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1 **Disentangling the dynamics of energy allocation to provide a** 2 **proxy of robustness in fattening pigs**

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4 Guillaume Lenoir^{1,2,3*}, Loïc Flatres-Grall³, Rafael Muñoz-Tamayo¹, Ingrid David² and Nicolas C.
5 Friggens¹

6

7 ¹Université Paris-Saclay, INRAE, AgroParisTech, UMR Modélisation Systémique Appliquée aux
8 Ruminants, 91120, Palaiseau, France

9 ²GenPhySE, INRAE, ENVT, Université de Toulouse, 31326 Castanet-Tolosan, France

10 ³AXIOM, 37310 Azay-sur-Indre, France

11 *Corresponding author

12

13 E-mail addresses:

14 GL: glenoir@axiom-genetics.com

15 LFG: loic.fg@mailo.fr

16 RMT: rafael.munoz-tamayo@inrae.fr

17 ID: Ingrid.david@inrae.fr

18 NF: Nicolas.friggens@agroparistech.fr

19

20 **Abstract**

21 **Background**

22 There is a growing need to improve robustness characteristics in fattening pigs, but this trait is
23 difficult to phenotype. Our first objective was to develop a robustness proxy on the basis of
24 modelling of longitudinal energetic allocation coefficient to growth for fattening pigs.
25 Consequently, the environmental variance of this allocation coefficient was considered as a proxy

26 of robustness. The second objective was to estimate its genetic parameters and correlation with
27 traits under selection as well with phenotypes routinely collected on farms. A total of 5848 pigs,
28 from Piétrain NN paternal line, were tested at the AXIOM boar testing station (Azay-sur-Indre,
29 France) from 2015 to 2022. This farm was equipped with automatic feeding system, recording
30 individual weight and feed intake at each visit. We used a dynamic linear regression model to
31 characterize the evolution of the allocation coefficient between cumulative net energy available,
32 estimated from feed intake, and cumulative weight gain during fattening period. Longitudinal
33 energetic allocation coefficients were analysed using a two-step approach, to estimate both its
34 genetic variance and the genetic variance in the residual variance, trait LSR.

35 **Results**

36 The LSR trait, that could be interpreted as an indicator of the response of the animal to
37 perturbations/stress, showed low heritability (0.05 ± 0.01). The trait LSR had high favourable genetic
38 correlations with average daily growth (-0.71 ± 0.06) and unfavourable with feed conversion ratio ($-$
39 0.76 ± 0.06) and residual feed intake (-0.83 ± 0.06). The analysis of the relationship between
40 estimated breeding values (EBV) LSR quartiles and phenotypes routinely collected on farms shows
41 the most favourable situation for animals from quartile with the weakest EBV LSR, *i.e.*, the most
42 robust.

43 **Conclusions**

44 These results show that selection for robustness based on deviation from energetic allocation
45 coefficient to growth can be considered in breeding programs for fattening pigs.

46 **Background**

47 The pig industry faces new challenges related to rapidly changing environmental conditions,
48 especially related to global warming (Hansen et al., 2012), and to growing societal concerns. For
49 several decades, breeding objectives were mainly focused on increasing animal productivity
50 (growth, feed efficiency...) at the expense of non-productive functions, *i.e.*, fitness (Puillet et al.,
51 2016; Rauw et al., 1998). These unfavorable consequences could be explained by trade-offs in
52 resource allocation between biological functions (Rauw, 2009). Indeed, when animals cannot obtain
53 more resources, *i.e.*, in limiting environments, allocation of these resources to a high priority
54 function must be to the detriment of another function (Stearns, 1992). In this situation the animal is
55 unable to maximize the expression of each biological function simultaneously. This changing
56 context requires having animals able to adapt to new environmental conditions with more limiting
57 resources, which can be associated with an improvement of robustness. Knap (2005) defined
58 robustness as “*the ability to combine a high production potential with resilience to stressors,*
59 *allowing for unproblematic expression of a high production potential in a wide variety of*
60 *environmental conditions*”. Generally, the production potential is associated to a phenotype of
61 interest, such as growth, feed efficiency or milk production, egg production. Incorporating one or
62 several traits to evaluate robustness of growing pigs in genetic evaluation would therefore be of
63 value for the development of more sustainable breeding goals (Berghof et al., 2019b). Accordingly,
64 when targeting robustness as a breeding objective, it is important to maintain simultaneously a high
65 level of production to meet industry’s economic expectations. However, until recently to it was very
66 difficult to phenotype traits such as robustness in farm animals and therefore on the way to improve
67 it.

68 In parallel, the increasingly common use of sensors in farms, especially automatic feeding system
69 (AFS) in pig industry, allows continuous individual recording of weight or feed intake over a long
70 period. This offers the possibility to characterize the dynamics of those phenotypes for each

71 individual in the face of variations in the environment. Several studies have used such longitudinal
72 data to quantify resilience indicators based on deviation between an expected trajectory of each
73 individual for a given non-perturbed environment and its observed trajectory on feed intake
74 (Nguyen-Ba et al., 2020) or body weight (Revilla et al., 2022). Definition and modelling of
75 individual potential trajectory are challenging issues in these approaches. Other studies developed
76 several resilience indicators based on the within individual variance of time series measurements
77 related to production, such as feed intake of growing pigs (Putz et al., 2019), milk yield for dairy
78 cows (Poppe et al., 2021) or egg production in laying hens (Bedere et al., 2022). These modeling
79 approaches have mainly addressed the characterization of robustness or resilience through the
80 analysis of one production variable. They are a substantial contribution in the phenotyping of
81 resilience but do not address the underlying biological mechanisms and the potential trade-offs in
82 the use of available resources between production and other functions. A robust animal can be
83 considered as an animal able to allocate a proportion of its resources to the right function at the right
84 time (Friggens et al., 2017). To our knowledge, the characterization of robustness based on the
85 temporal evolution of the allocation pattern has been little explored in growing pigs.

86 The acquisition of temporal data of feed intake and weight in growing pigs made it possible to
87 consider the development of allocation model based on these two variables to characterize
88 robustness. With this objective, we developed a conceptual model to represent the temporal pattern
89 of allocation of energy intake to growth in fattening pigs (Lenoir et al., 2022).

90 In the present study, the first objective was to develop a robustness indicator on the basis of
91 modelling of longitudinal energetic allocation coefficient to growth for fattening pigs.
92 Consequently, the environmental variance of this allocation coefficient was considered as a proxy
93 of robustness. This proxy should reflect the ability of an animal to express or adapt its production
94 potential in the face of changes in the environment relative to other animals that have been raised

95 under the same conditions. Our objective was to estimate its genetic parameters and correlation with
96 traits under selection as well as with phenotypes routinely collected on farms and associated to
97 robustness or health status.

98 **Methods**

99 **Study population**

100 A total of 25745 pigs from Piétrain NN Français paternal line (Pie NN), free from halothane-
101 sensitivity, of the AXIOM company were used in this study. Individuals from the Pie NN line were
102 born in 3 different farms integrated into the AXIOM breeding scheme and that comply with
103 AXIOM's biosafety and health requirements. A part of the males were selected before weaning and
104 then raised at the boar testing station of the breeding company AXIOM Genetics (Azay-sur-Indre,
105 France). The animals considered in the present dataset were 6885 entire males and 13012 females
106 raised and individually tested at their farm of birth from April 2014 to April 2022 and 5848 entire
107 males raised from September 2015 to April 2022 at the boar testing station.

108 The animals raised on their birth farm were born from 3943 litters, 6.5 ± 2.9 piglets per litter, and
109 from 321 sires, 80 ± 53.8 piglets per sire. To limit the risk of confounding between environmental
110 (*i.e.*, fattening group) and genetic effects, the sires were used at least in two mating groups in each
111 farm and in two different farms. Animals were transferred to fattening rooms when they were 75.7
112 ± 3.4 days of age (33.8 ± 7.8 kg body weight (BW)). Pigs were raised in fattening rooms for 68.6
113 ± 4.9 days until the individual testing at around 142.4 ± 4.6 days of age (103.4 ± 11 kg BW).

114 For males raised at the boar testing station, they were transferred every three weeks from birth farm
115 to the station at an average age of 27.3 ± 2.2 days with an average BW of 8.5 ± 1.7 kg. They were
116 raised in pens of 14 animals from the same birth farm. These groups of 14 pigs were never modified
117 at the different stages of breeding. Each fattening group consisted of animals sourced from between
118 one or three farrowing farms. These animals came from 2048 litters, 2.6 ± 1.5 piglets per litter, and

119 were born from 238 sires, 22.1 ± 15 piglets per sire. They were raised in quarantine and post-
120 weaning rooms for five and two weeks respectively and transferred to fattening rooms when they
121 were 76.4 ± 2.9 days of age (34.4 ± 5.4 kg BW). These pigs were raised in fattening rooms for 69 ± 4.7
122 days until the individual testing at around 145.4 ± 3.6 days of age (104.5 ± 11.1 kg BW). Fattening
123 rooms were equipped with AFS: Nedap pig performance testing feeding station (Nedap N.V.;
124 Groenlo, the Netherlands). Animals were fed ad-libitum with commercial diets adapted to their
125 physiological needs. The provided diets were non-limiting in amino acids. The boar testing station
126 environmental and technical conditions are described in detail in Lenoir et al. (2022a). The
127 pedigrees contained 27276 animals across 20 generations.

128 **Information recorded during the fattening period**

129 The performances recorded were the same in farrowing farms testing and boar testing station. Each
130 animal was individually weighed on arrival in the fattening room (initial body weight: IBW). When
131 the average weight of the group was approximately 100 kg, individual tests were performed for
132 animals weighing more than 70 kg (Institut Technique du Porc, 2004). Measurements made during
133 the test were: body weight (TBW), average ultrasonic backfat thickness (BF = mean of three
134 measurements in mm) and ultrasonic longissimus dorsi thickness (LD = one measurement in mm).
135 The BF and LD measures were transformed to correspond to their values at 100 kg liveweight
136 (BF100 and LD100 respectively) to compare animals at equivalent weight. This transformation was
137 done by applying linear coefficients that multiply the difference between 100 kg and TBW.
138 Coefficients used are 0.04 mm/kg for BF100 and 0.27 mm/kg for LD100 (Sourdioux et al., 2009).
139 The average daily gain (ADG) was calculated as the difference between TBW and IBW divided by
140 the number of days elapsed between the two weighings.

141 Additionally, at the boar testing station, BW (kg) and feed intake (FI; kg per visit) were recorded
142 each time the animal went into the AFS. The feed conversion ratio (FCR) was calculated as the ratio

143 between the total FI during the fattening period and the weight gain (TBW-IBW), expressed in
144 kg/kg. The average daily feed intake (DFI) was calculated as the total FI during the period divided
145 by the number of days elapsed. The residual feed intake (RFI) was also estimated for each animal as
146 the deviation between the recorded DFI and the potential average daily feed intake (PDFI) predicted
147 from requirements for maintenance and production. Based on the method proposed by Labroue et
148 al. (1999), the PDFI was estimated by linear regression, with the lm function in R (R Core Team,
149 2018), of DFI on average metabolic weight (AMW), ADG and BF100. The AMW was estimated
150 for each animal using the formula proposed by Noblet et al. (1991), $AMW = \frac{(TBW^{1.6} - IBW^{1.6})}{1.6(TBW - IBW)}$. In
151 addition, all medical treatments received by the animal were recorded. A visual observation of the
152 animals was carried out by the technician in charge of the measurements in order to note any
153 morphological defects, anomalies and clinical signs of disease according to a frame of reference
154 (Institut Technique du Porc, 2004), noted as "observable defects". These observations were made by
155 the same person within any given fattening group. The medical treatments and individual
156 observations were recorded from January 2019 to April 2022 on 3028 males fattened at the boar
157 testing station.

158 **Longitudinal data pre-treatment**

159 A pre-treatment process was performed on BW and FI, recorded each time the animal went into the
160 AFS, to validate them, identify quality issues and convert them on a daily scale. This process
161 followed the procedure proposed by Revilla et al. (2022) and modified by Lenoir et al. (2022a). In
162 summary, on the scale of the visit, a quadratic regression of BW on age + age² for each animal was
163 applied to eliminate aberrant BW. For a given animal and a given visit, if the ratio between the
164 residual value and the fitted value was > 0.15, the BW measurement was considered to be null. This
165 step was repeated a second time. Following this step, the body weight (BW_{it}; kg) was estimated
166 from the median of the non-null weights for each pig (*i*) and each fattening day since the transfer to

167 fattening room (t). For feed intake, if for a given animal the feed intake rate at a visit was lower or
168 higher than its mean take rate over the fattening period ± 4 standard deviations, the FI measurement
169 was considered to be missing. This missing value was estimated using a linear regression of FI on
170 feeding duration. The daily feed intake (FI_{it} ; kg) was calculated as the intakes during the visits of the
171 day t . Then BW_{it} and FI_{it} were validated at the pen scale to detect inconsistencies linked to the AFS
172 machine. When a control day was missing (due to a mechanic problem of AFS or loss of a RFID
173 tag), the missing BW_{it} and FI_{it} were estimated separately by using local regression model, “*proc*
174 *loess*” implement in SAS (SAS Institute Inc., 2013). Data recorded on day $t=0$ were excluded from
175 the dataset due to AFS calibration and animal adaptation. After data pre-treatment, the file included
176 405983 daily records associated to the 5848 males fattened at the testing station.

177 **Model for analysis**

178 **Modelling energetic allocation coefficient to growth**

179 As shown on Figure 1, the feed intake, i.e input of the system, is transformed in net energy intake
180 and allocated to several functions: maintenance, body development (protein deposition), body
181 reserves (lipid deposition) and other functions (van Milgen et al., 2005). The body weight gain, i.e.,
182 output of the system, is directly related to the protein and lipid deposition. Resource allocation is
183 regulated during the fattening period for each individual according to deterministic factors: genetic
184 potential and degree of maturity (Lewis and Emmans, 2020). Over the time, resource allocation
185 coefficient is also impacted by changes in environmental conditions, i.e., perturbations (Friggens et
186 al., 2017).

187 A dynamic regression model (DLM; West and Harrison, 1997) was used to estimate daily energetic
188 allocation coefficient to growth (α_{it} ; Lenoir et al., 2022b). First, FI_{it} was converted in net energy
189 intake in MJ (EI_{it}), using the net energy density of the feed of 9.85 MJ of NE/kg. Then, the net
190 energy available for growth at day t (NEA_{it}) was calculated as the difference between EI_{it} and the

191 net energy maintenance requirements at day t (MR_{it}), estimated according to Noblet et al. (2016).
192 The DLM to estimate the allocation coefficient of energy to weight gain for a given pig i at day t
193 (α_{it}) was built with two equations : an observation equation (1), relating cumulative weight gain at
194 day t (CW_{it} in kg) and cumulative net energy available at day $t-1$ ($CNEA_{it-1}$ in MJ), a system
195 equation (2), describing the changes in α_{it} (unobserved state variable) from day to day according to
196 a stochastic process.

$$197 \quad CW_{it} = \alpha_{it} * CNEA_{it-1} + v_{it} \quad \mathbf{v}_i \sim N(0, I\sigma_{iv}^2) \quad (1)$$

$$198 \quad \alpha_{it} = \alpha_{it-1} + w_{it} \quad \mathbf{w}_i \sim N(0, I\sigma_{iw}^2) \quad (2)$$

199 Where v_{it} was a random observation error for animal i ; σ_{iv}^2 is the observational variance i ; w_{it}
200 represented random and unpredictable changes in level between time $t-1$ and t ; and σ_{iw}^2 was the
201 system variance. The model was built using the R package dlm (Petris et al., 2009). The values of
202 α_{it} were calculated independently for each animal with a Kalman smoother algorithm. The value of
203 α_{it} at $t=1$ was not estimated because the consumption at $t-1$ was unknown.

204 ***Estimation of genetic variance in environmental variance***

205 Longitudinal energetic allocation coefficients (α_{it}) were analyzed with ASReml 4.2 software
206 (Gilmour et al., 2009) to estimate both its genetic variance and the genetic variance in the residual
207 variance (*i.e.*, environmental variance) using a two-step approach (SanCristobal-Gaudy et al., 1998;
208 Garreau et al., 2008).

209 ***First step: estimation of genetic variance in the energetic allocation coefficient***

210 The energetic allocation coefficient was analyzed by a random regression model (RR) with first
211 order Legendre polynomials (Robson, 1959) for the genetic and permanent environmental effects.
212 The common litter was significant as a random effect, tested using likelihood ratio (LRT) test, α -
213 risk of 5%, and included in the model, in addition to additive genetic and permanent environmental
214 effects. Fixed effects included in the model were selected at an p-value of 5% using the Wald F

215 statistic. The significant fixed effects were the fattening group (103 levels), as contemporary group,
216 and the joint effect of fattening group and the fattening pen (517 levels). The age k in days of the
217 animal at day t was include as a covariate. The residual variance was assumed constant over time.

218 *Second step: estimation of genetic variance in residual variance*

219 In the second step of the analysis, the residuals (e_{it} , residuals of animal i at time t) of the RR
220 model were used to compute log transformed squared residuals: $LSR_{it} = \ln(e_{it}^2)$ as an indicator of
221 animal robustness. A lower LSR value is assumed to be an indication of a higher animal robustness
222 to environmental perturbations, related to a smaller deviation from expected allocation of energy to
223 growth. To follow the assumption of the BLUP (best linear unbiased prediction; Henderson, 1977)
224 method, which should be applied to a non-selected base population, and to estimate the covariance
225 between traits, a multi-traits animal model including the four traits under selection (ADG, BF100,
226 LD100 and FCR, single measurement for all the animals) and the non-selected traits LSR (repeated
227 data for animal in station) and RFI was applied. For the LSR trait, the same fixed effects were fitted
228 as for α_{it} and the random effects included were common litter, permanent environmental and animal
229 additive genetic effects. For the four traits under selection, the fixed effects tested at an α -risk of 5%
230 using the Wald F statistic were the gender (2 levels), the fattening farm (4 levels) and the fattening
231 group within the fattening farm (443 levels). The significant random effects were common litter and
232 animal additive genetic. At this step, heritability (h^2) was calculated as the ratio of animal genetic
233 variance to the total phenotypic variance, *i.e.*, the sum of the genetic additive variance,
234 environmental variances (common litter, permanent environmental if necessary) and the residual
235 variance.

236 *Relation between LSR and routinely collected phenotypes*

237 To evaluate whether the LSR phenotype could be considered as a robustness proxy, the relationship
238 between estimated breeding value (EBV) for LSR and health phenotypes was studied. The 3028

239 males with LSR phenotype and known information over the fattening period (observations,
240 injections...) were divided into 4 quartiles according to their EBV for LSR, from Q1 for the most
241 favorable values (lower EBV LSR) to Q4 for the most unfavorable values (higher EBV LSR). We
242 studied the distribution of other phenotypes associated with animal health and robustness according
243 to the EBV LSR quartile. To compare the differences and frequencies in the scores among the four
244 EBV LSR classes, a Chi-square was performed. Statistical significance was set a priori at P less
245 than or equal to 0.05. These phenotypes are derived from measurements made during the animals
246 performance evaluations, and from the medical treatments recorded during the testing period. In
247 each class, we differentiated animals that can be selected (Selectable) from those that are dead or
248 weighing less than 70 kg at the day of the individual test or weighing 70 kg or more and with an
249 observable defect on the day of testing. We considered as an observable defect on the day of testing,
250 factors such as weak development and similar that were estimated to relate to the robustness of the
251 animal (Appendix 1). A second trait differentiated pigs that received at least one antibiotic or anti-
252 inflammatory injection during the testing period from those that didn't receive any injection (No
253 injection). We also differentiated pigs that were "Selectable" without receiving any antibiotic or
254 anti-inflammatory injection during the testing period (Selectable without injection) from the others.

255 **Results**

256 *Observed allocation coefficients and robustness indicators*

257 The descriptive statistics for the dataset used in this study are shown in Table 1. The observed
258 means and LSR were 0.099 ± 0.027 kg/MJ NE and -12.62 ± 2.50 , respectively. The phenotypic
259 correlations, estimated with *cor.test* function on R (R Core Team, 2018), for trait α_t were positive
260 with e_t (0.241 ± 0.002) and LSR (0.23 ± 0.002), which means that a higher energetic allocation rate to
261 growth was related to a higher variability. The phenotypic coefficients of variation were greater

262 than 20% for IBW, α_t and LSR, and between 10 and 20% for TBW, ADG, DFI and BF100,
263 indicating large phenotypic variation for these traits.

264 Figure 2 displays the α_t trajectories of two animals exhibiting different patterns. The first animal on
265 Figure 2a had a smoothed allocation trajectory over time close to its prediction from RR model
266 (Figure 2a), its average LSR value for was -14.6 ± 1.7 . The second animal on Figure 2b had higher
267 deviation between smoothed allocation and prediction likely in response to an environmental
268 perturbation, its average LSR value was higher than for the first individual (-12.3 ± 1.9).
269 Accordingly, the parameter LSR looks to be a useful indicator to quantify the effect of perturbation
270 of an animal and allows comparison within a population.

271 ***Genetic parameters of allocation coefficients, production and robustness indicator traits***

272 The changes in heritability for α_t over time estimated with the RR model are shown in Figure 3,
273 ranging from 0.20 ± 0.03 to 0.30 ± 0.03 . The heritabilities obtained with the RR model were stable
274 from 67 to 100 days of age, around 0.30 ± 0.03 , then decreased up to 150 days of age and then
275 stabilized around 0.20 ± 0.03 toward the end of the control period. The permanent environmental
276 ratios ranged from 0.51 ± 0.03 to 0.64 ± 0.03 . The estimates obtained decreased up to 128 days of age
277 and then increased again toward the end of the period.

278 Heritability estimates of the traits under selection, ADG, BF100, LD100 and FCR, were moderate,
279 ranging from 0.27 ± 0.03 to 0.45 ± 0.02 (Table 2). Heritability estimates for RFI and FCR were not
280 significantly different from each other, 0.29 ± 0.03 and 0.27 ± 0.03 respectively. The robustness
281 indicator LSR was lowly heritable, 0.05 ± 0.01 . The proportion of variance due to common litter
282 effects was similar for all traits, ranging from 0.04 ± 0.01 to 0.06 ± 0.01 , except in the LSR estimation,
283 which had a proportion of phenotypic variance explained by litter effect close to 0. The proportion
284 of phenotypic variance explained by permanent environment effect for LSR was moderate,
285 0.22 ± 0.01 .

286 The trait LSR had high negative genetic correlations with ADG, FCR and RFI, ranging from -
287 0.83 ± 0.06 to -0.71 ± 0.06 (Table 3). Estimates of genetic correlations of LSR with BF100 were low
288 and negative, and not significantly different than from 0 with LD100. The trait FCR had a high
289 genetic correlation with RFI, 0.90 ± 0.02 , and moderate genetic correlations with ADG and BF100,
290 0.52 ± 0.06 and 0.50 ± 0.05 , respectively. Estimates of the genetic correlations of ADG with BF100
291 and RFI were positive and moderate to high, 0.43 ± 0.04 and 0.61 ± 0.05 respectively.

292 *Relation between EBV LSR classes and collected phenotypes*

293 The percentage of “Selectable” animals was significantly related to the EBV LSR quartile (Figure
294 4). The quartile Q1, including animals with the lowest EBV LSR value, had the highest value with
295 91.7% of “Selectable” animals, and the quartile Q4 had the lowest percentage, 61.2%. The
296 difference between each quartile were significant. In the quartile Q1, 75% of the animals didn’t
297 receive any antibiotic or anti-inflammatory injection (“No injection”) over the control period. This
298 percentage was not significantly different than those observed for Q2 and Q3, 74.1% and 70.9%
299 respectively. The difference of percentage animals with “No injection” was significant between Q4,
300 68.7%, and Q1 or Q2. The proportion of animals “Selectable without injection” was significantly
301 higher in Q1 than in Q3 and Q4, 69.3%, 58.3% and 43.3% respectively. In summary, a lower EBV
302 LSR, *i.e.*, a higher robustness level, was associated with a better chance of being in good health, of
303 being “selectable” and with a lower use of medicines.

304 **Discussion**

305 Our objective was to propose a robustness indicator for fattening pigs from the characterization of
306 the energy allocation of the animal. This indicator is expected to be associated with the ability to
307 cope with different types of environment perturbations encountered, allowing optimal expression of
308 production potential. The originality of this work was to use two time-series variables measured in
309 order to model longitudinal an energetic allocation coefficient, α_t , over the fattening period. The

310 LSR trait was estimated as the daily deviation of α between the observed values (*i.e.*, calculated
311 with the DLM) and the fitted values estimated by the RR model. Then, we studied the genetic
312 background of LSR in order to assess its potential as selection trait for robustness in fattening pigs.
313 This study indicated that LSR had a low heritability trait and showed strong favorable genetic
314 correlation with growth and unfavorable with FCR and RFI.

315 ***Energetic allocation to growth, from concept to model***

316 When faced with one or more environmental disturbances, we can assume that a fattening pig has
317 two types of responses: a change in feed intake pattern or a modification in energy allocation, that is
318 to say a trade-off. These modifications in feed intake or in allocation patterns can affect or not the
319 body weight gain pattern of the animal. This study focused on the second hypothesis with the
320 objective to quantify robustness with a proxy estimated from variations in the energetic allocation
321 over time. To our knowledge, this approach has been little studied in pigs with a selection purpose.
322 The effects of environmental conditions on feed intake have been widely studied in pigs, mainly the
323 effects of temperature (Quiniou et al., 2000) and diseases (Kyriazakis et al., 1998). The
324 quantification of robustness or resilience through the analysis of variations in feed intake have also
325 been studied (Putz et al., 2019; Nguyen-Ba et al., 2020; Homma et al., 2021). With respect to
326 robustness, the effect of disturbances on growth pattern has been studied on pigs after weaning
327 (Revilla et al., 2019) or during the finishing period (Revilla et al., 2022).

328 Conceptually, for a fattening pig, it can be assumed that net energy is allocated between several
329 functions: maintenance, growth (daily protein and lipid deposition) and other functions such as
330 health or thermoregulation (Figure 1). We can assume that the proportion of the total available net
331 energy allocated to each function was regulated by a “valve” which increases or decreases
332 allocation over time. This modulation supposed that there would be a regulation in the allocation of
333 the net energy which would be linked on the one hand to a “desired allocation”, dependent on the

334 characteristics of the individual (genotype, age), and on the other hand to an “allocation permitted
335 by the environment”.

336 The model structure does not detail the full process as described in Figure 1, but provides a simple
337 and biological way to represent energy allocation. Based on these assumptions and on data available
338 in the context of the study, we built the model to estimate α_t based on daily feed intake and live
339 weight measurements over time. Energy allocation to maintenance was estimated from the
340 metabolic body weight based on the equation proposed by Noblet et al. (1999), although this is an
341 average estimate and we thus ignored any variability between sexes, breeds and individuals. The
342 mobilization of lipid reserves, allowing an increase in the net energy available, was not integrated
343 into the model. Indeed, the mobilization of body reserves, apart from glycogen, is rare in growing
344 animals (van Milgen and Noblet, 2003). In this context, we used a pragmatic approach to estimate
345 the energy available for growth at time t . This pragmatic approach is linked to the fact that it is not
346 possible, in a large population, to evaluate precisely for a given pig at a given time, the net energy
347 allocated to maintenance, to additional thermoregulation or physical activity, to protein deposition
348 and to lipid deposition.

349 In this study, we use DLM regression to model the relation between $CNEA_{it-1}$ and CW_{it} over time
350 because the DLM makes it possible to characterize allocation coefficient dynamics by a stochastic
351 process, without the requirement for a strong deterministic assumption. With this method, it is
352 possible to determine whether the allocation coefficient was increasing, decreasing or stagnating,
353 without assuming that it followed any given analytical trend, such as a linear, quadratic or cubic
354 trend (Michel and Makowski, 2013). Our approach takes advantage of the available dlm package in
355 R (Petris et al., 2009) which enabled processing of the full data in a small computation time (around
356 35 min for the 405104 measurements). In addition, this simple DLM approach could ultimately be
357 expanded to the development of multivariate models or the implementation of fixed (batch, herd...)

358 or random effects (Stygar and Kristensen, 2016). Another property of DLM is to produce one-step-
359 ahead forecasts of one or several variables especially to provide early warning to the farmer when
360 forecast error increases (Jensen et al., 2017). Dynamic linear models look to be powerful tools for
361 analyzing time-series variables.

362 *Estimation of genetic variance in allocation coefficient α_t*

363 We assumed that the “desired allocation” of net energy to growth was driven by two components:
364 the animal's genetic potential and its degree of maturity. In the first step, the objective was to
365 estimate the genetic variance in allocation coefficient α as affected by degree of maturity, which
366 evolves with the age of the pig. To achieve this, we used a RR model to estimate the genetic
367 variance α_t and the slope of allocation coefficient to growth over time for each individual. Random
368 regression using orthogonal polynomials models have been widely used in genetics, for example to
369 model feed intake or RFI in pigs or in rabbits (David et al., 2015; Shirali et al., 2017). The random
370 regression of order one was chosen to fit the additive genetic and permanent environmental effects,
371 there was no significant improve of the model, based on LRT test, with polynomials of higher
372 order. If the end of the measurement period had been at a weight closer to the maturity weight, a
373 quadratic random regression would probably be more suitable (Lewis and Emmans, 2020).

374 The trait α_t , describing the allocation of net energy in growth during fattening period, has moderate
375 heritabilities in the same range as those estimated for FCR or RFI and was strongly correlated with
376 them. In a previous study (Lenoir et al., 2022c), the trait considered was the average value of α_t and
377 not the repeated estimates, the heritability obtained was lower (0.16 ± 0.05) but was estimated from a
378 different dataset. For the trait RFI, the study of David et al. (2021) showed heritabilities ranging
379 from 0.19 ± 0.06 to 0.28 ± 0.06 , using a RR model with weekly estimation over 10 weeks in pigs.

380 *Genetic parameters for LSR and production traits*

381 The heritability of the trait LSR, which characterizes the environmental variance of α_t , was low but
382 non null. Generally, the heritability of environmental variance is lower than 0.10 (Mulder et al.,
383 2007). This estimate for LSR was in the same range as those published on different traits but with a
384 similar REML method such as: 0.012 ± 0.004 for rabbits birth weight (Garreau et al., 2008),
385 0.024 ± 0.002 for litter size in pigs (Sell-Kubiak et al., 2022), 0.029 ± 0.003 to 0.047 ± 0.004 for broiler
386 chicken body weight (Mulder et al., 2009). Other studies have been based on the analysis of the log-
387 transformed variance (LnVar) of residuals resulting from a modeling of one time-series variable.
388 This LnVar trait seems to have higher heritabilities than LSR: from 0.20 to 0.24 for milk production
389 (Poppe et al., 2021) or from 0.10 to 0.12 for egg production (Bedere et al., 2022). Some authors
390 have used the double hierarchical generalized linear model (DHGLM) allowing in the same
391 structural model to estimate the mean of the trait and its residual variance (Rönnegård et al., 2010).
392 In order to perform the multi-trait analysis, we chose to use a 2-step approach rather than the
393 DHGLM. In theory, the DHGLM model would make it possible to estimate a residual genetic
394 variance close to the results obtained by our two-step approach. However, it is much more complex
395 mathematically and has convergence issues, making it difficult to use in an operational breeding
396 program (Berghof et al., 2019a).

397 Heritability estimates for ADG and RFI were consistent with those reported in literature for Pietrain
398 or Large-White pigs raised in similar environmental conditions, which varied from 0.33 ± 0.03 to
399 0.48 ± 0.06 and from 0.21 ± 0.03 to 0.34 ± 0.05 (Saintilan et al., 2013; Déru et al., 2020). For carcass
400 traits (BF100 and LD100), heritabilities were also consistent with the values estimated by
401 Sourdioux et al. (2009) and Saintilan et al. (2013) in the Pietrain breed (BF100: 0.38 to 0.48;
402 LD100: 0.25 to 0.34). Our estimate of heritability for FCR was lower than the heritabilities
403 presented by Saintilan et al. (2013), Gilbert et al. (2017) and Déru et al. (2020), which varied from
404 0.30 ± 0.0 to 0.47 ± 0.08 .

405 ***Genetic correlations between robustness and production traits***

406 The growth trait ADG was strongly correlated with LSR. In the present rearing conditions, an
407 animal's ability to be robust, *i.e.*, to have low LSR value, is strongly linked to its ability to express
408 optimal growth regardless of the environment. Growth has been a major selection trait in the
409 Pietrain breed for over 20 years, and lack of growth was a major cause of culling at testing or of
410 non-selection. Nonetheless, even if the correlation was strong, it was not equal to 1, which implies
411 that the trait LSR added an additional information regarding the robustness of the animal compared
412 to ADG. Thus, if selection is made using these traits, they would allow us to improve animal's
413 robustness more than if the selection is made only on growth traits.

414 There were strong and unfavorable relationship between LSR and feed efficiency traits, FCR and
415 RFI. This could be related to the positive correlation between ADG and FCR, which was affected
416 by the way these two traits were estimated (Lenoir et al., 2022a). The traits ADG and FCR used in
417 selection were measured over an identical period for all pigs but were not standardized between
418 starting and finishing weights. Accordingly, some of the animals tested reached their mature weight
419 before testing, which led to a drop in feed conversion or residual feed intake even if they had
420 previously a strong growth. Thus, there were two different types of finisher pigs with low FCR or
421 RFI: those which had a strong growth but did not approach their mature weight during the testing
422 period, and those with a low daily feed intake associated with a low, near maturity, growth (Lenoir
423 et al., 2022a). We performed an additional analysis where we standardized the trait FCR between 40
424 and 100kg, the genetic correlation with LSR remained unfavorable but less strong, -0.34 ± 0.14 . The
425 standardization of the trait FCR modified the genetic correlation with ADG from moderately
426 unfavorable, 0.52 ± 0.06 , to close to zero or slightly favorable, -0.08 ± 0.09 . The correlation between
427 LSR and FCR or RFI could indicate that the most robust pigs during the testing period were not the
428 most efficient because they allocate a part of energy to other functions or maintenance. Indeed, a

429 selection for low RFI could impact the ability of the animals to modify their allocation of energy to
430 other functions to cope with environmental challenges (Gilbert et al., 2017). This antagonism
431 between short-term efficiency and resilience has been put forward by Friggens et al. (2017). In this
432 situation, it would seem that there is a compromise that does not make it possible to increase
433 robustness relatively easily without loss of selection response in feed efficiency. In contrast, several
434 studies have shown through divergent selection experiments on RFI, that animals from Low RFI
435 line (LRFI) adapted better to environmental challenges or at least are not disadvantaged compared
436 to animals from High RFI line (HRFI). Chatelet et al. (2018) showed that the health, growth
437 performance and feed intake of animals from the LRFI line were less impacted than those of
438 animals born from the HRFI line under poor hygienic conditions. In the same selection experiment,
439 the risk of being culled between 70 days of age and slaughter was 1.8 times less in the LRFI line
440 compared to the HRFI line (Gilbert et al., 2017). In another experience of selection Dunkelberger et
441 al. (2015) suggested that pigs for LRFI were more robust to PRRSV challenges; their growth was
442 less affected and they was less affected. These results seem to contradict the resource allocation
443 theory and the genetic correlation estimated in our study. This study was carried out on Pie NN line,
444 a sire line, and the different selection experiments on RFI were realized with animals from Large-
445 White (or Yorkshire), a dam line. The Pietrain sire line had been created and selected for several
446 generations on objectives of improving feed efficiency, growth and carcass characteristics,
447 potentially to the detriment of the other traits, such as robustness. Due to these characteristics and
448 orientations, it can be assumed that there is a different allocation pattern between these lines.

449 Genetic correlations between robustness and BF100 were slightly unfavorable. We can suppose that
450 the capacity to be robust could be associated with more important body reserves allowing the
451 animal to face perturbations.

452 ***Relation between EBV LSR classes and collected phenotypes***

453 Our study shows that model longitudinal energetic allocation to growth offers the opportunity to
454 develop a proxy of robustness that is heritable. Further, this proxy has to meet the expectations of
455 pig farmers, that is to say, it should identify animals that faced to environmental disturbances and
456 were present for testing in good health and with the least amount of medical injections. The analysis
457 of the relationship between EBV LSR quartiles and phenotypes routinely collected on farms shows
458 the most favorable situation for the most robust animals, *i.e.*, those from the quartile with the
459 weakest EBV LSR (Q1). Including LSR in the breeding goal would be an opportunity to improve
460 the robustness qualities of Pie NN line for the fattening period, in spite of the low heritability of
461 LSR. However, these results are evaluated over a short period of animal's life, it would be
462 appropriate to investigate the effects of a selection on the LSR trait over the whole lifespan of
463 related animals (dam, sire, pure or crossbred offspring). In a following step, it could be relevant to
464 study the link between the LSR trait and the reproductive performances of boars (spermatic
465 production) or females (fertility, productive longevity, survival).

466 ***Environmental conditions***

467 This studied was carried out in a higher biosecurity environment than regular farms, related to the
468 fact that a breeding company cannot take any risks with a purebred nucleus. The other
469 environmental conditions (feed characteristics, barn design, density...) were close to those found in
470 production farms in France, that is, designed to minimize exposure to environmental challenges.
471 When designing the selection conditions there is a need to balance between conditions that allow
472 full expression of performance and meet sanitary requirements versus conditions that favor
473 expression of robustness. Even though these environments are qualified as favorable, the animals
474 are subjected to stresses which can be chronic (social stress, heat wave). Rear animals under
475 challenging conditions seems to allow better phenotyping of the robustness of the animals (Gunia et
476 al., 2018). The difficulty of having conditions to evaluate robustness while evaluating production

477 potential could be partly overcome by the use of short-term challenges, such as feeding challenges.
478 Indeed, offspring of these purebred pigs, selected in one type of environment, are likely to be reared
479 in harder and more variable environments impacting robustness expression. This relationship
480 between the robustness expression and diverse rearing conditions cannot be dissociated from
481 Genotype x Environment (GxE) interaction (Falconer and Mackay, 1996). This interaction that may
482 cause reranking of sires, has a greater impact on traits based on variances than on traits based on
483 means (Bedere et al., 2022). The acquisition of data on related animals reared in farms newly
484 equipped with AFS makes it possible to consider evaluating the effects of the GxE interaction.

485 In this study, we proposed an approach for characterizing the robustness through the variability in
486 the allocation. However, when studying the allocation pattern, it is important to also assess the
487 acquisition trajectory (van Noordwijk and de Jong, 1986; Friggens et al., 2017). In a routine
488 selection approach, it would be relevant to add to the LSR trait, a trait making it possible to
489 characterize the robustness on acquisition

490 **Conclusions**

491 The trait LSR could be interpreted as an indicator of the response of the animal to
492 perturbations/stress, that is to say a robustness proxy. This study shows that LSR has a low
493 heritability but that it is possible to set up a selection on this trait. We found that this trait is
494 favourably genetically correlated with a growth trait (ADG) and unfavourably with feed efficiency
495 traits (FCR and RFI). Estimation of the economic value of LSR trait is a key issue before adding
496 this trait in breeding goals. Furthermore, improving robustness qualities also meets societal
497 expectations, the economic value of which is difficult to quantify.

498 **List of abbreviations**

499 α_i : daily energetic allocation coefficient to growth

- 500 ADG: average daily growth
- 501 AFS: automatic feeding system
- 502 AMW: average metabolic weight
- 503 BF: backfat thickness
- 504 BF100: backfat thickness estimated at 100 kg liveweight
- 505 BW: body weight
- 506 CNEA : cumulative net energy available for growth
- 507 CW: cumulative weight gain
- 508 DFI: daily feed intake
- 509 DLM: dynamic linear model
- 510 EBV: estimated breeding value
- 511 EI: net energy intake
- 512 FCR: feed conversion ratio
- 513 FI: feed intake
- 514 IBW: initial body weight
- 515 LD: longissimus dorsi thickness
- 516 LD100: longissimus dorsi thickness estimated at 100 kg liveweight
- 517 LSR: log transformed squared residuals, robustness indicator
- 518 MR: net energy maintenance requirement
- 519 NEA: net energy available for growth
- 520 PDFI: potential average daily feed intake
- 521 Pie NN: Piétrain NN Français free from halothane-sensitivity
- 522 RFI: residual feed intake
- 523 TBW: body weight at individual testing

524 **Declarations**

525 **Ethics approval and consent to participate**

526 Specific Experimental Animal Care and Use Committee approval was not needed because all the
527 data used in this study were obtained from preexisting databases provided by AXIOM. The data
528 used were from animals raised under commercial conditions that were cared for according to EU-
529 Council directive 2008/120/EC of 18 December 2008 laying down minimum standards for the
530 protection of pigs (<http://data.europa.eu/eli/dir/2008/120/oj>).

531 **Consent for publication**

532 Not applicable

533 **Availability of data and materials**

534 The datasets analysed during the current study are not publicly available because they are part of the
535 commercial breeding program of AXIOM. However, they are available from the corresponding
536 author on reasonable request.

537 **Competing interests**

538 RMT, NF and ID declare that they have no competing interests. GL and LFG are employed by
539 AXIOM. The datasets are of interest to commercial targets of AXIOM, but this interest did not
540 influence the results in this manuscript in any matter.

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544 **Authors' contributions**

545 GL, NF and RMT developed the conceptual model. RMT and GL implemented and tested the DLM
546 model. GL, ID and LFG carried out statistical analyses. GL drafted the paper. ID, LFG, NF, RMT
547 and GL participated in interpreting and discussing results. All authors read and approved the final
548 manuscript.

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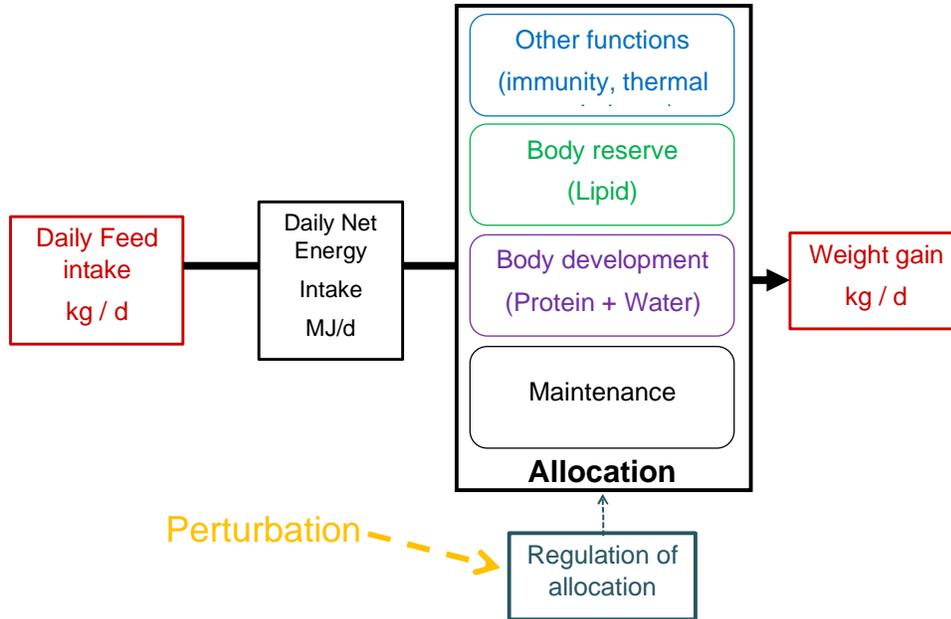
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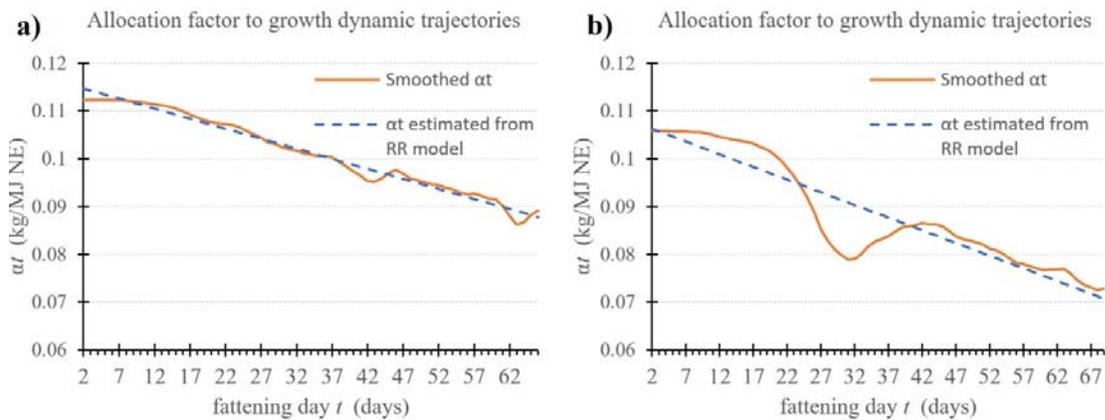
711 **Figures**



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713 **Figure 1.** Conceptual model of resource allocation in growing pig.
 714 In red : Variables recorded by AFS

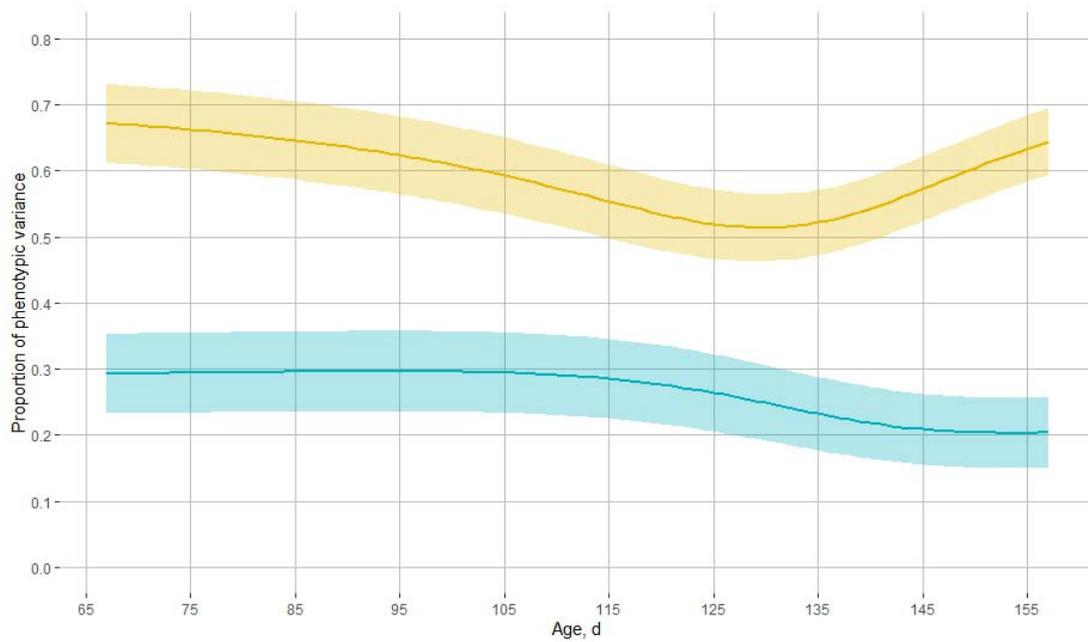
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717 **Figure 2.** Example of two dynamic trajectories of the allocation coefficients α_t during the whole
 718 fattening period for two animals: smoothed with DLM model (orange line) and its prediction from
 719 RR model (blue dotted line).

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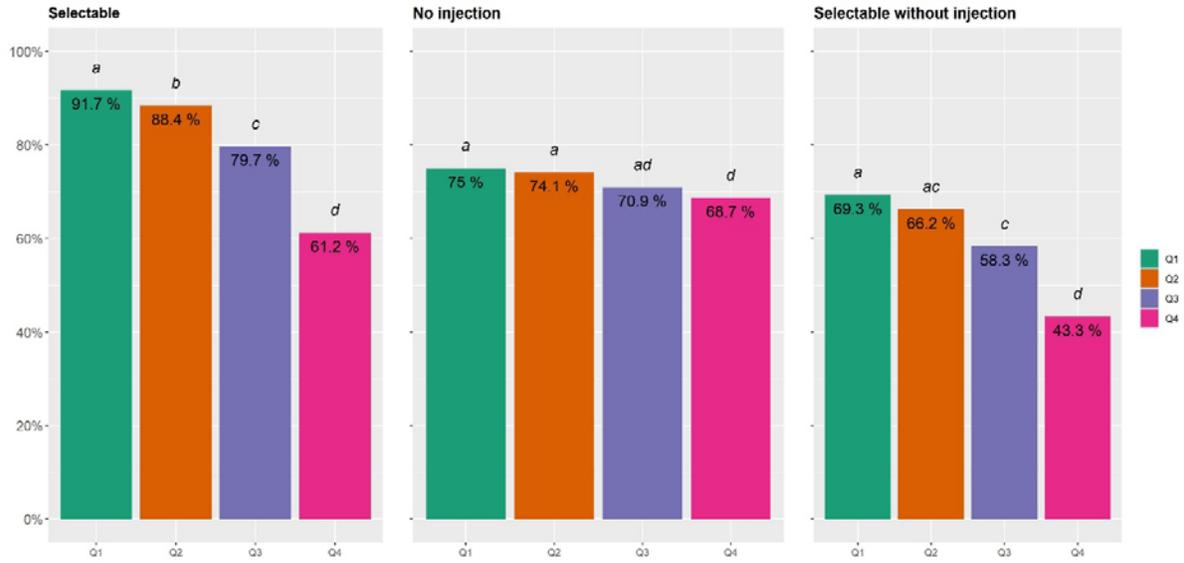


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723 **Figure 3.** Changes of heritability (h^2_k ; blue) and permanent environmental (p^2_k ; yellow) estimates
724 for energetic allocation coefficient α_i over age in days under the random regression model (RR)
725 using Legendre orthogonal polynomials. Shaded area: 95% confidence interval

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Figure 4. Distribution of percentages of pigs that can be selected (Selectable), that didn't receive any antibiotic or anti-inflammatory injection (No injection) or that were "Selectable" without receiving any antibiotic or anti-inflammatory injection during the testing period (Selectable without injection) depending of their estimated breeding value for robustness indicator (LSR) quartile. *Q1*: pigs with lowest EBV LSR values, i.e., higher robustness genetic potential; *Q4*: pigs with highest EBV LSR values, i.e., lower robustness genetic potential. Bars with different letters are significantly different ($P < 0.05$).

736 **Tables**

737 **Table 1.** Descriptive statistics of the variables recorded or estimated on fattening pigs

Trait (unit) ¹	Number of animals / records if repeated measures	Mean	SD	
				738
				739
IBW (kg)	25745	33.8	7.8	
TBW (kg)	25365	103.7	11.1	740
ADG (kg/d)	25322	0.977	0.109	
FCR (kg/kg)	8675	2.25	0.21	741
DFI (kg/d)	8675	2.19	0.29	742
RFI (kg/d)	8675	-0.005	0.169	
BF100 (mm)	25323	7.66	1.19	743
LD100 (mm)	25320	68.26	6.34	744
α_t (kg/MJ)	5848 / 405104	0.099	0.027	
e_t (kg/MJ)	5848 / 405104	0	0.0096	745
LSR	5848 / 405104	-12.62	2.50	746
				747
				748

749 ¹IBW: initial body weight; TBW: terminal body weight; ADG: average daily gain; FCR: feed conversion; DFI: daily
 750 feed intake; RFI: residual feed intake; BF100: backfat thickness estimated at 100kg liveweight; LD100: longissimus
 751 dorsi thickness estimated at 100 kg liveweight; α_t : allocation coefficient to growth; e_t : residual of RR model; LSR=
 752 log-squared residual, robustness indicator.

753 **Table 2.** Estimates of heritability (h^2), common litter effect ratio (c^2), permanent environmental
 754 effect ratio (p^2) and phenotypic variance (V_p) for the traits recorded (\pm standard error)

Trait ¹	h^2	c^2	p^2	V_p	
BF100	0.45 \pm 0.02	0.04 \pm 0.01	/	1.02 \pm 0.02	755
LD100	0.29 \pm 0.02	0.04 \pm 0.01	/	15.78 \pm 0.20	756
ADG	0.37 \pm 0.02	0.06 \pm 0.01	/	0.01 \pm 0.000	757
FCR	0.27 \pm 0.03	0.04 \pm 0.01	/	0.0222 \pm 0.000	758
RFI	0.29 \pm 0.03	0.04 \pm 0.01	/	0.034 \pm 0.000	759
LSR	0.05 \pm 0.01	0.004 \pm 0.004	0.22 \pm 0.01	5.56 \pm 0.033	760
					761
					762
					763

764 ¹BF100= backfat thickness estimated at 100kg liveweight; LD100= longissimus dorsi thickness estimated at 100 kg
 765 liveweight; ADG= average daily gain; FCR= feed conversion ratio; RFI: residual feed intake; LSR= log-squared
 766 residual, robustness indicator

767 **Table 3.** Estimates of genetic correlations ($r^2a \pm$ standard error) between robustness trait (LSR) and
 768 production traits

Trait ¹	LD100	ADG	FCR	RFI	LSR
BF100	-0.13 \pm 0.05	0.43 \pm 0.04	0.50 \pm 0.05	0.32 \pm 0.06	-0.19 \pm 0.07
LD100		-0.24 \pm 0.05	-0.09 \pm 0.05	-0.08 \pm 0.07	0.02 \pm 0.07
ADG			0.52 \pm 0.06	0.61 \pm 0.05	-0.71 \pm 0.06
FCR				0.90 \pm 0.02	-0.76 \pm 0.06
RFI					-0.83 \pm 0.06
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777 ¹BF100= backfat thickness estimated at 100kg liveweight; LD100= longissimus dorsi thickness estimated at 100 kg
 778 liveweight; ADG= average daily gain; FCR= feed conversion ratio; LSR= log-squared residual, robustness indicator

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780 **Additional information**

781 **Appendix 1.** List of individuals observations performed during the individual test from Lenoir et al.
 782 (2022a).

	783
	Observation
Observations taken into account to define the robustness traits	Abcess
	Cannibalism
	Capelet
	Weak development / Low body condition
	Callus
	Shortness of breath
	Necrotic ear
	Out of test (testing body weight < 70kg)
Shaker	
Observations not taken into account to define the robustness traits	Lack of leg soundness
	Low and short
	Conformation / Body development
	Culard
	Important conformation
	Fat animal
	Asymmetric hooves
	Teats default
Incorrect conformation	
Hernia	