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

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Abstract

Background

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

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

Results

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

Conclusions

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

Background

The pig industry faces new challenges related to rapidly changing environmental conditions,

especially related to global warming (Hansen et al., 2012), and to growing societal concerns. For

several decades, breeding objectives were mainly focused on increasing animal productivity

(growth, feed efficiency…) at the expense of non-productive functions, *i.e.*, fitness (Puillet et al.,

2016; Rauw et al., 1998). These unfavorable consequences could be explained by trade-offs in

resource allocation between biological functions (Rauw, 2009). Indeed, when animals cannot obtain

more resources, *i.e.,* in limiting environments, allocation of these resources to a high priority

function must be to the detriment of another function (Stearns, 1992). In this situation the animal is

unable to maximize the expression of each biological function simultaneously. This changing

context requires having animals able to adapt to new environmental conditions with more limiting

resources, which can be associated with an improvement of robustness. Knap (2005) defined

robustness as "*the ability to combine a high production potential with resilience to stressors,*

allowing for unproblematic expression of a high production potential in a wide variety of

environmental conditions". Generally, the production potential is associated to a phenotype of

interest, such as growth, feed efficiency or milk production, egg production. Incorporating one or

several traits to evaluate robustness of growing pigs in genetic evaluation would therefore be of

value for the development of more sustainable breeding goals (Berghof et al., 2019b). Accordingly,

when targeting robustness as a breeding objective, it is important to maintain simultaneously a high

level of production to meet industry's economic expectations. However, until recently to it was very

difficult to phenotype traits such as robustness in farm animals and therefore on the way to improve

it.

In parallel, the increasingly common use of sensors in farms, especially automatic feeding system

(AFS) in pig industry, allows continuous individual recording of weight or feed intake over a long

period. This offers the possibility to characterize the dynamics of those phenotypes for each

individual in the face of variations in the environment. Several studies have used such longitudinal

data to quantify resilience indicators based on deviation between an expected trajectory of each

individual for a given non-perturbed environment and its observed trajectory on feed intake

(Nguyen-Ba et al., 2020) or body weight (Revilla et al., 2022). Definition and modelling of

individual potential trajectory are challenging issues in these approaches. Other studies developed

several resilience indicators based on the within individual variance of time series mesurments

related to production, such as feed intake of growing pigs (Putz et al., 2019), milk yield for dairy

cows (Poppe et al., 2021) or egg production in laying hens (Bedere et al., 2022). These modeling

approaches have mainly addressed the characterization of robustness or resilience through the

analysis of one production variable. They are a substantial contribution in the phenotyping of

resilience but do not address the underlying biological mechanisms and the potential trade-offs in

the use of available resources between production and other functions. A robust animal can be

considered as an animal able to allocate a proportion of its resources to the right function at the right

time (Friggens et al., 2017). To our knowledge, the characterization of robustness based on the

temporal evolution of the allocation pattern has been little explored in growing pigs.

The acquisition of temporal data of feed intake and weight in growing pigs made it possible to

consider the development of allocation model based on these two variables to caracterize

robustness. With this objective, we developed a conceptual model to represent the temporal pattern

of allocation of energy intake to growth in fattening pigs (Lenoir et al., 2022).

In the present study, the first objective was to develop a robustness indicator on the basis of

modelling of longitudinal energetic allocation coefficient to growth for fattening pigs.

Consequently, the environmental variance of this allocation coefficient was considered as a proxy

of robustness. This proxy should reflect the ability of an animal to express or adapt its production

potential in the face of changes in the environment relative to other animals that have been raised

under the same conditions. Our objective was to estimate its genetic parameters and correlation with

traits under selection as well as with phenotypes routinely collected on farms and associated to

robustness or heatlh status.

Methods

98 **Methods**

Study population

Study population

A total of 25745 pigs from Piétrain NN Français paternal line (Pie NN), free from halothane-

sensitivity, of the AXIOM company were used in this study. Individuals from the Pie NN line were

born in 3 different farms integrated into the AXIOM breeding scheme and that comply with

AXIOM's biosafety and health requirements. A part of the males were selected before weaning and

then raised at the boar testing station of the breeding company AXIOM Genetics (Azay-sur-Indre,

France). The animals considered in the present dataset were 6885 entire males and 13012 females

raised and individually tested at their farm of birth from April 2014 to April 2022 and 5848 entire

males raised from September 2015 to April 2022 at the boar testing station.

The animals raised on their birth farm were born from 3943 litters, 6.5±2.9 piglets per litter, and

from 321 sires, 80±53.8 piglets per sire. To limit the risk of confounding between environmental

(*i.e.*, fattening group) and genetic effects, the sires were used at least in two mating groups in each

farm and in two different farms. Animals were transferred to fattening rooms when they were 75.7

±3.4 days of age (33.8±7.8 kg body weight (BW)). Pigs were raised in fattening rooms for 68.6

±4.9 days until the individual testing at around 142.4±4.6 days of age (103.4±11 kg BW).

For males raised at the boar testing station, they were transferred every three weeks from birth farm

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

raised in pens of 14 animals from the same birth farm. These groups of 14 pigs were never modified

at the different stages of breeding. Each fattening group consisted of animals sourced from between

one or three farrowing farms. These animals came from 2048 litters, 2.6±1.5 piglets per litter, and

were born from 238 sires, 22.1 ±15 piglets per sire. They were raised in quarantine and post-

weaning rooms for five and two weeks respectively and transferred to fattening rooms when they

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

days until the individual testing at around 145.4 ±3.6 days of age (104.5±11.1 kg BW). Fattening

rooms were equipped with AFS: Nedap pig performance testing feeding station (Nedap N.V.;

Groenlo, the Netherlands). Animals were fed ad-libitum with commercial diets adapted to their

physiological needs. The provided diets were non-limiting in amino acids. The boar testing station

environmental and technical conditions are described in detail in Lenoir et al. (2022a). The

pedigrees contained 27276 animals across 20 generations.

Information recorded during the fattening period

The performances recorded were the same in farrowing farms testing and boar testing station. Each

animal was individually weighed on arrival in the fattening room (initial body weight: IBW). When

the average weight of the group was approximately 100 kg, individual tests were performed for

animals weighing more than 70 kg (Institut Technique du Porc, 2004). Measurements made during

the test were: body weight (TBW), average ultrasonic backfat thickness (BF = mean of three

measurements in mm) and ultrasonic longissimus dorsi thickness (LD = one measurement in mm).

The BF and LD measures were transformed to correspond to their values at 100 kg liveweight

(BF100 and LD100 respectively) to compare animals at equivalent weight. This transformation was

done by applying linear coefficients that multiply the difference between 100 kg and TBW.

Coefficients used are 0.04 mm/kg for BF100 and 0.27 mm/kg for LD100 (Sourdioux et al., 2009).

The average daily gain (ADG) was calculated as the difference between TBW and IBW divided by

the number of days elapsed between the two weighings.

Additionally, at the boar testing station, BW (kg) and feed intake (FI; kg per visit) were recorded

each time the animal went into the AFS. The feed conversion ratio (FCR) was calculated as the ratio

between the total FI during the fattening period and the weight gain (TBW-IBW), expressed in

kg/kg. The average daily feed intake (DFI) was calculated as the total FI during the period divided

by the number of days elapsed. The residual feed intake (RFI) was also estimated for each animal as

the deviation between the recorded DFI and the potential average daily feed intake (PDFI) predicted

from requirements for maintenance and production. Based on the method proposed by Labroue et

al. (1999), the PDFI was estimated by linear regression, with the lm function in R (R Core Team,

2018), of DFI on average metabolic weight (AMW), ADG and BF100. The AMW was estimated

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

addition, all medical treatments received by the animal were recorded. A visual observation of the

animals was carried out by the technician in charge of the measurements in order to note any

morphological defects, anomalies and clinical signs of disease according to a frame of reference

(Institut Technique du Porc, 2004), noted as "observable defects". These observations were made by

the same person within any given fattening group. The medical treatments and individual

observations were recorded from January 2019 to April 2022 on 3028 males fattened at the boar

testing station.

Longitudinal data pre-treatment

A pre-treatment process was performed on BW and FI, recorded each time the animal went into the

AFS, to validate them, identify quality issues and convert them on a daily scale. This process

followed the procedure proposed by Revilla et al. (2022) and modified by Lenoir et al. (2022a). In

summary, on the scale of the visit, a quadratic regression of BW on age + age² for each animal was

applied to eliminate aberrant BW. For a given animal and a given visit, if the ratio between the

residual value and the fitted value was > 0.15, the BW measurement was considered to be null. This

step was repeated a second time. Following this step, the body weight (BW$_{it}$; kg) was estimated

from the median of the non-null weights for each pig (*i*) and each fattening day since the transfer to

fattening room (*t*). For feed intake, if for a given animal the feed intake rate at a visit was lower or

higher than its mean take rate over the fattening period ±4 standard deviations, the FI measurement

was considered to be missing. This missing value was estimated using a linear regression of FI on

feeding duration. The daily feed intake (FI_{it}; kg) was calculated as the intakes during the visits of the

day *t*. Then BW_{it} and FI_{it} were validated at the pen scale to detect inconsistencies linked to the AFS

machine. When a control day was missing (due to a mechanic problem of AFS or loss of a RFID

tag), the missing BW_{it} and FI_{it} were estimated separately by using local regression model, "*proc*

loess" implement in SAS (SAS Institute Inc., 2013). Data recorded on day *t*=0 were excluded from

the dataset due to AFS calibration and animal adaptation. After data pre-treatment, the file included

405983 daily records associated to the 5848 males fattened at the testing station.

Model for analysis

Modelling energetic allocation coefficient to growth

As shown on Figure 1, the feed intake, i.e input of the system, is transformed in net energy intake

and allocated to several functions: maintenance, body development (protein deposition), body

reserves (lipid deposition) and other functions (van Milgen et al., 2005). The body weight gain, *i.e.,*

output of the system, is directly related to the protein and lipid depostion. Resource allocation is

regulated during the fattening period for each individual according to deterministic factors: genetic

potential and degree of maturity (Lewis and Emmans, 2020). Over the time, resource allocation

coefficient is also impacted by changes in environmental conditions, *i.e.,* pertubations (Friggens et

al., 2017).

A dynamic regression model (DLM; West and Harrison, 1997) was used to estimate daily energetic

allocation coefficient to growth (α_{it}; Lenoir et al., 2022b). First, FI_{it} was converted in net energy

intake in MJ (EI_{it}), using the net energy density of the feed of 9.85 MJ of NE/kg. Then, the net

energy available for growth at day *t* (NEA_{it}) was calculated as the difference between EI_{it} and the

net energy maintenance requirements at day t (MR_{it}), estimated according to Noblet et al. (2016).

The DLM to estimate the allocation coefficient of energy to weight gain for a given pig i at day t

(α_{it}) was built with two equations : an observation equation (1), relating cumulative weight gain at

day t (CW_{it} in kg) and cumulative net energy available at day t-1 ($CNEA_{it-1}$ in MJ), a system

equation (2), describing the changes in α_{it} (unobserved state variable) from day to day according to

a stochastic process.

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

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

Where v_{it} was a random observation error for animal i; σ_{iv}^2 is the observational variance i; w_{it}

represented random and unpredictable changes in level between time $t-1$ and t; and σ_{iw}^2 was the

system variance. The model was built using the R package dlm (Petris et al., 2009). The values of

α_{it} were calculated independently for each animal with a Kalman smoother algorithm. The value of

α_{it} at t=1 was not estimated because the consumption at t-1 was unknown.

Estimation of genetic variance in environmental variance

Longitudinal energetic allocation coefficients (α_{it}) were analyzed with ASReml 4.2 software

(Gilmour et al., 2009) to estimate both its genetic variance and the genetic variance in the residual

variance (*i.e.,* environmental variance) using a two-step approach (SanCristobal-Gaudy et al., 1998;

Garreau et al., 2008).

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

The energetic allocation coefficient was analyzed by a random regression model (RR) with first

order Legendre polynomials (Robson, 1959) for the genetic and permanent environmental effects.

The common litter was significant as a random effect, tested using likelihood ratio (LRT) test, α-

risk of 5%, and included in the model, in addition to additive genetic and permanent environmental

effects. Fixed effects included in the model were selected at an p-value of 5% using the Wald F

statistic. The significant fixed effects were the fattening group (103 levels), as contemporary group,

and the joint effect of fattening group and the fattening pen (517 levels). The age k in days of the

animal at day t was include as a covariate. The residual variance was assumed constant over time.

Second step: estimation of genetic variance in residual variance

In the second step of the analysis, the residuals (e_{it}, residuals of animal i at time t) of the RR

model were used to compute log transformed squared residuals: $LSR_{it} = ln(e_{it}^2)$ as an indicator of

animal robustness. A lower LSR value is assumed to be an indication of a higher animal robustness

to environmental perturbations, related to a smaller deviation from expected allocation of energy to

growth. To follow the assumption of the BLUP (best linear unbiased prediction; Henderson, 1977)

method, which should be applied to a non-selected base population, and to estimate the covariance

between traits, a multi-traits animal model including the four traits under selection (ADG, BF100,

LD100 and FCR, single measurement for all the animals) and the non-selected traits LSR (repeated

data for animal in station) and RFI was applied. For the LSR trait, the same fixed effects were fitted

as for α_{it} and the random effects included were common litter, permanent environmental and animal

additive genetic effects. For the four traits under selection, the fixed effects tested at an α-risk of 5%

using the Wald F statistic were the gender (2 levels), the fattening farm (4 levels) and the fattening

group within the fattening farm (443 levels). The significant random effects were common litter and

animal additive genetic. At this step, heritability (h²) was calculated as the ratio of animal genetic

variance to the total phenotypic variance, *i.e.,* the sum of the genetic additive variance,

environmental variances (common litter, permanent environmental if necessary) and the residual

variance.

Relation between LSR and routinely collected phenotypes

To evaluate whether the LSR phenotype could be considered as a robustness proxy, the relationship

between estimated breeding value (EBV) for LSR and health phenotypes was studied. The 3028

males with LSR phenotype and known information over the fattening period (observations,

injections…) were divided into 4 quartiles according to their EBV for LSR, from Q1 for the most

favorable values (lower EBV LSR) to Q4 for the most unfavorable values (higher EBV LSR). We

studied the distribution of other phenotypes associated with animal health and robustness according

to the EBV LSR quartile. To compare the differences and frequencies in the scores among the four

EBV LSR classes, a Chi-square was performed. Statistical significance was set a priori at P less

than or equal to 0.05. These phenotypes are derived from measurements made during the animals

performance evaluations, and from the medical treatments recorded during the testing period. In

each class, we differentiated animals that can be selected (Selectable) from those that are dead or

weighing less than 70 kg at the day of the individual test or weighing 70 kg or more and with an

observable defect on the day of testing. We considered as an observable defect on the day of testing,

factors such as weak development and similar that were estimated to relate to the robustness of the

animal (Appendix 1). A second trait differentiated pigs that received at least one antibiotic or anti-

inflammatory injection during the testing period from those that didn't receive any injection (No

injection). We also differentiated pigs that were "Selectable" without receiving any antibiotic or

anti-inflammatory injection during the testing period (Selectable without injection) from the others.

Results

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

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

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

Genetic parameters of allocation coefficients, production and robustness indicator traits

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

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

The trait LSR had high negative genetic correlations with ADG, FCR and RFI, ranging from -

0.83±0.06 to -0.71±0.06 (Table 3). Estimates of genetic correlations of LSR with BF100 were low

and negative, and not significantly different than from 0 with LD100. The trait FCR had a high

genetic correlation with RFI, 0.90±0.02, and moderate genetic correlations with ADG and BF100,

0.52±0.06 and 0.50±0.05, respectively. Estimates of the genetic correlations of ADG with BF100

and RFI were positive and moderate to high, 0.43±0.04 and 0.61±0.05 respectively.

Relation between EBV LSR classes and collected phenotypes

The percentage of "Selectable" animals was significantly related to the EBV LSR quartile (Figure

4). The quartile Q1, including animals with the lowest EBV LSR value, had the highest value with

91.7% of "Selectable" animals, and the quartile Q4 had the lowest percentage, 61.2%. The

difference between each quartile were significant. In the quartile Q1, 75% of the animals didn't

receive any antibiotic or anti-inflammatory injection ("No injection") over the control period. This

percentage was not significantly different than those observed for Q2 and Q3, 74.1% and 70.9%

respectively. The difference of percentage animals with "No injection" was significant between Q4,

68.7%, and Q1 or Q2. The proportion of animals "Selectable without injection" was significantly

higher in Q1 than in Q3 and Q4, 69.3%, 58.3% and 43.3% respectively. In summary, a lower EBV

LSR, *i.e.*, a higher robustness level, was associated with a better chance of being in good health, of

being "selectable" and with a lower use of medicines.

304 Discussion

Our objective was to propose a robustness indicator for fattening pigs from the characterization of

the energy allocation of the animal. This indicator is expected to be associated with the ability to

cope with different types of environment perturbations encoutered, allowing optimal expresion of

production potential. The originality of this work was to use two time-series variables measured in

order to model longitudinal an energetic allocation coefficient, $α_t$, over the fattening period. The

LSR trait was estimated as the daily deviation of α between the observed values (*i.e.,* calculated

with the DLM) and the fitted values estimated by the RR model. Then, we studied the genetic

background of LSR in order to assess its potential as selection trait for robustness in fattening pigs.

This study indicated that LSR had a low heritability trait and showed strong favorable genetic

correlation with growth and unfavorable with FCR and RFI.

Energetic allocation to growth, from concept to model

When faced with one or more environmental disturbances, we can assume that a fattening pig has

two types of responses: a change in feed intake pattern or a modification in energy allocation, that is

to say a trade-off. These modifications in feed intake or in allocation patterns can affect or not the

body weight gain pattern of the animal. This study focused on the second hypothesis with the

objective to quantify robustness with a proxy estimated from variations in the energetic allocation

over time. To our knowledge, this approach has been little studied in pigs with a selection purpose.

The effects of environmental conditions on feed intake have been widely studied in pigs, mainly the

effects of temperature (Quiniou et al., 2000) and diseases (Kyriazakis et al., 1998). The

quantification of robustness or resilience through the analysis of variations in feed intake have also

been studied (Putz et al., 2019; Nguyen-Ba et al., 2020; Homma et al., 2021). With respect to

robustness, the effect of disturbances on growth pattern has been studied on pigs after weaning

(Revilla et al., 2019) or during the finishing period (Revilla et al., 2022).

Conceptually, for a fattening pig, it can be assumed that net energy is allocated between several

functions: maintenance, growth (daily protein and lipid deposition) and other functions such as

health or thermoregulation (Figure 1). We can assume that the proportion of the total available net

energy allocated to each function was regulated by a "valve" which increases or decreases

allocation over time. This modulation supposed that there would be a regulation in the allocation of

the net energy which would be linked on the one hand to a "desired allocation", dependent on the

characteristics of the individual (genotype, age), and on the other hand to an "allocation permitted

by the environment".

The model structure does not detail the full process as described in Figure 1, but provides a simple

and biological way to represent energy allocation. Based on these assumptions and on data available

in the context of the study, we built the model to estimate α_t based on daily feed intake and live

weight measurements over time. Energy allocation to maintenance was estimated from the

metabolic body weight based on the equation proposed by Noblet et al. (1999), although this is an

average estimate and we thus ignored any variability between sexes, breeds and individuals. The

mobilization of lipid reserves, allowing an increase in the net energy available, was not integrated

into the model. Indeed, the mobilization of body reserves, apart from glycogen, is rare in growing

animals (van Milgen and Noblet, 2003). In this context, we used a pragmatic approach to estimate

the energy available for growth at time t. This pragmatic approach is linked to the fact that it is not

possible, in a large population, to evaluate precisely for a given pig at a given time, the net energy

allocated to maintenance, to additional thermoregulation or physical activity, to protein deposition

and to lipid deposition.

In this study, we use DLM regression to model the relation between $CNEA_{it-1}$ and CW_{it} over time

because the DLM makes it possible to characterize allocation coefficient dynamics by a stochastic

process, without the requirement for a strong deterministic assumption. With this method, it is

possible to determine whether the allocation coefficient was increasing, decreasing or stagnating,

without assuming that it followed any given analytical trend, such as a linear, quadratic or cubic

trend (Michel and Makowski, 2013). Our approach takes advantage of the available dlm package in

R (Petris et al., 2009) which enabled processing of the full data in a small computation time (around

35 min for the 405104 measurements). In addition, this simple DLM approach could ultimately be

expanded to the development of multivariate models or the implementation of fixed (batch, herd…)

or random effects (Stygar and Kristensen, 2016). Another property of DLM is to produce one-step-

ahead forecasts of one or several variables especially to provide early warning to the farmer when

forecast error increases (Jensen et al., 2017). Dynamic linear models look to be powerful tools for

analyzing time-series variables.

Estimation of genetic variance in allocation coefficient α_t

We assumed that the "desired allocation" of net energy to growth was driven by two components:

the animal's genetic potential and its degree of maturity. In the first step, the objective was to

estimate the genetic variance in allocation coefficient α as affected by degree of maturity, which

evolves with the age of the pig. To achieve this, we used a RR model to estimate the genetic

variance α_t and the slope of allocation coefficient to growth over time for each individual. Random

regression using orthogonal polynomials models have been widely used in genetics, for example to

model feed intake or RFI in pigs or in rabbits (David et al., 2015; Shirali et al., 2017). The random

regression of order one was chosen to fit the additive genetic and permanent environmental effects,

there was no significant improve of the model, based on LRT test, with polynomials of higher

order. If the end of the measurement period had been at a weight closer to the maturity weight, a

quadratic random regression would probably be more suitable (Lewis and Emmans, 2020).

The trait α_t, describing the allocation of net energy in growth during fattening period, has moderate

heritabilities in the same range as those estimated for FCR or RFI and was strongly correlated with

them. In a previous study (Lenoir et al., 2022c), the trait considered was the average value of α_t and

not the repeated estimates, the heritability obtained was lower (0.16±0.05) but was estimated from a

different dataset. For the trait RFI, the study of David et al. (2021) showed heritabilities ranging

from 0.19±0.06 to 0.28±0.06, using a RR model with weekly estimation over 10 weeks in pigs.

Genetic parameters for LSR and production traits

The heritability of the trait LSR, which characterizes the environmental variance of α_t, was low but

non null. Generally, the heritability of environmental variance is lower than 0.10 (Mulder et al.,

2007). This estimate for LSR was in the same range as those published on different traits but with a

similar REML method such as: 0.012±0.004 for rabbits birth weight (Garreau et al., 2008),

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

chicken body weight (Mulder et al., 2009). Other studies have been based on the analysis of the log-

transformed variance (LnVar) of residuals resulting from a modeling of one time-series variable.

This LnVar trait seems to have higher heritabilities than LSR: from 0.20 to 0.24 for milk production

(Poppe et al., 2021) or from 0.10 to 0.12 for egg production (Bedere et al., 2022). Some authors

have used the double hierarchical generalized linear model (DHGLM) allowing in the same

structural model to estimate the mean of the trait and its residual variance (Rönnegård et al., 2010).

In order to perform the multi-trait analysis, we chose to use a 2-step approach rather than the

DHGLM. In theory, the DHGLM model would make it possible to estimate a residual genetic

variance close to the results obtained by our two-step approach. However, it is much more complex

mathematically and has convergence issues, making it difficult to use in an operational breeding

program (Berghof et al., 2019a).

Heritability estimates for ADG and RFI were consistent with those reported in literature for Pietrain

or Large-White pigs raised in similar environmental conditions, which varied from 0.33 ±0.03 to

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

traits (BF100 and LD100), heritabilities were also consistent with the values estimated by

Sourdioux et al. (2009) and Saintilan et al. (2013) in the Pietrain breed (BF100: 0.38 to 0.48;

LD100: 0.25 to 0.34). Our estimate of heritability for FCR was lower than the heritabilities

presented by Saintilan et al. (2013), Gilbert et al. (2017) and Déru et al. (2020), which varied from

0.30 ±0.0 to 0.47 ±0.08.

Genetic correlations between robustness and production traits

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

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

selection for low RFI could impact the ability of the animals to modify their allocation of energy to

other functions to cope with environmental challenges (Gilbert et al., 2017). This antagonism

between short-term efficiency and resilience has been put forward by Friggens et al. (2017). In this

situation, it would seem that there is a compromise that does not make it possible to increase

robustness relatively easily without loss of selection response in feed efficiency. In contrast, several

studies have shown through divergent selection experiments on RFI, that animals from Low RFI

line (LRFI) adapted better to environmental challenges or at least are not disadvantaged compared

to animals from High RFI line (HRFI). Chatelet et al. (2018) showed that the health, growth

performance and feed intake of animals from the LRFI line were less impacted than those of

animals born from the HRFI line under poor hygienic conditions. In the same selection experiment,

the risk of being culled between 70 days of age and slaughter was 1.8 times less in the LRFI line

compared to the HRFI line (Gilbert et al., 2017). In another experience of selection Dunkelberger et

al. (2015) suggested that pigs for LRFI were more robust to PRRSV challenges; their growth was

less affected and they was less affected. These results seem to contradict the resource allocation

theory and the genetic correlation estimated in our study. This study was carried out on Pie NN line,

a sire line, and the different selection experiments on RFI were realized with animals from Large-

White (or Yorkshire), a dam line. The Pietrain sire line had been created and selected for several

generations on objectives of improving feed efficiency, growth and carcass characteristics,

potentially to the detriment of the other traits, such as robustness. Due to these characteristics and

orientations, it can be assumed that there is a different allocation pattern between these lines.

Genetic correlations between robustness and BF100 were slightly unfavorable. We can suppose that

the capacity to be robust could be associated with more important body reserves allowing the

animal to face perturbations.

Relation between EBV LSR classes and collected phenotypes

Our study shows that model longitudinal energetic allocation to growth offers the opportunity to

develop a proxy of robustness that is heritable. Further, this proxy has to meet the expectations of

pig farmers, that is to say, it should identify animals that faced to environmental disturbances and

were present for testing in good health and with the least amount of medical injections. The analysis

of the relationship between EBV LSR quartiles and phenotypes routinely collected on farms shows

the most favorable situation for the most robust animals, *i.e.*, those from the quartile with the

weakest EBV LSR (Q1). Including LSR in the breeding goal would be an opportunity to improve

the robustness qualities of Pie NN line for the fattening period, in spite of the low heritability of

LSR. However, these results are evaluated over a short period of animal's life, it would be

appropriate to investigate the effects of a selection on the LSR trait over the whole lifespan of

related animals (dam, sire, pure or crossbred offspring). In a following step, it could be relevant to

study the link between the LSR trait and the reproductive performances of boars (spermatic

production) or females (fertility, productive longevity, survival).

Environmental conditions

This studied was carried out in a higher biosecurity environment than regular farms, related to the

fact that a breeding company cannot take any risks with a purebred nucleus. The other

environmental conditions (feed characteristics, barn design, density…) were close to those found in

production farms in France, that is, designed to minimize exposure to environmental challenges.

When designing the selection conditions there is a need to balance between conditions that allow

full expression of performance and meet sanitary requirements versus conditions that favor

expression of robustness. Even though these environments are qualified as favorable, the animals

are subjected to stresses which can be chronic (social stress, heat wave). Rear animals under

challenging conditions seems to allow better phenotyping of the robustness of the animals (Gunia et

al., 2018). The difficulty of having conditions to evaluate robustness while evaluating production

potential could be partly overcome by the use of short-term challenges, such as feeding challenges.

Indeed, offspring of these purebred pigs, selected in one type of environment, are likely to be reared

in harder and more variable environments impacting robustness expression. This relationship

between the robustness expression and diverse rearing conditions cannot be dissociated from

Genotype x Environment (GxE) interaction (Falconer and Mackay, 1996). This interaction that may

cause reranking of sires, has a greater impact on traits based on variances than on traits based on

means (Bedere et al., 2022). The acquisition of data on related animals reared in farms newly

equipped with AFS makes it possible to consider evaluating the effects of the GxE interaction.

In this study, we proposed an approach for characterizing the robustness through the variability in

the allocation. However, when studying the allocation pattern, it is important to also assess the

acquisition trajectory (van Noordwijk and de Jong, 1986; Friggens et al., 2017). In a routine

selection approach, it would be relevant to add to the LSR trait, a trait making it possible to

characterize the robustness on acquisition

Conclusions

The trait LSR could be interpreted as an indicator of the response of the animal to

perturbations/stress, that is to say a robustness proxy. This study shows that LSR has a low

heritability but that it is possible to set up a selection on this trait. We found that this trait is

favourably genetically correlated with a growth trait (ADG) and unfavourably with feed efficiency

traits (FCR and RFI). Estimation of the economic value of LSR trait is a key issue before adding

this trait in breeding goals. Furthermore, improving robustness qualities also meets societal

expectations, the economic value of which is difficult to quantify.

List of abbreviations

α_t: daily energetic allocation coefficient to growth

ADG: average daily growth

AFS: automatic feeding system

AMW: average metabolic weight

BF: backfat thickness

BF100: backfat thickness estimated at 100 kg liveweight

BW: body weight

CNEA : cumulative net energy available for growth

CW: cumulative weight gain

DFI: daily feed intake

DLM: dynamic linear model

EBV: estimated breeding value

EI: net energy intake

FCR: feed conversion ratio

FI: feed intake

IBW: initial body weight

LD: longissimus dorsi thickness

LD100: longissimus dorsi thickness estimated at 100 kg liveweight

LSR: log transformed squared residuals, robustness indicator

MR: net energy maintenance requirement

NEA: net energy available for growth

PDFI: potential average daily feed intake

Pie NN: Piétrain NN Français free from halothane-sensitivity

RFI: residual feed intake

TBW: body weight at individual testing

Declarations

Ethics approval and consent to participate

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

Consent for publication

Not applicable

Availability of data and materials

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

Competing interests

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

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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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References

Bedere, N., Berghof, T.V.L., Peeters, K., Pinard-van der Laan, M.-H., Visscher, J., David, I., Mulder, H.A.,
2022. Using egg production longitudinal recording to study the genetic background of resilience in
purebred and crossbred laying hens. Genet. Sel. Evol. 54, 26. https://doi.org/10.1186/s12711-022-
00716-8
Berghof, T.V.L., Bovenhuis, H., Mulder, H.A., 2019a. Body Weight Deviations as Indicator for Resilience in
Layer Chickens. Front. Genet. 10.
Berghof, T.V.L., Poppe, M., Mulder, H.A., 2019b. Opportunities to Improve Resilience in Animal Breeding
Programs. Front. Genet. 9, 692. https://doi.org/10.3389/fgene.2018.00692
Chatelet, A., Gondret, F., Merlot, E., Gilbert, H., Friggens, N.C., Le Floc'h, N., 2018. Impact of hygiene of
housing conditions on performance and health of two pig genetic lines divergent for residual feed
intake. Animal 12, 350–358. https://doi.org/10.1017/S1751731117001379
David, I., Huynh Tran, V.-H., Gilbert, H., 2021. New residual feed intake criterion for longitudinal data.
Genet. Sel. Evol. 53, 53. https://doi.org/10.1186/s12711-021-00641-2
David, I., Ruesche, J., Drouilhet, L., Garreau, H., Gilbert, H., 2015. Genetic modeling of feed intake. J. Anim.
Sci. 93, 965–977. https://doi.org/10.2527/jas.2014-8507
Déru, V., Bouquet, A., Hassenfratz, C., Blanchet, B., Carillier-Jacquin, C., Gilbert, H., 2020. Impact of a high-
fibre diet on genetic parameters of production traits in growing pigs. animal 14, 2236–2245.
https://doi.org/10.1017/S1751731120001275
Dunkelberger, J.R., Boddicker, N.J., Serão, N.V.L., Young, J.M., Rowland, R.R.R., Dekkers, J.C.M., 2015.
Response of pigs divergently selected for residual feed intake to experimental infection with the
PRRS virus. Livest. Sci. 177, 132–141. https://doi.org/10.1016/j.livsci.2015.04.014
Falconer, D.S., Mackay, T.F.C., 1996. Introduction to Quantitative Genetics, 4th ed. Pearson Education
Limited, Essex, UK.
Friggens, N.C., Blanc, F., Berry, D.P., Puillet, L., 2017. Review: Deciphering animal robustness. A synthesis to
facilitate its use in livestock breeding and management. Animal 11, 2237–2251.
https://doi.org/10.1017/S175173111700088X

Garreau, H., Bolet, G., Larzul, C., Robert-Granié, C., Saleil, G., SanCristobal, M., Bodin, L., 2008. Results of four generations of a canalising selection for rabbit birth weight. Livest. Sci. 119, 55–62. https://doi.org/10.1016/j.livsci.2008.02.009

Gilbert, H., Billon, Y., Brossard, L., Faure, J., Gatellier, P., Gondret, F., Labussière, E., Lebret, B., Lefaucheur, L., Le Floch, N., Louveau, I., Merlot, E., Meunier-Salaün, M.-C., Montagne, L., Mormede, P., Renaudeau, D., Riquet, J., Rogel-Gaillard, C., van Milgen, J., Vincent, A., Noblet, J., 2017. Review: divergent selection for residual feed intake in the growing pig. Animal 11, 1427–1439. https://doi.org/10.1017/S175173111600286X

Gilmour, A.R., Gogel, B.J., Cullis, B.R., Thompson, R., 2009. ASREML user guide release 3.0 [WWW Document]. URL https://www.vsni.co.uk/downloads/asreml/release3/UserGuide.pdf (accessed 8.4.21).

Gunia, M., David, I., Hurtaud, J., Maupin, M., Gilbert, H., Garreau, H., 2018. Genetic Parameters for Resistance to Non-specific Diseases and Production Traits Measured in Challenging and Selection Environments; Application to a Rabbit Case. Front. Genet. 9, 467. https://doi.org/10.3389/fgene.2018.00467

Hansen, J., Sato, M., Ruedy, R., 2012. Perception of climate change. Proc. Natl. Acad. Sci. 109, E2415. https://doi.org/10.1073/pnas.1205276109

Henderson, C.R., 1977. Best Linear Unbiased Prediction of Breeding Values Not in the Model for Records. J. Dairy Sci. 60, 783–787. https://doi.org/10.3168/jds.S0022-0302(77)83935-0

Homma, C., Hirose, K., Ito, T., Kamikawa, M., Toma, S., Nikaido, S., Satoh, M., Uemoto, Y., 2021. Estimation of genetic parameter for feed efficiency and resilience traits in three pig breeds. Animal 15, 100384. https://doi.org/10.1016/j.animal.2021.100384

Institut Technique du Porc, 2004. La sélection porcine collective en France, ITP. ed. Paris.

Jensen, D.B., Toft, N., Kristensen, A.R., 2017. A multivariate dynamic linear model for early warnings of diarrhea and pen fouling in slaughter pigs. Comput. Electron. Agric. 135, 51–62. https://doi.org/10.1016/j.compag.2016.12.018

Knap, P., 2005. Breeding robust pigs. Aust. J. Exp. Agric. 45, 763–773. https://doi.org/10.1071/EA05041

Kyriazakis, I., Tolkamp, B.J., Hutchings, M.R., 1998. Towards a functional explanation for the occurrence of anorexia during parasitic infections. Anim. Behav. 56, 265–274. https://doi.org/10.1006/anbe.1998.0761

Labroue, F., Maignel, L., Sellier, P., Noblet, J., 1999. Consommation résiduelle chez le porc en croissance alimenté à volonté Méthode de calcul et variabilité génétique, in: Journ. Rech. Porcine Fr. pp. 167–174.

Lenoir, G., Flatres-Grall, L., Friggens, N.C., David, I., 2022a. Robustness scores in fattening pigs based on routinely collected phenotypes: determination and genetic parameters. J. Anim. Sci. 100, skac157. https://doi.org/10.1093/jas/skac157

Lenoir, G., Kashefifard, K., Chesnet, C., Flatres-Grall, L., Muñoz-Tamayo, R., 2022b. Dynamic data of body weight and feed intake in fattening pigs, and the determination of energetic allocation factors using a dynamic linear model. Anim. - Open Space 1, 100014. https://doi.org/10.1016/j.anopes.2022.100014

Lenoir, G., Muñoz-Tamayo, R., Flatres-Grall, L., David, I., Friggens, N.C., 2022c. Towards the characterisation of animal robustness by dynamic energy allocation indicators in fattening pigs. Presented at the WCGALP 2022, Rotterdam. Netherlands.

Lewis, R.M., Emmans, G.C., 2020. The relationship between feed intake and liveweight in domestic animals. J. Anim. Sci. 98, skaa087. https://doi.org/10.1093/jas/skaa087

Michel, L., Makowski, D., 2013. Comparison of Statistical Models for Analyzing Wheat Yield Time Series. PLOS ONE 8, 1–11. https://doi.org/10.1371/journal.pone.0078615

Mulder, H.A., Bijma, P., Hill, W.G., 2007. Prediction of Breeding Values and Selection Responses With Genetic Heterogeneity of Environmental Variance. Genetics 175, 1895–1910. https://doi.org/10.1534/genetics.106.063743

631   Mulder, H.A., Hill, W.G., Vereijken, A., Veerkamp, R.F., 2009. Estimation of genetic variation in residual
632   variance in female and male broiler chickens. Animal 3, 1673–1680.
633   https://doi.org/10.1017/S1751731109990668

634   Nguyen-Ba, H., Milgen, J. van, Taghipoor, M., 2020. A procedure to quantify the feed intake response of
635   growing pigs to perturbations. animal 14, 253–260. https://doi.org/10.1017/S1751731119001976

636   Noblet, J., Dourmad, J.-Y., Milgen, J. van, 2016. Etat des lieux et perspectives sur la nutrition du porc.
637   Presented at the 48. Journées de la Recherche Porcine, IFIP - Institut du Porc, Paris, France, pp. 85–
638   96.

639   Noblet, J., Karège, C., Dubois, S., 1991. Influence of growth potential on energy requirements for
640   maintenance in growing pigs, in: Energy Metabolism of Farm Animals, EAAP Publication. EAAP
641   Publication, pp. 107–110.

642   Noblet, J., Karege, C., Dubois, S., van Milgen, J., 1999. Metabolic utilization of energy and maintenance
643   requirements in growing pigs: effects of sex and genotype. J. Anim. Sci. 77, 1208–1216.
644   https://doi.org/10.2527/1999.7751208x

645   Petris, G., Petrone, S., Campagnoli, P., 2009. Dynamic Linear Models with R, Use R. Springer, New York, NY,
646   USA. https://doi.org/10.1007/b135794_1

647   Poppe, M., Mulder, H.A., Veerkamp, R.F., 2021. Validation of resilience indicators by estimating genetic
648   correlations among daughter groups and with yield responses to a heat wave and disturbances at
649   herd level. J. Dairy Sci. 104, 8094–8106. https://doi.org/10.3168/jds.2020-19817

650   Puillet, L., Réale, D., Friggens, N.C., 2016. Disentangling the relative roles of resource acquisition and
651   allocation on animal feed efficiency: insights from a dairy cow model. Genet. Sel. Evol. 48, 72.
652   https://doi.org/10.1186/s12711-016-0251-8

653   Putz, A.M., Harding, J.C.S., Dyck, M.K., Fortin, F., Plastow, G.S., Dekkers, J.C.M., PigGen Canada, 2019. Novel
654   Resilience Phenotypes Using Feed Intake Data From a Natural Disease Challenge Model in Wean-to-
655   Finish Pigs. Front. Genet. 9, 660. https://doi.org/10.3389/fgene.2018.00660

656   Quiniou, N., Dubois, S., Noblet, J., 2000. Voluntary feed intake and feeding behavior of grouphoused
657   growing pigs are affected by ambient temperature and body weight. Livest. Prod. Sci. 63, 245–253.
658   https://doi.org/10.1016/S0301-6226(99)00135-9

659   R Core Team, 2018. R: A Language and Environment for Statistical Computing. R Foundation for Statistical
660   Computing, Vienna, Austria.

661   Rauw, W., 2009. Introduction, in: Resource Allocation Theory Applied to Farm Animal Production. Cabi
662   Publishing, Wallingford, UK, pp. 1–21.

663   Rauw, W., Kanis, E., Noordhuizen-Stassen, E.N., Grommers, F.J., 1998. Undesirable side effects of selection
664   for high production efficiency in farm animals: a review. Livest. Prod. Sci. 56, 15–33.
665   https://doi.org/10.1016/S0301-6226(98)00147-X

666   Revilla, M., Friggens, N.C., Broudiscou, L.P., Lemonnier, G., Blanc, F., Ravon, L., Mercat, M.J., Billon, Y.,
667   Rogel-Gaillard, C., Le Floch, N., Estellé, J., Muñoz-Tamayo, R., 2019. Towards the quantitative
668   characterisation of piglets' robustness to weaning: a modelling approach. Animal 13, 2536–2546.
669   https://doi.org/10.1017/S1751731119000843

670   Revilla, M., Lenoir, G., Flatres-Grall, L., Muñoz-Tamayo, R., Friggens, N.C., 2022. Quantifying growth
671   perturbations over the fattening period in swine via mathematical modelling. Peer Community J. 2.
672   https://doi.org/10.24072/pcjournal.82

673   Revilla, M., Lenoir, G., Flatres-Grall, L., Muñoz-Tamayo, R., Friggens, N.C., 2021. Quantifying growth
674   perturbations over the fattening period in swine via mathematical modelling. bioRxiv
675   2020.10.22.349985. https://doi.org/10.1101/2020.10.22.349985

676   Robson, D.S., 1959. A Simple Method for Constructing Orthogonal Polynomials When the Independent
677   Variable is Unequally Spaced. Biometrics 15, 187–191. https://doi.org/10.2307/2527668

678   Rönnegård, L., Felleki, M., Fikse, F., Mulder, H.A., Strandberg, E., 2010. Genetic heterogeneity of residual
679   variance - estimation of variance components using double hierarchical generalized linear models.
680   Genet. Sel. Evol. 42, 8. https://doi.org/10.1186/1297-9686-42-8

Saintilan, R., Merour, I., Brossard, L., Tribout, T., Dourmad, J.-Y., Sellier, P., Bidanel, J.P., Milgen, J. van,
Gilbert, H., 2013. Genetics of residual feed intake in growing pigs: Relationships with production
traits, and nitrogen and phosphorus excretion traits. J. Anim. Sci. 91, 2542.
https://doi.org/10.2527/jas.2012-5687
SanCristobal-Gaudy, M., Elsen, J.-M., Bodin, L., Chevalet, C., 1998. Prediction of the response to a selection
for canalisation of a continuous trait in animal breeding. Genet. Sel. Evol. 30, 423–451.
https://doi.org/10.1186/1297-9686-30-5-423
SAS Institute Inc., 2013. SAS/STAT® 13.1 User's Guide.
Sell-Kubiak, E., Knol, E.F., Lopes, M., 2022. Evaluation of the phenotypic and genomic background of
variability based on litter size of Large White pigs. Genet. Sel. Evol. 54, 1.
https://doi.org/10.1186/s12711-021-00692-5
Shirali, M., Strathe, A.B., Mark, T., Nielsen, B., Jensen, J., 2017. Joint analysis of longitudinal feed intake and
single recorded production traits in pigs using a novel Horizontal model1. J. Anim. Sci. 95, 1050–
1062. https://doi.org/10.2527/jas.2016.0606
Sourdioux, M., Lenoir, G., Guery, L., Bahon, D., Tribout, T., Bidanel, J.P., 2009. Estimation des paramètres
génétiques pour des critères de croissance et carcasse en race Piétrain et en lignée composite
Piétrain négative halothane., in: Journ. Rech. Porcine Fr.
Stearns, S.C., 1992. The Evolution of Life Histories. Oxford University Press, Oxford, UK.
Stygar, A.H., Kristensen, A.R., 2016. Monitoring growth in finishers by weighing selected groups of pigs - A
dynamic approach. J. Anim. Sci. 94, 1255–1266. https://doi.org/10.2527/jas.2015-9977
van Milgen, J., Noblet, J., 2003. Partitioning of energy intake to heat, protein, and fat in growing pigs. J
Anim Sci 81, E86–E93.
van Milgen, J., Noblet, J., Valancogne, A., Dubois, S., Dourmad, J.Y., 2005. InraPorc⬜: un modèle pour
analyser les performances et évaluer les stratégies alimentaires chez le porc en croissance.
Presented at the Journées Recherche Porcine, Paris, France, pp. 291–298.
van Noordwijk, A., de Jong, G., 1986. Acquisition and Allocation of Resources: Their Influence on Variation
in Life History Tactics. Am. Nat. 128, 137–142. https://doi.org/10.1086/284547
West, M., Harrison, J., 1997. Bayesian forecasting and dynamic models, 2nd ed. Springer-Verlag, New York,
NY, USA.

Figures

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

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

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

727
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).
735

Tables

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
IBW (kg)	25745	33.8	7.8
TBW (kg)	25365	103.7	11.1
ADG (kg/d)	25322	0.977	0.109
FCR (kg/kg)	8675	2.25	0.21
DFI (kg/d)	8675	2.19	0.29
RFI (kg/d)	8675	-0.005	0.169
BF100 (mm)	25323	7.66	1.19
LD100 (mm)	25320	68.26	6.34
α_t **(kg/MJ)**	5848 / 405104	0.099	0.027
e_t **(kg/MJ)**	5848 / 405104	0	0.0096
LSR	5848 / 405104	-12.62	2.50

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

Table 2. Estimates of heritability (h²), common litter effect ratio (c²), permanent environmental effect ratio (p²) and phenotypic variance (Vp) for the traits recorded (± standard error)

Trait[1]	h²	c²	p²	Vp
BF100	0.45 ±0.02	0.04 ±0.01	/	1.02 ±0.02
LD100	0.29 ±0.02	0.04 ±0.01	/	15.78 ±0.20
ADG	0.37 ±0.02	0.06 ±0.01	/	0.01 ±0.0001
FCR	0.27 ±0.03	0.04 ±0.01	/	0.0222 ±0.0007
RFI	0.29 ±0.03	0.04 ±0.01	/	0.034 ±0.0006
LSR	0.05 ±0.01	0.004 ±0.004	0.22 ±0.01	5.56 ±0.033

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

Table 3. Estimates of genetic correlations (r²a ± standard error) between robustness trait (LSR) and production traits

Trait[1]	LD100	ADG	FCR	RFI	LSR
BF100	-0.13 ±0.05	0.43 ±0.04	0.50 ±0.05	0.32 ±0.06	-0.19 ±0.07
LD100		-0.24 ±0.05	-0.09 ±0.05	-0.08 ±0.07	0.02 ±0.09
ADG			0.52 ±0.06	0.61 ±0.05	-0.71 ±0.03
FCR				0.90 ±0.02	-0.76 ±0.04
RFI					-0.83 ±0.06

 [1]BF100= 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

Additional information

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

	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