23). This points to a certain degree of

26 genetic determinism variation along the studied period. Nonetheless, in particular for the feed

efficiency trait (RFI), this variation seems irrelevant given the low estimated heritabilities and the low
level of genetic heterogeneity along the fattening period.

Highlights

- Feed efficiency related traits exhibit along-fattening genetic heterogeneity
- This heterogeneity is, however, rather limited
- Its consideration in breeding programs is not expected to improve the responses
- Properly modeling such genetic heterogeneity would request large datasets

1. Introduction

The costs associated with feeding growing pigs is the most important portion of the total production costs in pig production (Gutierrez and Patience, 2012). Therefore, to reduce daily feed intake (DFI) while maintaining performance of growing pigs is expected to result in economic benefits and for this reason such a trait is often considered, either directly or indirectly, in breeding programs for pigs (Stewart et al., 1990). Any direct consideration of feed efficiency traits (feed conversion ratio (FCR) or residual feed intake (RFI) (Merks et al., 2012)) would require recording both performance traits (daily weight gain (DWG), backfat thickness (BF) or live body weight (BW)) as well as feed intake. Nonetheless, important improvements in feed efficiency can be also achieved by indirect selection of performance traits genetically correlated with FCR or RFI. In this regard, the role of BF is paramount and most of the commercial pig breeding programs rely on the reduction of BF to enhance the efficiency of the growing animals. Reducing BF thickness, in addition, will yield carcasses with characteristics that better fit the desires of consumers, i.e. with reduced fat content.

The availability of longitudinal records, i.e. multiple measurements recorded throughout the fattening period, on performance and feed intake traits allows for the study of the evolution of genetic parameters

52 involved in the control of these traits, heritabilities and genetic correlation between the traits. There is

53 already evidence that the genetic correlations between production and feed efficiency traits change

54 with the age (Cai et al., 2011; Wetten et al., 2012), as well as the genetic variances and the heritabilities

55 of traits (Shirali et al., 2017; Tran et al., 2017; Chaudhary et al., 2019). This variation in the genetic

56 parameters along the fattening period could be responsible for the changes in the accuracy of the

57 estimated breeding values for DWG, DFI, FCR and RFI from early to late ages during the fattening

58 period (Arthur et al., 2008). The objective of this study was to estimate the changes in genetic

59 parameters as the pig ages for performance and feed efficiency traits in a Duroc population, with the

60 additional aim of identifying the optimal moment in which to record performance traits to indirectly

61 improve overall feed efficiency in the studied population.

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63 2. Material and Methods

64 Phenotypic records of 1,499 Duroc pigs were collected in 13 batches from 2007 to 2019 at the

65 experimental Center of Porcine Evaluation (Monells, Girona, Spain). These batches comprised a total

66 of 128 pens (pigs per pen averaged 11.8 ± 1.4) with an individual-space IVOG electronic feeding

67 station (Insentec, Markenesse, the Netherlands) in each pen. The complete known pedigree for these

68 animals is composed of 6,179 individuals. This Duroc line was founded in 1991 (Tibau et al., 1999)

69 initially selected as a multipurpose line but later, in around 2005, the line was specialized as a maternal

70 line focusing on increasing prolificacy while reducing backfat thickness (BF). The average (range) age

71 at the first live weight control was 70 (53-85) days, while that for the last control was 180 (160-200)

72 days. Despite this, as the recording of BF only was systematically conducted when the animals were

73 older than 110 days old, we limited the period of study for all the traits from this age onward, i.e. 90

74 days from 110 d to 200 d.

75 During the fattening period, animals were fed *ad libitum* with a standard diet satisfying their nutritional

76 requirements. Measurements for individual body weight (BW, kg) and BF (mm) were recorded several

77 times during the fattening period, there were variations on the number of measurements per animal,

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78 ranging from 3 – 10 records per animal. BF was measured using ultrasonic techniques (PIGLOG 105,

79 SFK-Technology, Herlev, Denmark). The individual feed intake (DFI, kg) records were collected

80 using electronic feeders following the procedure described by Sánchez et al. (2017). Descriptive

81 statistics of the three raw studied traits are presented in the Table 1.

82 Table 1 around here

83 A multi-trait random regression animal model was fitted to DFI, BW and BF. The same model was

84 considered for the three traits and its equation, in scalar form, is the following:

85 $Y_{jklmiot} = B_{jt} + S_{kt} + \mathbf{\Phi'_3}(age_{io}) \times \boldsymbol{\beta}_t + \mathbf{\Phi'_1}(age_{io}) \times \mathbf{c}_{mt} + \mathbf{\Phi'_1}(age_{io}) \times \mathbf{l}_{lt} + \mathbf{\Phi'_1}(age_{io}) \times \mathbf{p}_{it}$

86 $\qquad + \mathbf{\Phi'_1}(age_{io}) \times \mathbf{a}_{it} + e_{jklmiot}$,

87 where the subscript t refers to each one of the three studied traits (DFI, BW and BF), the considered

88 systematic effects were the batch (B_{jt}, 13 levels), the sex (S_{kt}, 2 levels: females and castrated males)

89 and a Legendre polynomial regression of degree three on the age, $\boldsymbol{\beta}_t$ is a vector that includes, the effects

90 associated with the four coefficients, $\mathbf{\Phi_3}'(age_{io})$, of the Legendre polynomial. These Legendre

91 coefficients are a function of the age of the animal i when its oth record was obtained. Similarly; pen

92 ($\mathbf{c}_{mt}$, 128 levels), litter ($\mathbf{l}_{lt}$, 562 levels), permanent environmental ($\mathbf{p}_{it}$, 1,499 levels) and additive

93 genetic ($\mathbf{a}_{it}$, 6,179 levels) effects were fitted as regression on Legendre functions of degree 1 (two

94 coefficients) for the age of the animal i when its oth record was obtained. The residual term ($e_{jklmiot}$)

95 was assumed to be heteroskedastic with respect to the age, see below.

96 Model parameters were estimated using a Bayesian MCMC procedure, thus prior distribution of all

97 the unknowns had to be specified. Uniform and independent distributions were *a priori* assumed for

98 the elements of **B**, **S** and **β,** i.e. batch, sex and regression coefficients on Legendre functions of age.

99 Pen, litter, permanent environment and additive genetic effects were assumed, *a priori*, to follow

100 independent multivariate normal distributions with these specifications: $\mathbf{c}|\mathbf{C_0} \sim MVN(\mathbf{0}, \mathbf{C_0} \otimes \mathbf{I})$;

101 $\mathbf{l}|\mathbf{L_0} \sim MVN(\mathbf{0}, \mathbf{L_0} \otimes \mathbf{I})$; $\mathbf{p}|\mathbf{P_0} \sim MVN(\mathbf{0}, \mathbf{P_0} \otimes \mathbf{I})$ and $\mathbf{a}|\mathbf{G_0} \sim MVN(\mathbf{0}, \mathbf{G_0} \otimes \mathbf{A})$, respectively. The

102 identity matrices **I** have dimensions equal to the number of levels of the different factors previously

103 described and **A** is the numerator relationship matrix between individuals in the pedigree. $\mathbf{C_0}$, $\mathbf{L_0}$, $\mathbf{P_0}$

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104 and $\mathbf{G_0}$ contain the co-variances associated with the two regression coefficients for each one of the

105 studied traits, i.e. dimension 6. The operator   denotes the Kronecker product. As has been stated,

106 heterogeneous residual variances were assumed, three different residual co-variance matrices were

107 defined for the intervals 110-140,141-170 and 171-200. The normal prior distribution for the residuals

108 can be expressed as $\mathbf{e}|\mathbf{R} \sim MVN(\mathbf{0}, \mathbf{R})$, where the covariance matrix has the following form:

109
$$\mathbf{R} = \begin{bmatrix} \mathbf{R_{0,110-140}} & \mathbf{I_{110-140}} & \mathbf{0} & & \mathbf{0} \\ \mathbf{0} & \mathbf{R_{0,141-170}} & \mathbf{I_{141-170}} & & \mathbf{0} \\ \mathbf{0} & & \mathbf{0} & \mathbf{R_{0,171-210}} & \mathbf{I_{171-200}} \end{bmatrix}$$

110 $\mathbf{R_{0,110-140}}$, $\mathbf{R_{0,141-170}}$ and $\mathbf{R_{0,171-200}}$ are 3x3 matrices with the residual (co)variances between traits in

111 the respective periods; and $\mathbf{I_{110-140}}$, $\mathbf{I_{141-170}}$ and $\mathbf{I_{171-200}}$ are identity matrices with dimension equal to

112 the number of records in each period. Similarly with the systematic effects, uniform prior within their

113 domain were assumed for all the elements of the variance component matrices: $\mathbf{C_0}$, $\mathbf{L_0}$, $\mathbf{P_0}$, $\mathbf{G_0}$,

114 $\mathbf{R_{0,110-140}}$, $\mathbf{R_{0,141-170}}$ and $\mathbf{R_{0,171-200}}$.

115 Marginal posterior distribution of the variance components were sampled using the Gibbs Sampling

116 algorithm using the program gibbsf90test, which is a new version of the gibbs3f90 program (Misztal

117 et al., 2015). Chains of 1,000,000 samples were run and the first 600,000 iterations were discarded in

118 order to allow the algorithm to reach convergence to the marginal posterior distributions. Then, one

119 sample every 10 iterations was saved. We chose this sampling scheme because we observed that

120 shorter burn-in period did not permit passing the different convergence criteria we considered. One

121 such convergence test of the Markov chains was the Geweke test function   in coda R package

122 (Plummer et al., 2006) applied to the genetic variance components of the model (Table A1 in the

123 Additional File 1). Another criterion to assess for convergence was just the visual inspection of the

124 chain trace plots (see Figure A1 and A2 in the Additional File 1). We also ran two chains having the

125 same random seed but with different starting values, in one of them the starting values were set to the

126 estimates obtained in a previous EM-REML analysis using the software remlf90 (Misztal et al., 2015).

127 In the other chain, the starting values were set to those after the first iteration of the EM-REML

128 algorithm. By comparing the posterior mean obtained with both chains we could assess whether the

129 effect of the starting value vanished, in our case this comparison resulted in numerically equivalent

130 estimates.

131 From the saved samples of the marginal posterior distribution of the variance components in the

132 aforementioned model, it was possible to derive variance components of other related traits. One of

133 these was daily weight gain (DWG), this trait was obtained from the first derivative of the Legendre

134 polynomial functions of BW for pen, litter, permanent environmental and additive genetic effects.

135 From the polynomial functions of the different factors for DFI, BW, BF and DWG, variance

136 components were obtained for all the days under study (110-200 days), this was done for pen, litter,

137 permanent environmental, additive genetic and residual effects.

138 Once matrices of (co)variance for all the factors and traits were defined on a daily basis, variance

139 components for residual feed intake (RFI) were derived using the procedure proposed by Strathe et al.

140 (2014). This method relies on considering RFI as a DFI conditional on BF, BW and DWG; thus, for

141 each day (d) along the fattening period it was necessary to obtain the regression coefficient vector ($\mathbf{B_d}$)

142 that allows conditioned DFI to be obtained:

143 $$\mathbf{b_d} = \begin{bmatrix} 1 & b_{BW,d} & b_{BF,d} & b_{DWG,d} \end{bmatrix}$$

144 $b_{BW,d}$, $b_{BF,d}$ and $b_{DWG,d}$ are phenotypic regression coefficients for the day d obtained from the 4x4

145 phenotypic co-variance matrix on the day d.

146 $$\begin{bmatrix} b_{BW,d} \\ b_{BF,d} \\ b_{DWG,d} \end{bmatrix} = \begin{bmatrix} \sigma^2_{Phe,BW,d} & \sigma_{Phe,BW-BF,d} & \sigma_{Phe,BW-DWG,d} \\ \sigma_{Phe,BW-BF,d} & \sigma^2_{Phe,BF,d} & \sigma_{Phe,BF-DWG,d} \\ \sigma_{Phe,BW-DWG,d} & \sigma_{Phe,BF-DWG,d} & \sigma^2_{Phe,DWG,d} \end{bmatrix}^{-1} \begin{bmatrix} \sigma_{Phe,DFI-BW,d} \\ \sigma_{Phe,DFI-BF,d} \\ \sigma_{Phe,DFI-DWG,d} \end{bmatrix}$$

147 The phenotypic covariance matrix was obtained as $\mathbf{Phe_d} = \mathbf{C_d} + \mathbf{L_d} + \mathbf{P_d} + \mathbf{G_d} + \mathbf{R_d}$. Pen, litter,

148 permanent environmental, additive genetic and residual variances for RFI on the day d were defined

149 as:

150 $$\sigma^2_{X,RFI,d} = \mathbf{b_d} \times \mathbf{X_d} \times \mathbf{b'_d},$$

151   where $\mathbf{X_d}$ represents the covariance matrix on day d for either cage (**C**), litter (**L**), permanent (**P**),

152   genetic (**G**), and residual (**R**) effects.

153   Similarly, covariances between days can be obtained with this general equation:

154    $$\sigma_{x,RFI,d1,d2} = \mathbf{b_{d1}} \times \mathbf{X_{d1,d2}} \times \mathbf{b'_{d2}}$$

155   In this context the sub-index x aims to represent any one of the effects in the model: pen, litter,

156   permanent environmental, additive genetic and residual, as well as the covariance matrix between days

157   associated with it. In the formula, $\mathbf{X_{d1,d2}}$ represents the covariances within (in the diagonal) and

158   between (out of the diagonal) traits for the effects referring to d1 and d2. The phenotypic variance of

159   RFI on the day d can be defined as $\sigma^2_{Phe,RFI,d} = \sigma^2_{C,RFI,d} + \sigma^2_{L,RFI,d} + \sigma^2_{P,RFI,d} + \sigma^2_{G,RFI,d} + \sigma^2_{R,RFI,d}$.

160   Daily variances for RFI ($\sigma^2_{X,RFI,d}$) and DWG ($\sigma^2_{X,DWG,d}$) and covariances between days (for example

161   for RFI = $\sigma_{X,RFI,d1,d2}$) can be organized in 90 x 90 matrices (90 = 200 d − 110 d). Again, the sub-index

162   x refers to any model effect: pen, litter, permanent environmental, additive genetic and residual. We

163   can name these matrices: $\mathbf{C_{all,RFI}}$, $\mathbf{L_{all,RFI}}$, , $\mathbf{P_{all,RFI}}$, $\mathbf{G_{all,RFI}}$ and $\mathbf{R_{all,RFI}}$ for RFI; and $\mathbf{C_{all,DWG}}$,

164    $\mathbf{L_{all,DWG}}$, , $\mathbf{P_{all,DWG}}$, $\mathbf{G_{all,DWG}}$ and $\mathbf{R_{all,DWG}}$ for DWG .

165   From these matrices we can obtain overall (averages along the whole fattening period) variance

166   components for the different factors with these quadratic forms

167    $$\sigma^2_{C,oRFI} = \mathbf{h} \times \mathbf{C_{all,RFI}} \times \mathbf{h'};$$

168    $$\sigma^2_{L,oRFI} = \mathbf{h} \times \mathbf{L_{all,RFI}} \times \mathbf{h'};$$

169    $$\sigma^2_{P,oRFI} = \mathbf{h} \times \mathbf{P_{all,RFI}} \times \mathbf{h'};$$

170    $$\sigma^2_{G,oRFI} = \mathbf{h} \times \mathbf{G_{all,RFI}} \times \mathbf{h'} \text{ , and}$$

171    $$\sigma^2_{R,oRFI} = \mathbf{h} \times \mathbf{R_{all,RFI}} \times \mathbf{h'}$$

172   Equivalent expressions of these quadratic forms were used for computing variance components of

173   oDWG. In these formulae **h** is a vector weighting the different days along the fattening period we

174   assigned the same weight to all the days, thus all the elements of vector **h** were equal to $\frac{1}{90}$. Finally,

175   phenotypic variances of oRFI and oDWG were obtained as:

176 $$\sigma^2_{Phe,oRFI} = \sigma^2_{C,oRFI} + \sigma^2_{L,oRFI} + \sigma^2_{P,oRFI} + \sigma^2_{G,oRFI} + \sigma^2_{R,oRFI} \text{ , and}$$

177 $$\sigma^2_{Phe,oDWG} = \sigma^2_{C,oDWG} + \sigma^2_{L,oDWG} + \sigma^2_{P,oDWG} + \sigma^2_{G,oDWG} + \sigma^2_{R,oDWG}$$

178   All the above-mentioned computations of parameters for the derived traits were conducted for each

179   sample of the marginal posterior distribution of the model parameters, thus it was possible to fully

180   characterize the marginal posterior distribution of genetic parameters for the derived traits.

181   **3. Results**

182   Figure 1 shows the heritability patterns for the studied traits DFI, BW, BF, DWG and RFI. To properly

183   quantify the magnitude of the estimates for the different moments along the fattening period the

184   estimates for every 15 days are presented in the Table 2. Fairly constant heritability patterns were

185   observed for DFI (0.15), BF (0.37) and DWG (0.34). BW is the trait for which the largest differences

186   in heritability across age were observed, from around 0.18 at 110 d. to around 0.32 at 200 d. The

187   heritability of RFI also showed a fairly constant pattern but at low values, before 140 d of age, the

188   estimates were between from 0.08 and 0.12, from this age onward the heritability estimates were as

189   high as 0.06. The observed broken-line patterns for the heritabilities are a consequence of the assumed

190   heterogeneous residual variance pattern, with peaks at 140 and 170 days. This pattern gets translated

191   to the phenotypic covariance structure and thus, if the transition from one period to the other is not

192   smooth then it could be possible to observe it in the phenotypic variance pattern, i.e. the denominator

193   of the heritability.

194   Figure 1 around here

195   Regarding the heritability of the overall growth and the overall RFI we observed that the marginal

196   posterior mean (marginal posterior standard deviation) of oRFI and oDWG were 0.07(0.01) and

197   0.34(0.09), respectively.

198 In order to assess the magnitude of the genetic correlations within each trait across the fattening period

199 we reported in Table 3 the marginal posterior mean (standard deviations) of the genetic correlations

200 between the trait recorded at different days along the fattening period and the trait recorded at day 120

201 of age. High correlations were observed for BF and BW, the lowest values being 0.82 and 0.71,

202 respectively. In the case of DFI and also for RFI, the genetic correlations with the respective trait at

203 120 d, reached much lower values at the end of the fattening period. For both traits the correlation

204 between the performance recorded at 200 days and that recorded on day 120 cannot be said to be

205 statistically different from zero. The genetic correlations between ADG and oADG were equal to one

206 as a consequence of the definitions of these traits, ADG was the first derivative of BW and oADG is

207 the integral of ADG along the fattening period.

208 The pattern of daily genetic correlations between performance and RFI are shown in Figure 2. To

209 quantitatively assess the magnitude of these correlations we also show the values (posterior means

210 (posterior standard deviations)) of these correlation estimates every 15 days in the Table 4. All the

211 patterns are fairly flat, i.e. constant along the fattening period, and the only genetic correlation that

212 seems to show a pattern statistically different from zero is that with DFI; for the other three traits, those

213 conditioning the DFI when computing RFI, the patterns always lay around zero.

214 Figure 2 around here

215 It would be relevant to assess the genetic correlation of overall measurements of daily RFI (oRFI) and

216 growth (oDWG) with other performance traits (Figure 3 and Table 5).

217 Figure 3 around here

218 The correlation patterns of oRFI with the other traits (Figure 3 panel B) can be said to be fairly similar

219 to those observed with the daily measurements of RFI, i.e. constant along the fattening period and only

220 different from zero with DFI, and also with BF at the latest ages. The patterns for the correlations with

221 oDWG (Figure 3 panel A), on the contrary, clearly showed a non-constant trend along the fattening

222 period, from around 150 days onward, the patterns are flat at around 0.90, 0.85 and 0.60 for the

223 correlations between oDWG, and DFI, BW and BF, respectively. Before this age, linearly increasing

224   patterns are observed for the three correlations, starting on 0.32, 0.15 and 0.08 at 110 days of age, for

225   the genetic correlations with DFI, BW and BF, respectively.

226   To finish with the description of the genetic correlation patterns, presentation of the correlations along

227   the fattening period between the performance traits is needed. These traits could be seen as the major

228   criteria driving any indirect selection procedure aiming to improve the feed efficiency of the

229   population. Figure 4 (Table 6) shows these patterns for the correlations between DFI and the

230   performance traits (BW, BF and DWG) as well as the patterns for the genetic correlations between

231   BW and, BF and DWG; and between BW and BF. Only those correlations involving DWG can be said

232   to show a non-constant pattern along the fattening period. These patterns are fairly linear for the

233   correlations between BF and DWG and BW and DWG, changing from 0.08 and 0.15 at 110 days of

234   age, respectively; to 0.62 and 0.89 for the same parameters at 200 d. The genetic correlation pattern

235   between DFI and DWG was not linear, from about 140 d onward a high correlation estimate was

236   obtained (0.85-0.90), before that age the pattern shows a linear trend, starting with an estimate value

237   of 0.32 at 110 days of age. The other two genetic correlations involving DFI showed relatively flat

238   patterns, around 0.65 and 0.70 for those between DFI and BF, and DFI and BW, respectively.

239   Similarly, the genetic correlation between BF and BW had a constant pattern around 0.5 for the whole

240   fattening period.

241   Figure 4 around here

242   **4. Discussion**

243   The estimated heritabilities for DFI, BF and DWG are in the range of previous estimates obtained from

244   the same population based on studies using single-measure traits (Herrera-Cáceres et al., 2020). With

245   regard to RFI, the only study that reported an heritability estimate for RFI in the current Duroc

246   population was the work by Sánchez et al. (2017). In this study the estimate was based on a

247   repeatability model, and the obtained value was around 0.12, relatively close to the estimate we found

248   in this study for the average RFI along the fattening period (oRFI) (0.07). Other FE definitions, like

249   for example feed conversion ratio (feed intake / growth) (FCR) were estimated to have a clearly higher

250   heritability, around 0.21 (Herrera-Cáceres et al., 2020). We initially tried to estimate parameters for

251   FCR, and we did it by approximating the ratio using linear index, in the same way as Lin (1980) did.

252   We finally decided not to formally describe the results from this approximation since some artifacts

253   on the daily genetic correlation patterns were evidenced. We show them Figure A3 of the Additional

254   File 1. The correlation estimates change from high negative to high positive values along the fattening

255   period. We believe this behavior is a consequence of the fact that DWG was obtained as the first

256   derivative of the BW polynomial function, and this implies two points: i) Constant variance

257   components for the DWG along the fattening period, ii) Null residual variance for the DWG, the

258   residual variance for BW was a piecewise constant function; thus, its first derivative will be zero. In

259   spite of this fitting artifacts, most likely associated with the reduced degree of the used polynomial

260   functions, when FCR was averaged along the fattening period, oFCR, computed in a similar way as

261   oRFI, the estimated heritability value was 0.20(0.10), a value close to the estimate reported by Herrera-

262   Cáceres et al., (2020).

263   The estimated high correlations (as low as 0.7 (Table 3)) between measurements on different days for

264   BF and BW (Table 3), jointly with the constant heritability (except for BW) patterns along the

265   fattening period (Figure 1) are indications of a common genetic control of the traits along the fattening

266   period. In the case of DFI, and consequently also for RFI, there is, however, a certain degree of genetic

267   heterogeneity along the fattening period (Table 3), however this heterogeneity seems rather irrelevant

268   since the heritability of this FE trait is very low. As a consequence of this a certain degree of the genetic

269   heterogeneity along the fattening period for DFI and BW the genetic correlations between oRFI and

270   BF seems also to show a non-constant pattern along the fattening period, and something similar

271   happens with the correlations involving oDWG and the other performance traits: DFI, BW and BF

272   (Figure 3). In previous studies (Huisman et al., 2002; Coyne et al., 2017) a general result or conclusion,

273   similar to ours, is that there is a certain degree of variation on the genetic control along the fattening

274   period for some of the FE-component traits as well as for certain FE definitions.

275   Our results could be said to be highly dependent on the fact that a polynomial of degree one was

276   considered in the random regression. This reduced degree imposes the constraint that only quadratic

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277 changes in the variance components could be evidenced. In other published studies (Cai et al., 2011)

278 a higher degree was assumed, increasing the flexibility of the functions. We decided to keep the

279 polynomial function to its minimum degree in order to avoid a number of artifacts that were evidenced

280 when a higher degree was employed. We assumed that these artifacts were a consequence of the

281 reduced number of records available for this study, which prevented a good quality for the Markov

282 chains, i.e. extremely low effective sample sizes and falling to pass convergence diagnosis tests.

283 In general, the observed patterns for the genetic correlation between the different traits (DWG, BF and

284 BW) and RFI (Figure 2 and Table 4) make sense according to the definition of this FE trait. RFI was

285 generated as the residual of a linear regression, at phenotypic level, between DFI and a number of

286 performance traits (BW, BF and DWG). This definition imposes the constraint of null phenotypic

287 correlations between RFI and the traits conditioning DFI, but it does not guarantee the genetic

288 correlations to also be null, nonetheless low values would be expected. In our case, only between BF

289 and RFI at around 170 days of age the genetic correlation was declared to be statistically different from

290 zero (Table 4). When the FE trait was averaged along the whole fattening period (oRFI) this positive

291 genetic correlation between RFI and BF was a bit more evident, being statistically positive from 150

292 days of age onward. No previous estimates for the correlation between RFI and BF were reported in

293 the population under study, in other populations (Gilbert et al., 2007; Cai et al., 2008 and Shirali et al.,

294 2018) when the analyses were based on single measurement traits, in agreement with the expected

295 null phenotypic correlations also null genetic correlations were estimated between RFI and BF. We

296 did not find any previous report in the literature on the correlation pattern between RFI and BF along

297 the fattening obtained using longitudinal models.

298 In this study, we aimed to assess whether it would be possible to take advantage of any variation in the

299 genetic control along the fattening period of feed efficiency, performance, and intake traits. The

300 existence of such variation could allow us to define the traits of interest at ages so that the biological

301 constraints in the genetic correlation structures that exist between the traits that could be considered in

302 an index to indirectly improve feed efficiency could be partially alleviated. One example of such

303 biological constraint is the unfavorable correlation between BF and BW or BF and growth (Herrera-

304 Cáceres et al., 2020; Sanchez et al., 2017). Our results indicate that although a certain degree of genetic

305 determinism exists in the control of the traits along the fattening period, it does not seem to be high

306 enough to take advantage of it. At the latest ages the correlation between BF and BW was estimated

307 to be around 0.6 (Table 6) while at the lowest ages (at around 120 d) this correlation is still clearly

308 positive 0.4. Given that this correlation still being positive at low ages, a marginal advantage, probably

309 not paying off the effort of controlling animals at two ages, could be expected if for example BF is

310 recorded at the end of the fattening period, while BW would be recorded at early ages. Also note that

311 the genetic correlation between BW at early ages (120 d) and at the end of the fattening period, is still

312 relatively high (0.7) (Table 3).

313 Previous longitudinal studies of FE and performance traits in pigs conclude that the genetic control of

314 this type of traits, to some extent, varies with the age (Cai et al., 2011; Wetten et al., 2012; Shirali et

315 al., 2017; Tran et al., 2017; Chaudhary et al., 2019). It has to be clarified that in these studies,

316 polynomials of higher degree were used, which allows for further flexibility for the genetic parameter

317 patterns. In this regard, we have been cautious in reducing the degree of the polynomial to its minimum

318 to omit estimation artifacts associated with our limited data set size. In some of the previously indicated

319 studies data sets of similar size to ours were used; and in some cases, suspicious patterns of parameters

320 are reported. In spite of this, the authors, based on these patterns, positively conclude there is a strong

321 genetic heterogeneity of the traits under study along the fattening period. We, on the contrary, want to

322 prevent about the difficulty of using random regression models with limited amount of phenotypic

323 data.

324

325 **5. Conclusions**

326 Our initial hypothesis of the performance, intake and feed efficiency traits having a heterogeneous

327 genetic determinism along the fattening period, at least for the period we have considered, can be

328 confirmed. Nonetheless, it seems to be difficult to take advantage of this genetic heterogeneity to

329 improve the responses in a selection process for feed efficiency. On one hand, because of the

330 magnitude of such heterogeneity, which is low; and also due to the reduced heritability of the FE trait

331 we have explored, i.e. longitudinal RFI.

332

340

341 **Ethics approval and consent to participate**

342 Animals used in this study come from a commercial population raised under selection nucleus

343 conditions, following all the applicable Spanish and European Union laws with regard to welfare and

344 health control. The fattening period of the animals was conducted at the Institut de Recerca i

345 Tecnologia Agroalimentàries (IRTA) experimental facilities, and for this control period a research

346 protocol was approved by IRTA's Animal Care and Use Committee.

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Tables

415 **Table 1.-** Descriptive statistics for the studied traits in three different periods along fattening.

Period	DFI (kg/d)			BW (kg)			BF (mm)		
	MEAN	SD	N	MEAN	SD	N	MEAN	SD	N
110 d - 140 d	2.58	0.63	28,266	66.03	10.47	2,402	10.75	2.57	1,666
141 d - 170 d	2.96	0.73	37,985	92.49	12.67	2,784	14.98	3.85	1,827
171 d - 200 d	2.96	0.85	15,081	117.85	14.04	1,581	20.0	4.6	1,486

416 DFI: daily feed intake, BW: live body weight, BF: backfat thickness, N: number of records.

417

418 **Table 2**.- Marginal posterior Mean(SD) of the heritabilities for production and feed efficiency traits
419 at different ages during the fattening period.

Age (d)	DFI	BW	BF	DWG	RFI
110	0.14(0.04)	0.18(0.05)	0.26(0.04)	0.34(0.09)	0.12(0.04)
125	0.14(0.04)	0.20(0.07)	0.34(0.05)	0.34(0.09)	0.08(0.02)
140	0.12(0.03)	0.24(0.08)	0.36(0.05)	0.34(0.09)	0.03(0.01)
155	0.16(0.04)	0.27(0.09)	0.39(0.06)	0.34(0.09)	0.03(0.01)
170	0.13(0.03)	0.29(0.10)	0.36(0.05)	0.34(0.09)	0.02(0.01)
185	0.16(0.04)	0.31(0.10)	0.37(0.06)	0.34(0.09)	0.04(0.01)
200	0.19(0.04)	0.32(0.10)	0.38(0.06)	0.34(0.09)	0.06(0.02)

420 DFI: daily feed intake, BW: live body weight, BF: backfat thickness, DWG: daily weight gain, RFI:
421 residual feed intake.
422

423 **Table 3.-** Marginal posterior Mean(SD) of the genetic correlation between each trait at different ages
424 and that particular trait at 120 days of age.

Age (d)	$r(DFI, DFI_{120})$	$r(BW, BW_{120})$	$r(BF, BF_{120})$	$r(DWG, DWG_{120})$	$r(RFI, RFI_{120})$
110	0.97(0.02)*	0.98(0.01)*	0.98(0.01)*	1.00(0.00)*	0.99(0.01)*
125	0.99(0.00)*	1.00(0.00)*	1.00(0.00)*	1.00(0.00)*	1.00(0.00)*
140	0.87(0.05)*	0.95(0.02)*	0.96(0.01)*	1.00(0.00)*	0.91(0.04)*
155	0.68(0.11)*	0.88(0.05)*	0.92(0.02)*	1.00(0.00)*	0.57(0.15)*
170	0.50(0.15)*	0.81(0.08)*	0.88(0.03)*	1.00(0.00)*	0.15(0.23)
185	0.37(0.17)*	0.76(0.10)*	0.84(0.04)*	1.00(0.00)*	-0.12(0.23)
200	0.27(0.18)	0.71(0.11)*	0.82(0.04)*	1.00(0.00)*	-0.26(0.23)

425 DFI: daily feed intake, BW: live body weight, BF: backfat thickness, DWG: daily weight gain, RFI:
426 residual feed intake.
427

Table 4.- Marginal posterior Mean(SD) of the genetic correlation between production and feed
efficiency traits at different ages during the fattening period.

Age (d)	$r(RFI,DFI)$	$r(RFI,BW)$	$r(RFI,BF)$	$r(RFI,DWG)$
110	0.63(0.15)*	-0.14(0.21)	0.14(0.16)	-0.12(0.19)
125	0.47(0.18)*	-0.19(0.20)	0.06(0.15)	-0.11(0.18)
140	0.4(0.16)*	-0.17(0.18)	0.16(0.14)	-0.02(0.17)
155	0.42(0.14)*	-0.10(0.16)	0.21(0.12)	0.09(0.16)
170	0.51(0.14)*	0.04(0.17)	0.25(0.13)*	0.17(0.17)
185	0.57(0.14)*	0.09(0.19)	0.22(0.15)	0.20(0.19)
200	0.60(0.14)*	0.11(0.20)	0.21(0.16)	0.20(0.20)

DFI: daily feed intake, BW: live body weight, BF: backfat thickness, DWG: daily weight gain, RFI:
residual feed intake. *Probability of the correlation being greater than 0 > 0.95 or < 0.05.

Table 5. Marginal posterior Mean(SD) of the genetic correlations between production traits at
different ages and overall RFI.

Age (d)	$r(RFIo,DFI)$	$r(RFIo,BW)$	$r(RFIo,BF)$	$r(RFIo,DWG)$	$r(DWGo,DFI)$	$r(DWGo,BW)$	$r(DWGo,BF)$	$r(DWGo,DWG)$
110	0.22(0.19)	-0.22(0.16)	-0.20(0.14)	0.08(0.16)	0.32(0.20)	0.15(0.22)	0.08(0.15)	1.00(0.00)*
125	0.33(0.17)*	-0.18(0.16)	0.00(0.13)	0.08(0.16)	0.60(0.13)*	0.41(0.19)*	0.31(0.14)*	1.00(0.00)*
140	0.40(0.14)*	-0.14(0.16)	0.13(0.12)	0.08(0.16)	0.82(0.07)*	0.61(0.14)*	0.44(0.13)*	1.00(0.00)*
155	0.41(0.14)*	-0.10(0.16)	0.21(0.12)*	0.08(0.16)	0.92(0.03)*	0.73(0.10)*	0.52(0.11)*	1.00(0.00)*
170	0.40(0.14)*	-0.07(0.16)	0.27(0.11)*	0.08(0.16)	0.93(0.03)*	0.81(0.07)*	0.57(0.10)*	1.00(0.00)*
185	0.38(0.14)*	-0.05(0.16)	0.31(0.11)*	0.08(0.16)	0.91(0.04)*	0.86(0.05)*	0.60(0.10)*	1.00(0.00)*
200	0.36(0.14)*	-0.03(0.16)	0.33(0.11)*	0.08(0.16)	0.88(0.05)*	0.89(0.04)*	0.62(0.09)*	1.00(0.00)*

DFI: daily feed intake, BW: live body weight, BF: backfat thickness, DWG: daily weight gain, oRFI:
overall residual feed intake. *Probability of the correlation being greater than 0 > 0.95 or < 0.05.

Table 6. Marginal posterior Mean(SD) of the genetic correlation between production and feed
efficiency traits at different ages during the fattening period.

Age (d)	$r(DFI,BF)$	$r(DFI,BW)$	$r(DFI,DWG)$	$r(BF,DWG)$	$r(BW,BF)$	$r(BW,DWG)$
110	0.55(0.14)*	0.57(0.17)*	0.32(0.20)	0.08(0.15)	0.44(0.13)*	0.15(0.22)
125	0.62(0.11)*	0.63(0.15)*	0.60(0.13)*	0.31(0.14)*	0.42(0.14)*	0.41(0.19)*
140	0.67(0.08)*	0.69(0.11)*	0.82(0.07)*	0.44(0.13)*	0.46(0.13)*	0.61(0.14)*
155	0.67(0.08)*	0.71(0.10)*	0.92(0.03)*	0.52(0.11)*	0.50(0.12)*	0.73(0.10)*
170	0.64(0.08)*	0.72(0.09)*	0.93(0.03)*	0.57(0.10)*	0.54(0.11)*	0.81(0.07)*
185	0.61(0.09)*	0.71(0.10)*	0.91(0.04)*	0.60(0.10)*	0.57(0.10)*	0.86(0.05)*
200	0.59(0.10)*	0.70(0.10)*	0.88(0.05)*	0.62(0.09)*	0.59(0.10)*	0.89(0.04)*

DFI: daily feed intake, BW: live body weight, BF: backfat thickness, DWG: daily weight gain, RFI:
residual feed intake. *Probability of the correlation being greater than 0 > 0.95 or < 0.05.
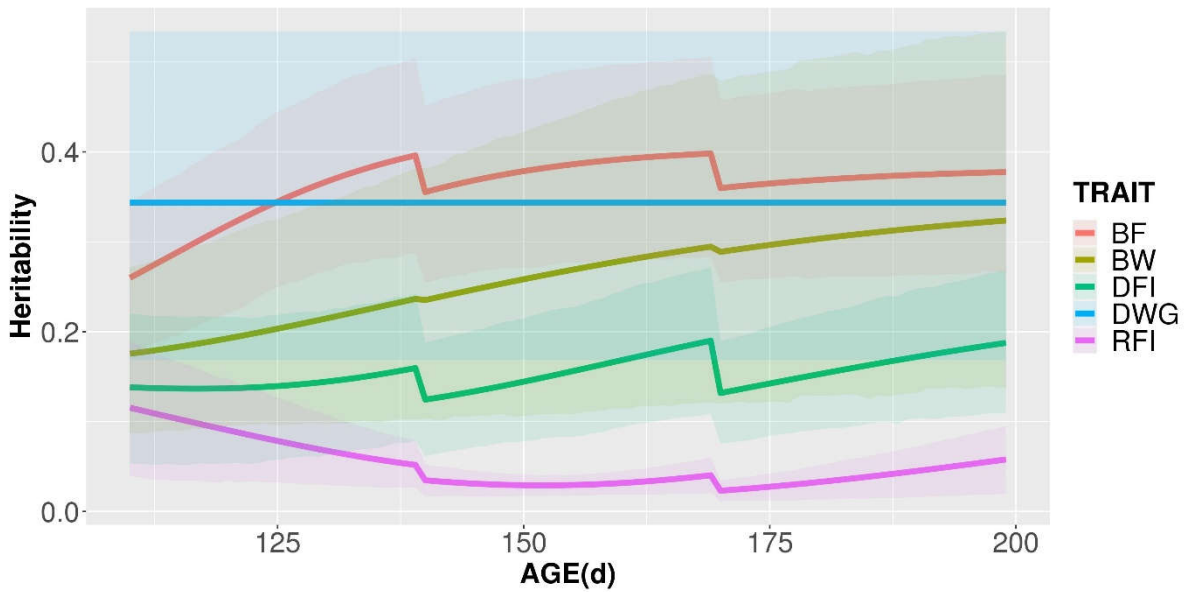
Figures
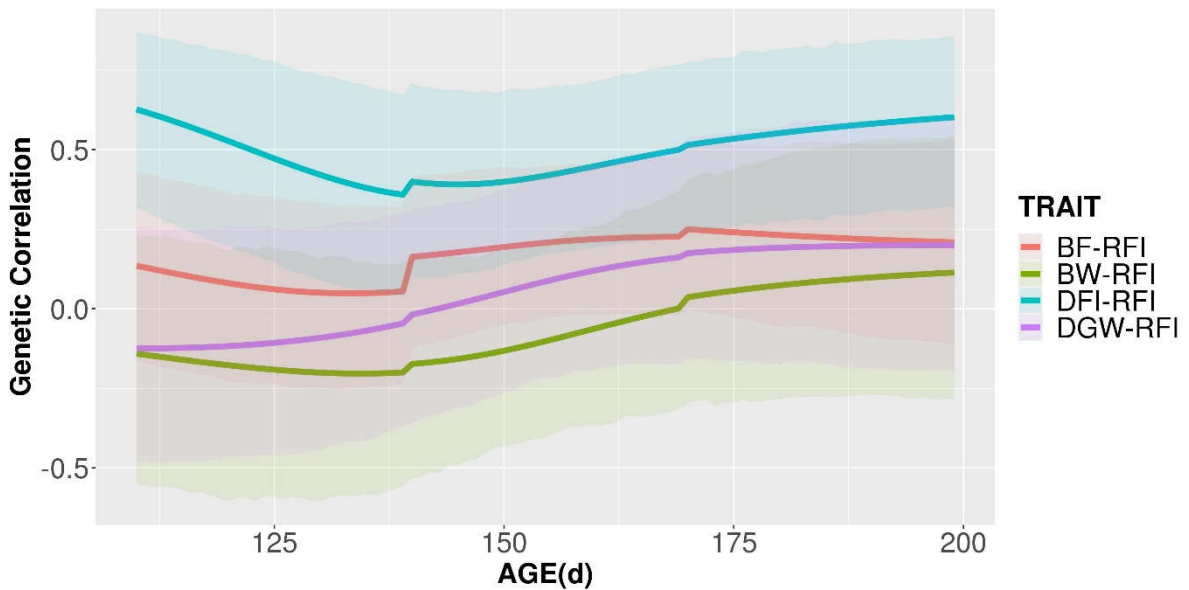
Figure 1 Heritability patterns along the fattening period for daily feed intake (DFI), live body weight (BW), backfat thickness (BF) and daily weigh gain (DWG) and residual feed intake (RFI). The solid lines represent posterior means, and the colored transparent areas represent 95HPD regions.
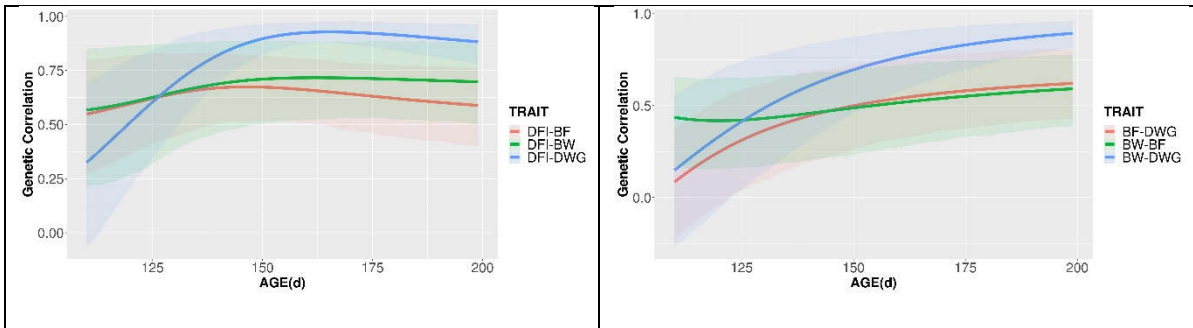

Figure 2 Pattern along the fattening period of the estimated genetic correlations between production (DFI: daily feed intake, BW: live body weight, BF: backfat thickness and DWG: daily weight gain) and feed efficiency trait (RFI: residual feed intake). The solid lines represent posterior means, and the colored transparent areas represent 95HPD regions.
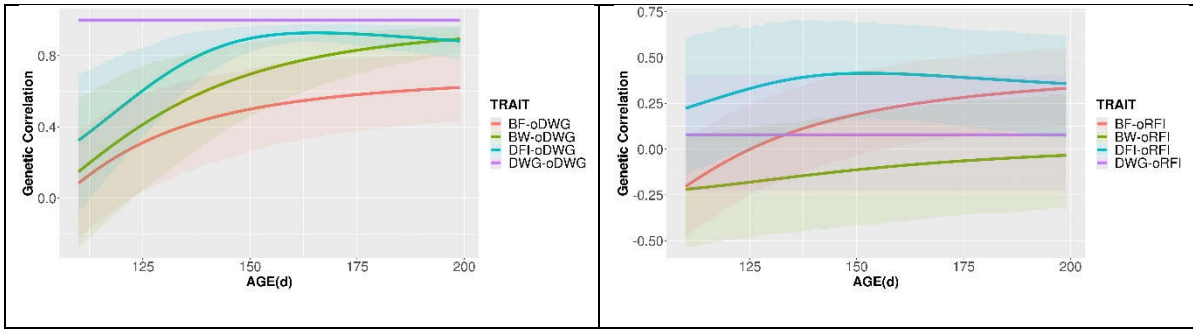
Figure 3 Pattern along the fattening period of the genetic correlations between daily traits (DFI: feed intake, BW: live body weight, BF: backfat thickness and DWG: weight gain) and average along the fattening period of residual feed intake (oRFI) and daily weight gain (oDWG). The solid lines represent posterior means and the colored transparent areas represent 95HPD regions

Figure 4 Pattern along the fattening period of the genetic correlations between production traits (DFI: daily feed intake, BW: live body weight, BF: backfat thickness and DWG: daily weight gain). The solid lines represent posterior means and the colored transparent areas represent 95HPD regions