



HAL
open science

Genetic determinism of sensitivity to environmental challenges using daily feed intake records in three lines of pigs

Tomasi Tusingwiire, Carolina Garcia-Baccino, Céline Carillier, Bruno Ligonesche, Catherine Larzul, Zulma Vitezica

► To cite this version:

Tomasi Tusingwiire, Carolina Garcia-Baccino, Céline Carillier, Bruno Ligonesche, Catherine Larzul, et al.. Genetic determinism of sensitivity to environmental challenges using daily feed intake records in three lines of pigs. *Journal of Animal Science*, 2024, 10.1093/jas/skae330 . hal-04782881

HAL Id: hal-04782881

<https://hal.science/hal-04782881v1>

Submitted on 8 Jan 2025

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



Distributed under a Creative Commons Attribution - NonCommercial 4.0 International License



Genetic determinism of sensitivity to environmental challenges using daily feed intake records in three lines of pigs

Tomasi Tusingwiire,^{†,1}  Carolina Garcia-Baccino,[‡] Céline Carillier-Jacquin,[†] Bruno Ligonesche,[‡] Catherine Larzul,[†] and Zulma G. Vitezica[†]

[†]GenPhySE, Université de Toulouse, INRAE, ENVT, Castanet-Tolosan, France

[‡]SAS NUCLEUS, Le Rheu, France

¹Corresponding author: tomasi.tusingwiire@inrae.fr

Abstract

In pig breeding, environmental challenges can affect the welfare and productivity of animals. Resilient animals have the capacity to be minimally affected by these environmental challenges. Understanding the genetic basis of sensitivity to these environmental challenges is crucial for selecting more resilient animals, thereby enhancing welfare and productivity. The aims of this study were to 1) estimate the probability of the occurrence of an unrecorded environmental challenge on a given day using daily feed intake (DFI) data and 2) evaluate the genetic determinism of environmental sensitivity in three pig lines bred in real selection conditions. Data comprised of 100,799, 186,247, and 304,826 DFI records from 1,618, 2,517, and 3,788 Landrace (LA), Large White (LW), and Piétrain (PI) male pigs, respectively. The pedigree included 3,730, 5,649, and 9,293 animals for LA, LW, and PI, respectively. The probabilities of an unrecorded environmental challenge on a given day were estimated via a mixture model. The probabilities (P) of being “high coefficient of variation days” were then taken as reference and used in genetic analysis as an environmental descriptor to describe the environment. DFI records were analyzed using two linear models: a linear reaction norm animal model (RNAM) and the animal model. (Co)variance components were estimated using average-information restricted maximum likelihood (AI-REML). The means of the probabilities of the occurrence of an environmental challenge for LA, LW, and PI were 0.24, 0.10, and 0.22, respectively, indicating that the probability of an environmental challenge was low for most of the days. The genetic correlations between the intercept and the slope obtained from the RNAM for LA, LW, and PI were -0.52 , 0.06 , and -0.36 , respectively. These findings suggest that selecting hypothetically for decreased DFI in nonstressful conditions would result in pigs with increased DFI in stressful conditions in the LA and PI lines, whereas it would have a minor impact on the environmental sensitivity of LW. The proportion of resilient animals for LA, LW, and PI was 75.0, 74.2, and 72.2%, respectively, implying that most of the animals were resilient. The study demonstrated that the slope of DFI is heritable and can effectively be used as an indicator of sensitivity to environmental challenges. These results are valuable in improving the resilience of livestock species to environmental challenges through genetic selection.

Lay Summary

Selecting resilient animals, those minimally affected by disturbances or able to quickly recover, is vital for improving pig welfare and productivity. While pigs in selection farms benefit from monitored and more stable environmental conditions, they still face potential challenges that are unrecorded and of unknown origin. Hence, resilience in pigs remains important. Using daily feed intake data, we estimated the probability of occurrence of an unrecorded environmental challenge and evaluated the genetic determinism of sensitivity to these challenges. In our study, the probability of being a stressful day was low for all the studied pig lines. Most animals in all the lines were less sensitive to environmental challenges. These results can be utilized in the genetic selection of resilient animals.

Key words: environmental sensitivity, genetic correlation, probability, reaction norm model, unrecorded challenges

Abbreviations: ACF, automatic concentrate feeder; AM, animal model; BV, breeding value; CG, contemporary groups; DFI, daily feed intake; EBV, estimated breeding values; LA, Landrace; LW, Large White; PI, Piétrain; p , probability; RNM, reaction norm model; RNAM, reaction norm animal model; RFID, radio frequency identification tag

Introduction

Growing pigs face environmental variations, such as infectious diseases, management practices, and interactions with other animals, to which they may have to adapt (Knap, 2005; Nguyen-Ba et al., 2020). The impacts of these perturbations on an animal's performance can be observed in real production conditions, even though they are not always recorded, and their origin is unknown (Nguyen-Ba et al., 2020). They can significantly affect their physiological, behavioral, and

affective states, resulting in reduced productivity, poor health, and reduced welfare; hence, animals must constantly acclimatize to the changing environments (Colditz and Hine, 2016). Therefore, resilience in pigs remains important. Resilience can be defined as the capacity of the animal to be minimally affected by disturbances or to rapidly return to the state that pertained before exposure to the disturbances (Colditz and Hine, 2016). Therefore, animals that are highly resilient have

Received May 31, 2024 Accepted October 25, 2024.

© The Author(s) 2024. Published by Oxford University Press on behalf of the American Society of Animal Science.

This is an Open Access article distributed under the terms of the Creative Commons Attribution-NonCommercial License (<https://creativecommons.org/licenses/by-nc/4.0/>), which permits non-commercial re-use, distribution, and reproduction in any medium, provided the original work is properly cited.

For commercial re-use, please contact reprints@oup.com for reprints and translation rights for reprints. All other permissions can be obtained through our RightsLink service via the Permissions link on the article page on our site—for further information please contact journals.permissions@oup.com.

the ability to reach their genetic production potential under challenging production conditions. This is because resilient animals are more likely to cope with any given environmental challenges, and over sufficiently long periods of time, they have higher chances of survival than less resilient animals (Friggens et al., 2022).

Measuring resilience requires longitudinal data to quantify the extent to which the environmental challenge evokes a response from the animal and the rate at which it subsequently recovers (Friggens et al., 2022). The development of precision livestock farming technologies and their growing adoption in a large number of farms (Lora et al., 2020) has made it possible to continuously record longitudinal data at the individual level on performance and behavior, including feed consumption, live weight, rumination activity levels, milk yield, body temperature, and body condition score (Friggens et al., 2022). For example, automatic feeders have recently become popular for collecting daily feed intake (DFI) data, making it possible to evaluate the day-to-day fluctuations in feed, which could be used as a measure of a pig's response to disturbances or challenges (Putz et al., 2019; Nguyen-Ba et al., 2020; Homma et al., 2021; Gorssen et al., 2023).

In pig breeding, sire lines such as Piétrain (PI) are predominantly selected to improve feed efficiency and meat quality traits, while maternal lines such as Large White (LW) and Landrace (LA) are primarily selected to improve reproductive and maternal traits (Homma et al., 2021). Differences in breeding programs can lead to distinct responses to environmental challenges among these breeds, which might be reflected in differences in feeding behaviors such as DFI. For example, of the three pig breeds, LA has the highest DFI followed by LW, while PI has the lowest DFI (Labroue et al., 1997, 1999; Baumung et al., 2006; Fernández et al., 2011). It is important to note that variations in DFI within breeds exist. Large changes in DFI within a restricted period of time may indicate that the pig is less resilient and more susceptible to environmental stressors than pigs with smaller fluctuations under the same conditions (Nguyen-Ba et al., 2020). Since animal welfare and resilience are becoming indispensable in modern pig breeding, selection methods that can improve pig resilience and welfare are needed (Knap, 2020; Kavlak and Uimari, 2024).

One powerful tool for studying resilience in animal populations is the reaction norm model (RNM). In an RNM, the breeding value (BV) of each animal is modeled as a function of a continuous environmental descriptor (Waters et al., 2022). There are two BV per animal: the intercept and the reaction norm slope. The BV of the intercept represents an individual's genetic merit in nonstressful environments (environment-independent), whereas the reaction norm slope measures how much an individual's phenotype fluctuates across different environmental conditions, indicating its environmental sensitivity or plasticity (Shariati et al., 2007; Chen et al., 2021; Cheng et al., 2022; Waters et al., 2022; Silva Neto et al., 2023). By quantifying the genetic variation in environmental sensitivity, breeders can identify animals or genetic lines that are more resilient to environmental fluctuations, thus facilitating the development of more robust and adaptable livestock populations.

Recently, Garcia-Baccino et al. (2021) presented a data-driven method to estimate the probability that, on a given day, an unrecorded environmental challenge occurred, using a mixture model of phenotypic variances. These probabilities were then used as an environmental descriptor in an RNM to

evaluate the genetic determinism of resilience to environmental challenges. The authors used the method in a dataset of Romane male lambs born on an experimental farm with DFI records. However, to date, the method has only been tested under experimental conditions. The aims of this study were to 1) estimate the probability of occurrence of an unrecorded environmental challenge on a given day using DFI data and 2) evaluate the genetic determinism of environmental sensitivity in three commercial pig lines bred in real selection conditions.

Materials and Methods

Data used in this study were provided by SAS NUCLEUS (Le Rheu, France). Animal care and use committee approval was not obtained for this study because the data were obtained from an existing database.

Animals and phenotypes

Data utilized in the analysis were collected from LA, LW, and PI male pigs. LA and LW were each raised separately on one selection farm, whereas PI pigs were raised on three different selection farms, each with 1,596 animals on average. Over a 3-yr period (from 2021 to 2023), for each batch (a group of animals of the same age and weight), a cohort of 47 (ranging from 23 to 55), 67 (ranging from 49 to 79), and 65 (ranging from 48 to 76) male pigs for LA, LW, and PI, respectively, were continuously recorded for feed consumption. For each batch, the animals were kept in groups of 10 to 14 animals within each pen. Each pen was equipped with an automatic concentrate feeder (ACF), and each animal was equipped with a unique radio frequency identification tag. The animals were automatically identified by the ACF at each time they approached the feeder and the amount of feed consumed was recorded, defining a "visit." A 7-d "adaptation" period was required for animals to get used to the new environment and learn how to use the ACF. After the adaptation period, animals were recorded for an average of 63 d (ranging from 53 to 68 d), 74 (ranging from 61 to 79 d), and 64 (ranging from 38 to 76 d) for LA, LW, and PI, respectively, starting at approximately 30 to 100 kg body weight. All the pigs were fed ad libitum during the whole period. In addition, all the pigs had free access to water for the whole period. Records from the adaptation period and those that had technical errors (e.g., data recording and transfer problems) were removed from the analysis.

After quality control, the number of visits across all batches of each breed is presented in Table 1. For each animal and each day, feed intakes per visit were summed up to obtain the DFI (kg/day, Table 1). Since data were collected on growing animals, the natural logarithm of the daily coefficient of variation (CV) of DFI was used to quantify variability since DFI (and its variance) increases as an animal grows bigger over time. The CV of DFI was calculated across animals on a given day within each batch and breed. This resulted in a total of 1,502, 3,944, and 4,741 d for LA, LW, and PI, respectively, across all the batches within each breed. For the genetic analysis, pedigrees were extracted from the collective National French pig programs and were tracked back for six generations for each breed (Table 1).

Estimation of probabilities of the occurrence of an unrecorded environmental challenge

The probabilities of the occurrence of an unrecorded environmental challenge on a given day were estimated via a mixture

Table 1. Data structure for visit records (Vi) and DFI (kg/day) in three pig lines¹

Line	Animals in datasets	Number of visits	Mean Vi ² (SD)	Number of DFI records	Mean DFI (SD)	Number of batches	Animals in pedigree
LA	1,618	2,750,259	27.0 (20.19)	100,799	2.50 (0.68)	24	3,730
LW	2,517	9,901,187	53.2 (24.12)	186,247	2.43 (0.75)	53	5,649
PI	4,788	6,219,930	20.4 (15.23)	304,826	2.36 (0.60)	74	9,293

¹Landrace (LA), Large White (LW), and Piétrain (PI).

²MeanVi = mean visit per pig per day.

model using the method proposed by (Garcia-Baccino et al., 2021). The analyses were performed per batch in each breed to avoid the variability related to the fact that there were animals of varying ages (different batches) on the same day. This ensured homogeneity among animals within the batch, which is required by the method. The *normalmixEM* function from the R package *mixtools* (Benaglia et al., 2009) was used to fit the Gaussian mixture model. For instance in PI, the Gaussian mixture model was implemented to the data consisting of 304,826 values of log(CV) of DFI registered for 4,741 d during the 3 yr. To confirm a mixture of two components, the *emtest.norm* function from the *MixtureInf* R package was used.

We also calculated the posterior probabilities for each day (within each batch) belonging to the first or second component of the mixture distribution. Days with a high probability of belonging to the first component were “low CV days,” whereas days with a high probability of belonging to the second component were “high CV days.” Days with a high probability of having high CV (stressful days) showed high variability in DFI and are most likely related to the occurrence of an unrecorded environmental challenge (Garcia-Baccino et al., 2021). The probabilities (p) of being “high CV days” were taken as a reference and used in genetic analysis as a continuous covariable.

Estimation of variance components

Phenotypes (DFI) were analyzed using univariate best linear unbiased prediction models for each breed. Two linear models were considered: a reaction norm animal model (RNAM), including the probabilities that at a given date, an unrecorded environmental challenge occurred, as a covariate (environmental descriptor) (Garcia-Baccino et al., 2021) and an animal model (AM) without reaction norm terms. The probabilities ranged from a nonchallenging environment ($p = 0$) to a challenging one ($p = 1$). According to (Dekkers, 2021), to use RNAM, two conditions must be met: 1) a quantitative measure of environmental quality and 2) a functional relationship between the environmental variable and the trait of interest. Both, the trait (DFI) and the environmental descriptor (p , the probability of occurrence of an environmental challenge) used in this study satisfy these conditions. The model was described as:

$$y_{ijk} = CG_i + b_1 day_j + a_{0,k} + a_{1,k} * p_j + pe_{0,k} + pe_{1,k} * p_j + e_{ijk},$$

where y_{ijk} is the observation of DFI (kg) in a given contemporary group i , on day j for animal k . The first term is the contemporary groups defined by concatenating batch and ACF in LA and LW with 136 and 197 levels, respectively, and farm, batch, and ACF in PI (434 levels). The covariate of day j was included to take into account the effect of the growth of pigs on DFI over the recording period; $a_{0,k}$ is the BV of the level (or intercept of DFI) and corresponds to the classical

BV for an animal k , and it is environment-independent; $a_{1,k}$ is the BV for the slope of DFI for animal k and quantifies environmental sensitivity; p_j is the probability that on day j an unrecorded environmental challenge occurred; $pe_{0,k}$ is the permanent environmental effect of animal k (intercept); $pe_{1,k}$ is the permanent environmental effect for p_j (Slope); and e_{ijk} , is the residual effect.

The covariance between a_0 and a_1 were assumed to follow a bivariate distribution with $Var \begin{bmatrix} a_0 \\ a_1 \end{bmatrix} \sim N(0, A \otimes \begin{bmatrix} \sigma_{a0}^2 & \sigma_{a0,a1} \\ \sigma_{a0,a1} & \sigma_{a1}^2 \end{bmatrix})$, and pe_0 and pe_1 were assumed to follow a bivariate distribution with $Var \begin{bmatrix} a_{pe0} \\ a_{pe1} \end{bmatrix} \sim N(0, I \otimes \begin{bmatrix} \sigma_{pe0}^2 & \sigma_{pe0,a1} \\ \sigma_{pe0,a1} & \sigma_{pe1}^2 \end{bmatrix})$, where A is the pedigree-based relationship matrix, I is an identity matrix; \otimes is the Kronecker product; σ_{a0}^2 , σ_{a1}^2 , and $\sigma_{a0,a1}$ are the variance of the intercept of the animal, the variance of the slope for the animal and their covariance, respectively; σ_{pe0}^2 , σ_{pe1}^2 , and $\sigma_{pe0,a1}$ are the variance of the permanent environmental effect of the intercept, the variance of the slope for the permanent environmental effect and their covariance, respectively. The residual variances were assumed to be homogeneous and follow the distribution $e_{ijk} \sim N(0, I\sigma_e^2)$, based on preliminary analysis.

(Co)variance components were estimated using average-information restricted maximum likelihood (AI-REML) implemented in BLUPF90 + software (Lourenco et al., 2022) available at (<https://nce.ads.uga.edu/wiki/doku.php?id=start>). The RNAM and AM models were compared with Akaike's information criterion (AIC; Akaike, 1974). After obtaining the (co)variances, heritability (h_{pj}^2) estimates that change across the environmental condition (i.e., from $p = 0$ to $p = 1$) was calculated as follows: $h_{pj}^2 = \frac{\sigma_{apj}^2}{\sigma_{apj}^2 + \sigma_{pepj}^2 + \sigma_e^2}$, where the total genetic variance for a given level of the covariate p_j was calculated as $\sigma_{apj}^2 = \sigma_{a0}^2 + 2p\sigma_{a0,a1} + p^2\sigma_{a1}^2$. The variance due to the permanent environment was computed in a similar way.

Using the (co)variances estimated from RNAM, the genetic correlation between the BV in a nonchallenging environment ($p = 0$) and the BV at a given probability of occurrence of an environmental challenge (p) was calculated as in (Garcia-Baccino et al., 2021): $r_g(a_0, a_p) = \frac{cov(a_0, a_p)}{\sqrt{var(a_0) var(a_p)}} = \frac{\sigma_{a0}^2 + \sigma_{a0,a1} * p}{\sqrt{\sigma_{a0}^2(\sigma_{a0}^2 + p^2\sigma_{a1}^2 + 2p\sigma_{a0,a1})}}$. If the $r_g = 1$, it indicates the similar ranking of animals in challenging and nonchallenging environments; if the r_g drops below 0.8, there is evidence of reordering of animal rank (Shariati et al., 2007; Hayes et al., 2016; Chen et al., 2021).

From reaction norm analysis, the slope was used as a measure of an animal's sensitivity to environmental challenges (Shariati et al., 2007; Garcia-Baccino et al., 2021). When the slope $a_{1,k} = 0$, it indicates that an animal is not sensitive to the environmental challenge, and when the slope of $a_{1,k}$ is greater or lower than 0,

it indicates that the animal is sensitive to environmental challenges (Garcia-Baccino et al., 2021). Therefore, we used a plasticity scale based on the change in EBV from a nonchallenging environment ($p = 0$) and challenging environmental condition ($p = 1$) (expressed in terms of genetic standard deviation) to classify animals as less sensitive (within 1 SD) and more sensitive to environmental challenges (less or greater than 1 SD).

Results

Descriptive statistics

Table 1 shows the description of the data for the three pig lines. As expected, LA pigs had the highest DFI, followed by LW, and PI had the lowest DFI. On the other hand, LW had the highest number of visits, followed by LA, and PI had the lowest number of visits per day. According to the study by Baumung et al. (2006), LW animals had the highest number of visits to the feeding station, combined with shorter time spent in it and a lower amount of feed consumed per meal. LA pigs had fewer visits per hour, which is compensated for by staying longer in the feeding station and consuming more per visit. PI animals had the lowest number of visits per day, which can be related to this breed's characteristic intake behavior. Similar results were found by Fernández et al. (2011) for the same lines.

Estimation of the probabilities of the occurrence of an unrecorded environmental challenge in pigs

The application of the mixture model to the natural logarithm of the CV of DFI data for LA, LW, and PI allowed for the identification of two different components, each indicat-

ing a subgroup of days (Figure 1). It can be seen on the right side of each histogram that there is a subgroup of days that appear to have values of the log(CV) of DFI that are higher than most of the records on the left side. We used a parametric bootstrap (based on the assumption that the original dataset is a random sample from a specific distribution) to confirm the presence of at least two components in each breed. Figure 1 also shows the two density distributions in each breed: the red for the first component and the green for the second. Notably, these components exhibit heteroscedasticity and distinct means. Specifically, the first component has a mean (SD) of -1.67 (0.15), -1.67 (0.12), and -1.77 (0.16) for LA, LW, and PI, respectively. Conversely, the second component has a mean (SD) of -1.21 (0.23), -1.28 (0.28), and -1.38 (0.40) for LA, LW, and PI, respectively.

The EM approach for mixture models allows us to estimate the probability that each day belongs to the second component of the mixture (probability of being a “high CV day” or a stressful day). These probabilities are presented in Figures 2–4 (for a random sample of nine batches) for LA, LW and PI, respectively. For LA, LW, and PI, the means of these probabilities were 0.24, 0.10, and 0.22, respectively. These values suggest that for most of the days, the probability of the occurrence of an environmental challenge was low. In Figures 2–4, some days had a probability of the occurrence of an environmental challenge greater than 0.9. Across all batches within each breed, the proportion of days with a probability of the occurrence of an environmental challenge greater than 0.9 was around 10% for LA and PI (12.58% in LA and 8.65% in PI) but about a half for LW (4.16%). Most of the days had a probability of

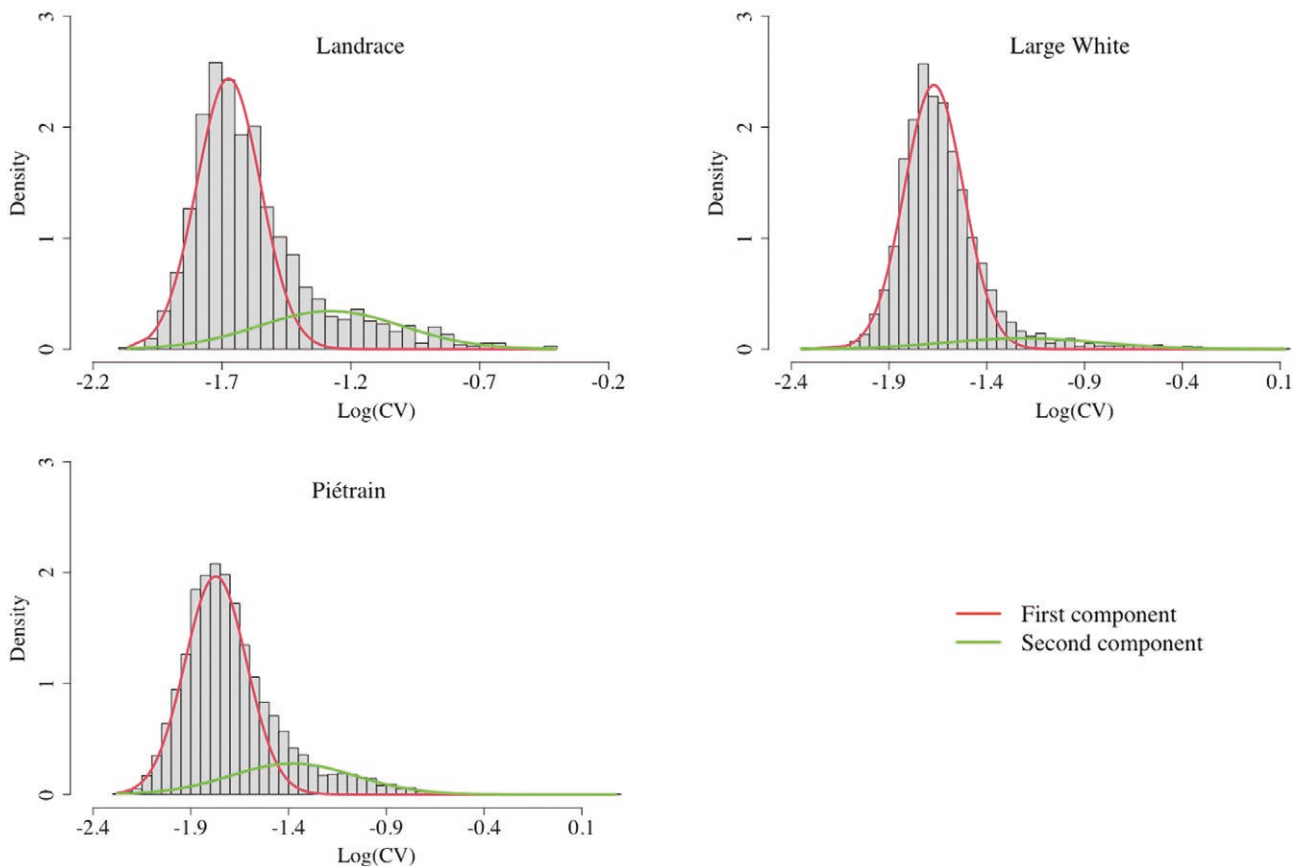


Figure 1. The plot of the log-transformed CV of DFI data of the fitted two-component normal mixture model in three pig breeds.

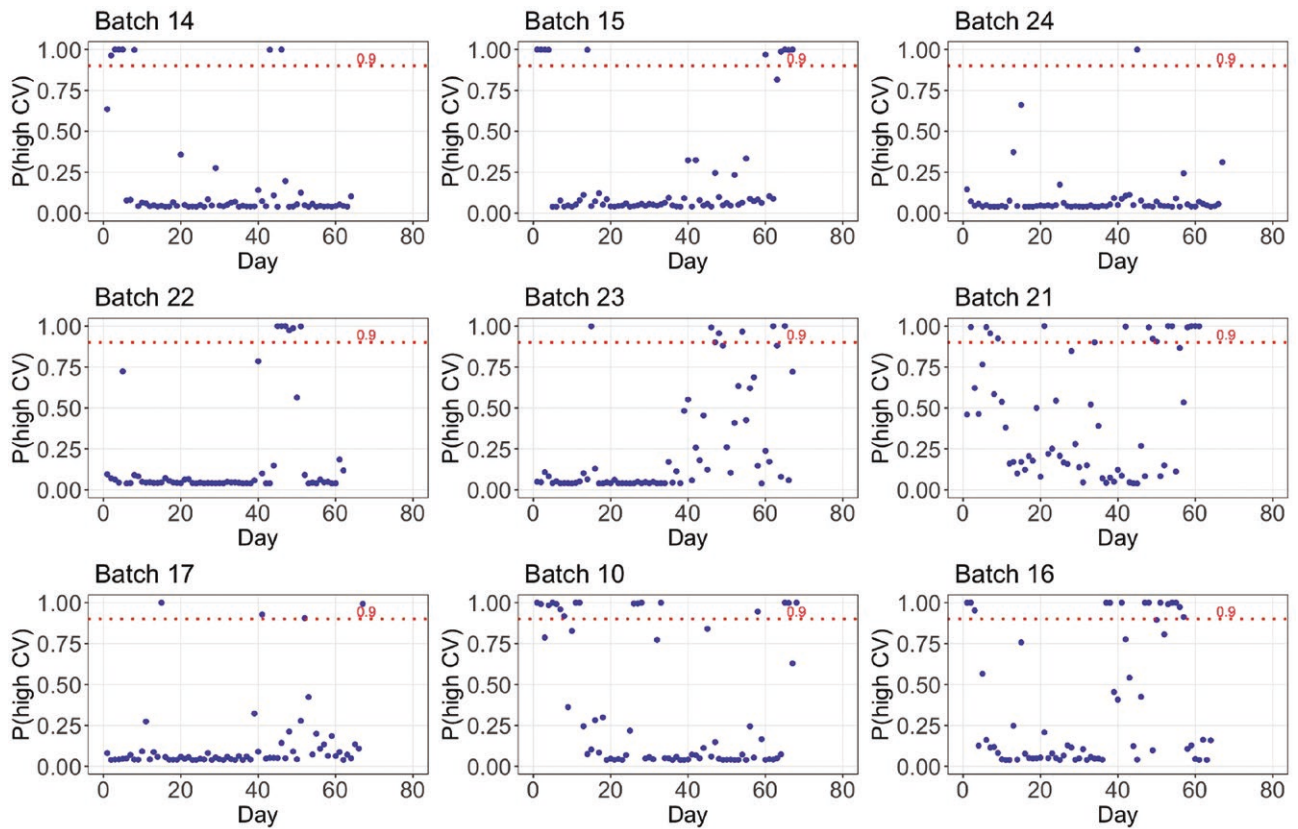


Figure 2. Probabilities of showing a high CV (for a random sample of nine batches) related to the occurrence of an environmental challenge for each day for Landrace.

the occurrence of an environmental challenge lower than 0.25 (75.37% in LA, 91.84% in LW, and 77.30% in PI).

After identifying days with high probabilities of the occurrence of an environmental challenge (probabilities greater than 0.9), we conducted an in-depth follow-up analysis of the history of each batch. We checked whether there were any recorded disturbances (perturbations) on the farm corresponding to these days. It was established that some of the “high CV days” corresponded to management operations such as ear tagging, weighting, ACF repair, movement of animals from one pen to another, leg problems, ACF blockage, and animal illness. However, for some of the days with high probabilities of being stressful (greater than 0.9), there were no explanations, and we assume that these correspond to the occurrence of unrecorded environmental challenges.

When we look at the AIC, model RNAM fitted the data much better than AM (RNAM had the lowest AIC for all lines: 136,961.10 vs. 142,235.09 in LA, 243,377.55 vs. 248,463.25 in LW, and 355,294.19 vs. 368,447.14 in PI). These results justify the inclusion of the probability of the occurrence of an environmental challenge (the $\log(\text{CV of DFI})$) in the genetic analysis.

Genetic correlations

The genetic correlations (and their SE) between the intercept and the slope obtained from the RNAM for all the lines are shown in Table 2. The genetic correlation between the intercept (a_0) and the slope (a_1 , environmental sensitivity) in LA and PI was of moderate magnitude and negative (−0.53 and −0.36, respectively), whereas the genetic correlation was of low magnitude and positive (0.06) in LW. These results suggest that selecting hypothetically for decreased DFI in non-

stressful conditions (the most common ones) would result in pigs with increased DFI in stressful conditions in LA and PI lines. In contrast, in LW, a hypothetical selection for increased or decreased DFI would have a minor impact on the animal’s sensitivity to challenging environmental conditions. These results are in line with those reported in the literature. Schnyder et al. (2001) investigated the genetic variation in feed intake curves of French LA and LW using a random regression model. In their study, they found that the genetic correlations between the intercept and the slope (linear term) were −0.62 and 0.01 for LA and LW, respectively. Hermesesch et al. (2006) found a genetic correlation of 0.07 between the intercept and slope of average DFI of boars from three terminal sire lines recorded in a commercial group-housed environment.

The genetic correlations between EBV in a nonstressful environment ($p = 0$) and EBV at a given probability of the occurrence of an environmental challenge for all the lines are shown in Figure 5. When p is lower than 0.1 (less stressful environments), the genetic correlations are closer to 1 for all the lines and start to decrease as p increases beyond 0.1, reaching their respective minimum values of 0.47, 0.63, 0.17 and for LA, LW, and PI, respectively, at $p = 1$. The genetic correlation across the environmental gradient decreased fastest in PI, followed by LA, with LW exhibiting the slowest decrease. These results suggest that LW was the least sensitive to environmental challenges, whereas PI was the most sensitive to environmental challenges. In addition, low genetic correlations between stressful and nonstressful environments (for instance, in PI) indicate changes in the ranking of animals across different environmental conditions. This implies that selection only under completely nonstressful conditions

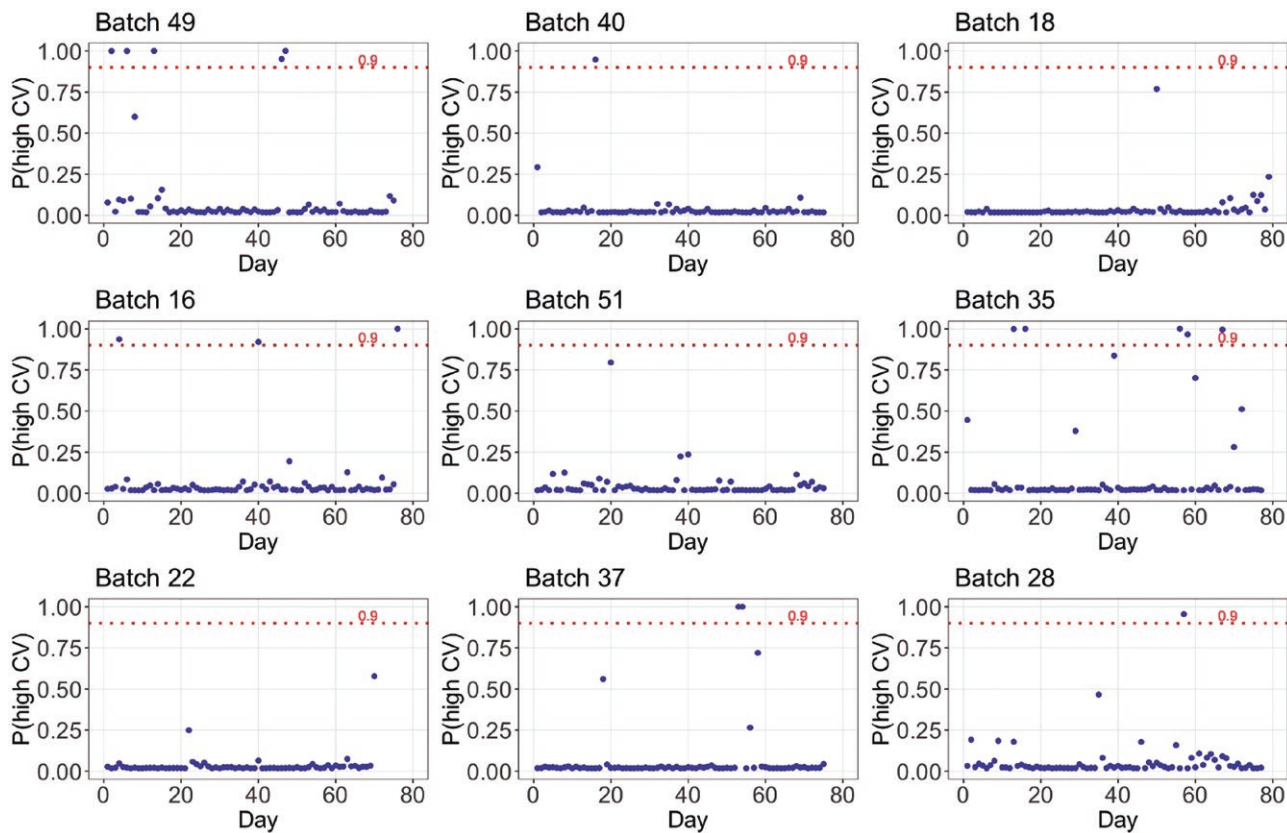


Figure 3. Probabilities of showing a high CV (for a random sample of nine batches) related to the occurrence of an environmental challenge for each day for LW.

can be ineffective for trait expression in completely stressful conditions (Garcia-Baccino et al., 2021). Furthermore, among the lines studied, the LW had the lowest re-ranking of animals across different environmental conditions, as evidenced by the high genetic correlation (0.63) between EBV at $p = 0$ and EBV at $p = 1$. It should be noted that PI is known to be more sensitive to stress than other lines (Foury et al., 2007; Malancus et al., 2022).

Variance component estimates

Table 2 presents the estimates of variance components for DFI obtained from the RNAM and the AM models for all the lines. The additive genetic variance of the intercept for DFI was highest in LA followed by LW and PI. Gao et al. (2021) found an additive genetic variance of DFI in Danish LA as 0.10, which is higher than the value obtained in the current study. The additive genetic variance of DFI reported by Johnson et al. (1999) in LW was 0.02. Núñez et al. (2023) reported an additive genetic variance of DFI of 0.02 for PI. However, Do et al. (2013) reported additive genetic variance of 0.42 and 0.44 of average DFI for LA and LW, respectively. The additive genetic variance of average DFI is higher than that of DFI because averaging DFI over the whole testing period reduces the noise in the data.

Figure 6 shows the estimates of the genetic variance of the slope for DFI for increasing probabilities of the occurrence of an environmental challenge for LA, LW and PI. The environmental sensitivity variance was 0 in a nonstressful environmental condition ($p = 0$) (as expected) and increases as p increases (more stressful environmental conditions) in all the lines. Its maximum value was 0.055, 0.080, and 0.097 (Table 2)

for LA, LW and PI, respectively. A larger variance of the slope (sensitivity) (for instance, PI) would suggest that pigs have high variation in their feed intake in response to changes in environmental conditions. Based on the results shown in Table 2 and Figure 6, the proportion of the additive genetic variance explained by the slope was 51.4, 63.5, and 78.9% for LA, LW, and PI. As expected, PI showed the highest level of variation in DFI when there is the occurrence of environmental challenges.

Heritability estimates of DFI for increasing probabilities of the occurrence of an environmental challenge for LA, LW, and PI are shown in Figure 7. Heritability estimates of DFI varied from a nonchallenging environment ($p = 0$) to a challenging environment ($p = 1$), with values ranging from 0.119 to 0.172 for LA, 0.167 to 0.253 for LW, and 0.103 to 0.235 for PI. In LA, due to the negative covariance between the intercept and the slope, the heritability of DFI decreased from $p = 0$ to $p = 0.6$, then remained constant until $p = 0.8$, after which it slightly increased until $p = 1$. The heritability of DFI in PI also decreased from $p = 0$ to $p = 0.2$, and then increased for higher values of p . For LW, the heritability of DFI increased from low to moderate as values of p increased. The heritability estimates of DFI across the environmental gradient were highest in LW and lowest for LA especially at higher values of p . The behavior of heritability (heritability changing across the environmental gradient) in this study is comparable to those reported in previous studies, e.g., in Garcia-Baccino et al. (2021) and Waters et al. (2022) in sheep; Chen et al. (2021) and Madsen et al. (2018) in pigs; Shariati et al. (2007), Zhang et al. (2019), and Carvalho Filho et al. (2022) in cattle.

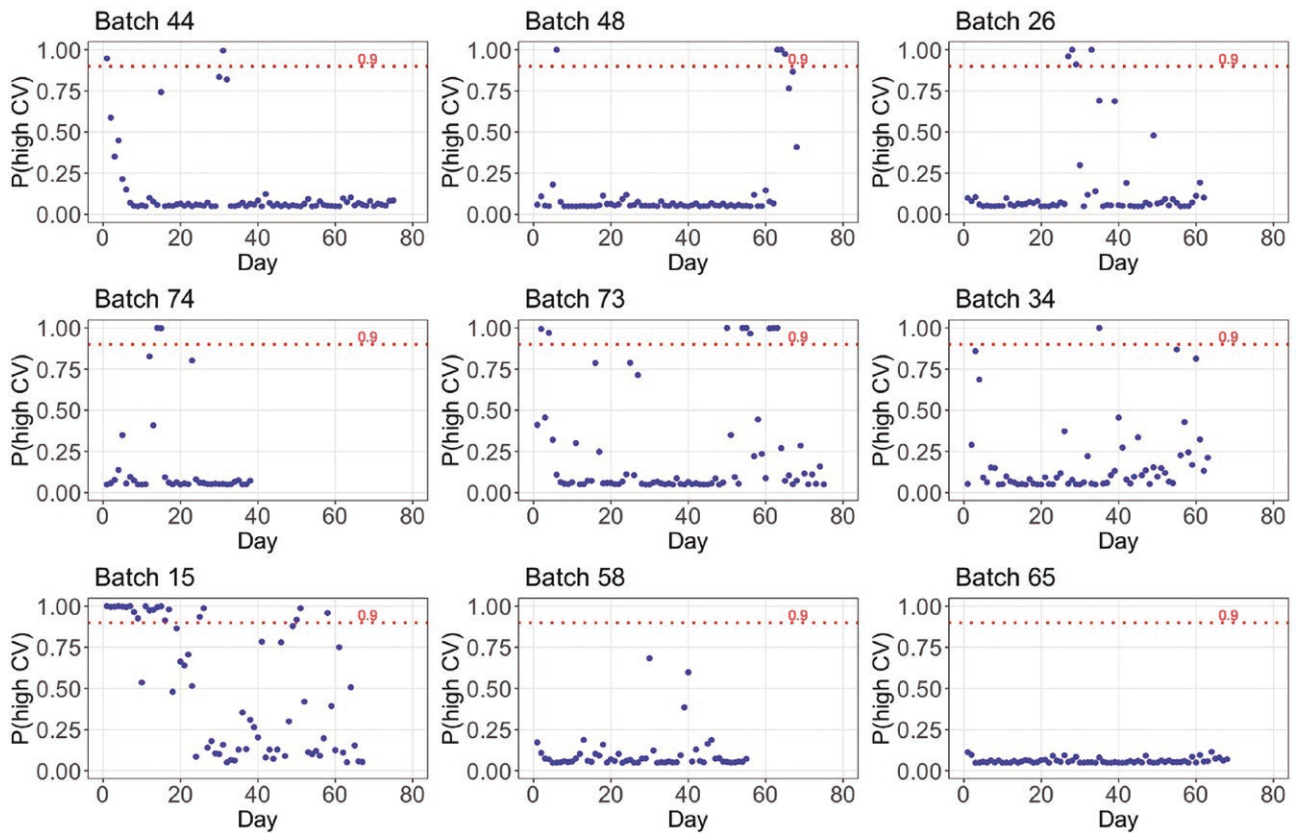


Figure 4. Probabilities of showing a high CV (for a random sample of nine batches) related to the occurrence of an environmental challenge for each day for Piétrain.

Table 2. Genetic parameter estimates (\pm SE) for DFI (kg) obtained from AM and RNAM in three pig lines

Parameters	Landrace		Large White		Piétrain	
	AM	RNAM	AM	RNAM	AM	RNAM
σ_{a0}^2	0.042 \pm 0.007	0.052 \pm 0.008	0.046 \pm 0.006	0.046 \pm 0.006	0.024 \pm 0.030	0.026 \pm 0.003
σ_{a1}^2	–	0.055 \pm 0.014	–	0.080 \pm 0.018	–	0.097 \pm 0.012
$\sigma_{a0,a1}$	–	–0.028 \pm 0.009	–	0.003 \pm 0.008	–	–0.018 \pm 0.005
σ_{pe0}^2	0.032 \pm 0.007	0.033 \pm 0.005	0.026 \pm 0.004	0.027 \pm 0.004	0.024 \pm 0.002	0.025 \pm 0.002
σ_{pe1}^2	–	0.140 \pm 0.012	–	0.200 \pm 0.016	–	0.114 \pm 0.009
$\sigma_{pe0,pe1}$	–	–0.018 \pm 0.006	–	0.019 \pm 0.006	–	–0.015 \pm 0.003
σ_e^2	0.228 \pm 0.001	0.211 \pm 0.001	0.213 \pm 0.001	0.203 \pm 0.001	0.187 \pm 0.001	0.175 \pm 0.001
$r_{a0,a1}$	–	–0.523 \pm 0.128	–	0.055 \pm 0.133	–	–0.359 \pm 0.077

σ_{a0}^2 = additive genetic variance for the intercept; σ_{a1}^2 = additive genetic variance for slope; $\sigma_{a0,a1}$ = additive genetic covariance between level and slope; σ_{pe0}^2 = permanent environmental variance for level; σ_{pe1}^2 = permanent environmental variance for slope; $\sigma_{pe0,pe1}$ = permanent environmental covariance between level and slope; σ_e^2 = residual variance; $r_{a0,a1}$ = genetic correlation between intercept and slope.

Kavлак et al. (2021) estimated heritabilities of DFI in LW by classifying the records into five test periods of 20 d each in Finnish pig lines and reported heritability estimates varying from 0.14 to 0.30 for the different periods. Wetten et al. (2012) investigated the heritability of DFI curves for growing pigs (Duroc and LA) using random regression models and obtained heritabilities ranging from 0.09 to 0.11. Gao et al. (2021) used a random regression model to estimate the heritability of DFI in Danish LA and found heritability ranging from 0.15 to 0.36 across the test period. Our results are in agreement with those published in the literature.

Identification of resilient animals

The change in EBV from nonchallenging environmental conditions ($p = 0$) to challenging environmental conditions ($p = 1$) expressed in genetic standard deviation is shown in Figure 8. This was used to identify potentially resilient and sensitive animals. Animals were categorized into three groups depending on the pattern of the change of EBV.

In the first group (shown in violet in Figure 8), the EBV of DFI decreased as the conditions became more stressful (as probability increases), while in the third group (shown in gray in Figure 8), the EBV of DFI increased as the environmental

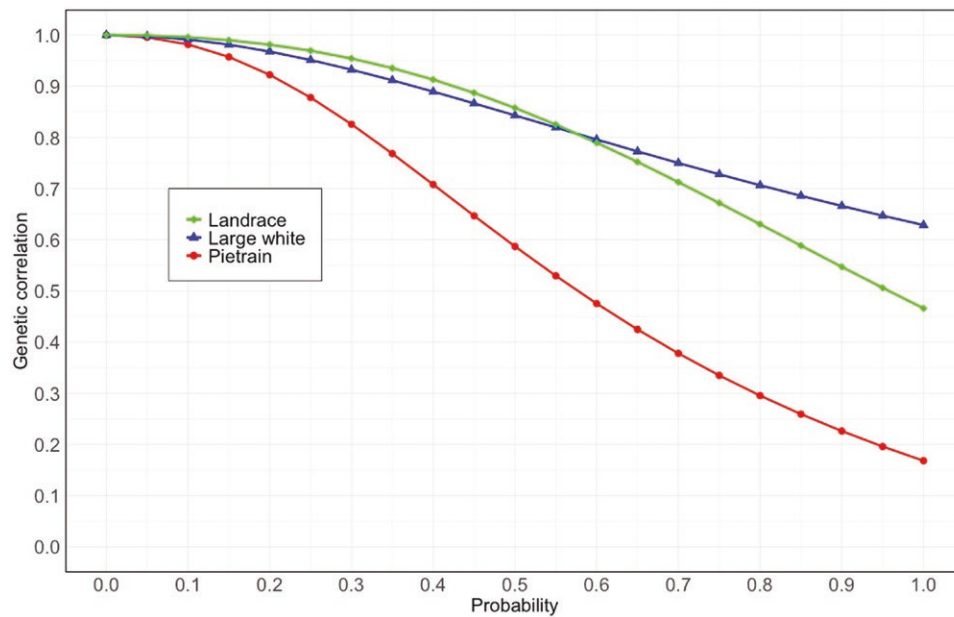


Figure 5. Genetic correlation between BVs of DFI in a nonchallenging environment ($P = 0$) and BVs at different probabilities of the occurrence of an environmental challenge ($p > 0$).

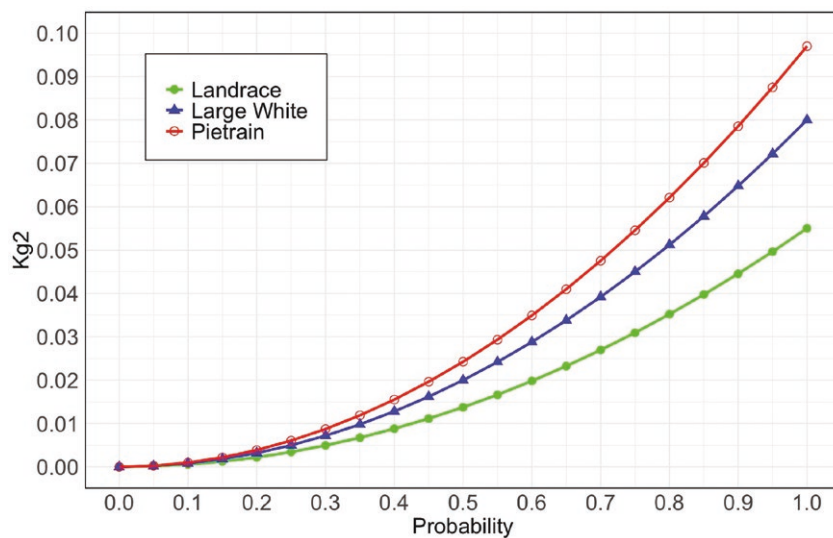


Figure 6. Variance estimates of the slope of the reaction norm of DFI for different probabilities of the occurrence of an environmental challenge.

conditions became more stressful. The second group (shown in blue on Figure 8) consists of animals whose slopes remain relatively constant as p increases. This second group includes animals with positive or negative slopes or slopes close to 0, but their EBV change within ± 1 SD. For LA, LW, and PI, 75.0%, 74.2%, and 72.2% of the animals, respectively, were in the second group and so can be termed resilient. In other words, most of the animals have the ability to maintain performance despite the change in environmental conditions.

Discussion

The identification of variability in animal responses to the presence of environmental challenges can be performed using artificially introduced disturbances or perturbations (Bai et al., 2020; Nguyen-Ba et al., 2020; Laghouaouta et al., 2021; Luttman et al., 2023). In contrast to phenotyping

during experimentally imposed stressful conditions, Colditz and Hine (2016) proposed that phenotyping should be done during an animal's exposure to a stressful event that is inherent to their management environment. In this study, we used a data-driven approach which involves estimating the probability of the occurrence of an unrecorded environmental challenge on a given day (Garcia-Baccino, 2021). First, we used DFI data recorded in routine to estimate the probabilities (environmental descriptor) in pigs reared in real selection conditions. Second, we evaluated the genetic determinism of environmental sensitivity in three pig lines (LA, LW, and PI).

Estimation of the probabilities of the occurrence of an unrecorded environmental challenge in pigs

The approach of Garcia-Baccino et al. (2021) is regarded as data-driven because the estimation of the probabilities of the occurrence of an environmental challenge is solely based on

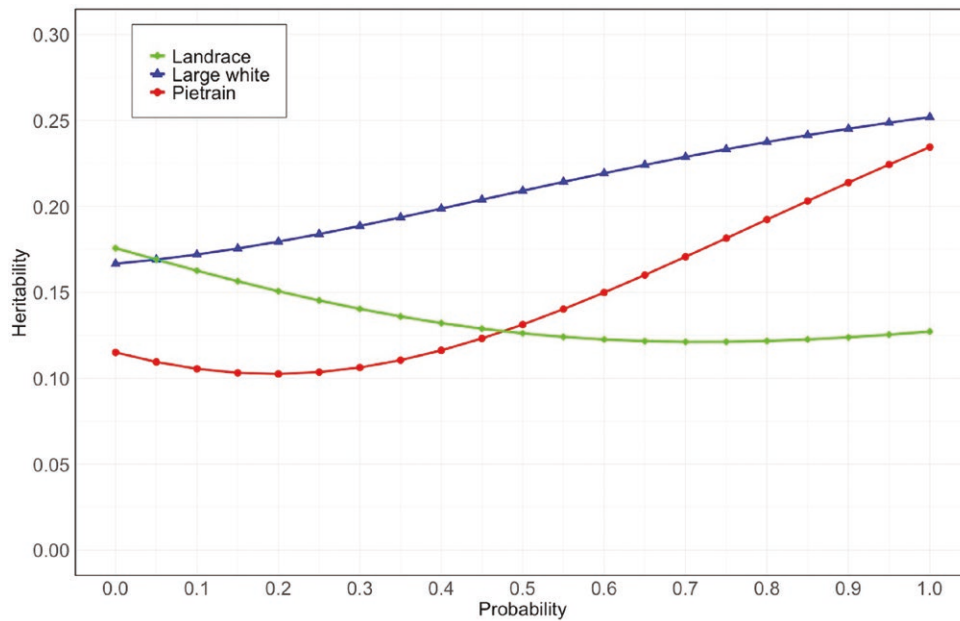


Figure 7. Heritability estimates of DFI for different probabilities of the occurrence of the environmental challenge.

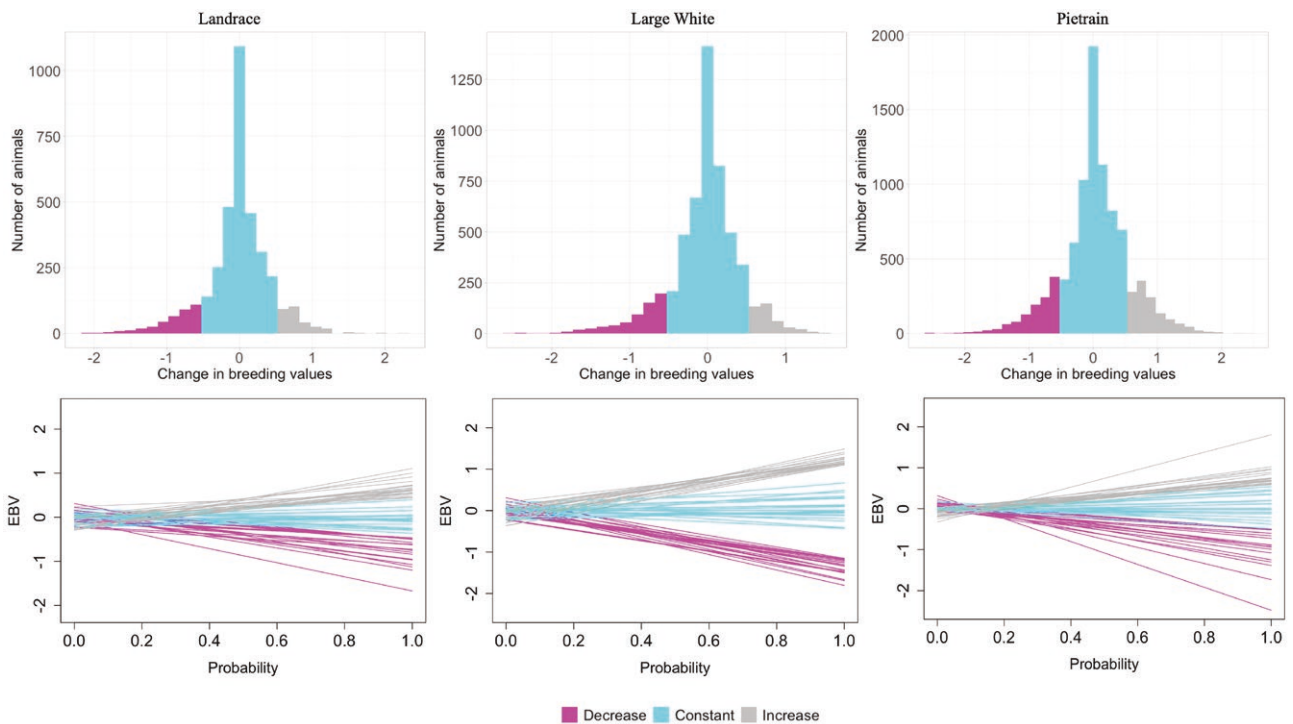


Figure 8. Change in EBV between a nonchallenging environmental condition ($p = 0$) and an extremely challenging condition ($p = 1$) expressed in terms of genetic standard deviation. Three groups were identified according to the pattern of reaction to environmentally challenging conditions (Decrease: animals with EBV that decrease for higher values of p ; Constant: animals with EBV that tend to remain relatively constant for higher values of p within a range of ± 1 genetic standard deviations; Increase: animals with EBV that increase for higher values of p). The reaction norms of DFI are shown for 20 randomly selected animals from each of the three groups for each breed.

phenotypic data collected routinely, without the need for additional information (e.g., climatic variables). With this method, there is no need to introduce challenges or perturbations physically. It captures events that occur on the farm even if they are not documented. Furthermore, it does not require the estimation of the target curve and deviations from the curve to detect the occurrence of an environmental challenge (Garcia-Baccino et al., 2021), unlike other methods, such as the procedure pro-

posed by Nguyen-Ba et al. (2020) to quantify the feed intake responses of growing pigs to perturbations. Garcia-Baccino et al. (2021) illustrated the method using data from DFI records from Romane lambs raised on a single experimental farm over an 8-yr period, with one cohort per year. In this study, we implemented the method using data from DFI recorded routinely in three lines (PI, LW, and LA) reared in five different selection farms (three farms for PI one for LW, and one for LA)

during a 3-yr period, with overlapping batches each. Since the method requires homogeneity among animals within groups, the analysis was performed on each batch within each breed. The method was able to capture the differences between the lines in their response to environmental challenges. These environmental challenges and their sources are unknown. However, [Martínez-Miró et al. \(2016\)](#) categorized animal stressors into social, environmental, metabolic, immunological, and human interactions. When a posterior investigation was done on days that had a high probability of the occurrence of a challenge, it was confirmed that some of the days corresponded to the days with documented disturbances on the farm that were associated with animal illness, change in management, environmental conditions like storm, animal handling operations such as ear tagging, weighing of animals, and other human interventions such as ACF repair and animal movement of animals from one pen to another. However, for some other days with a high probability of the occurrence of an environmental challenge, no disturbances were documented on the farms, and no explanation could be given; thus, they are assumed to correspond to days with unrecorded environmental challenges ([Garcia-Baccino et al., 2021](#)). Stressors like pathogens, heat stress, mycotoxins, social interaction, dust, and problems in access to feed and water events have been reported to cause stress to pigs ([Patience and Ramirez, 2022](#)), though not all are recorded on the farm.

Genetic correlation

The genetic correlation between the intercept and the slope can be interpreted as the genetic correlation between the overall performance (genetic potential) and environmental sensitivity. A high genetic correlation (positive or negative) between the intercept and the slope of the reaction norms suggests that selection for the preferred (high or low) trait level in nonchallenging environments would lead to increased environmental sensitivity in challenging environments ([Knap, 2005](#); [Garcia-Baccino et al., 2021](#)). The correlation indicates the trade-off between “baseline” ability of growth and “environmental coping” ability of the pig.

In the current study, we observed a low positive genetic correlation between the intercept and slope for LW but moderate negative genetic correlations between the intercept and slope for LA and PI. This shows that the three lines exhibit different patterns of environmental sensitivity. The low genetic correlation between the intercept and the slope observed in LW suggests that selecting for decreased DFI would have a minimal effect on the animal’s sensitivity to challenging environmental conditions. This means that it is possible to hypothetically select for both decreased DFI and resilience. In other words, the EBV for the intercept (EBV for the genetic potential of the animal) will not affect the EBV of the slope (EBV for environmental sensitivity) or vice versa ([Madsen et al., 2018](#)). The negative and moderate genetic correlation between the slope and intercept for LA and PI suggests that a hypothetical selection for decreased DFI in nonchallenging environments would result in pigs with increased DFI in challenging environmental conditions or vice versa. Similar results were reported by [Garcia-Baccino et al. \(2021\)](#) in Romane sheep.

In our study, we observed a decrease in genetic correlation between EBVs in a nonchallenging environment and EBV at a given probability of the occurrence of an environmental challenge as the probability of the occurrence of an environmental challenge increased. Genetic correlations between different

environments that are lower than 0.8 have been suggested as evidence of $G \times E$ interaction ([Robertson, 1959](#); [Shariati et al., 2007](#); [Hayes et al., 2016](#); [Chen et al., 2021](#)). In our study, we uncovered GxE for DFI in pigs, although the magnitude of GxE was lower in LW than in PI and LA. In addition, low genetic correlations between stressful and nonstressful environments indicate the re-ranking of animals in different environmental conditions, implying that selection solely under completely nonstressful conditions can be ineffective for trait expression in completely stressful conditions. Thus, selection in nonstressful conditions should also consider performance under stressful conditions to avoid or reduce negative effects due to environmental changes.

While our results revealed differences in terms of environmental sensitivity among LA, LW, and PI pig lines, note that LA and LW were each raised separately on one selection farm. Thus, a potential confounding effect of farm-specific conditions could exist in these lines, and the results should be interpreted with caution.

Heritability estimates

In this study, heritability estimates of DFI for both lines varied across the environmental gradient (from $p = 0$ to $p = 1$). This is attributed to variation in additive genetic variance across the environmental gradient ([Carvalho Filho et al., 2022](#)). Heritability estimates that vary across the environmental gradient were also observed by [Garcia-Baccino et al. \(2021\)](#) for DFI in Romane sheep; [Waters et al. \(2022\)](#) for body weight in Australian sheep; [Chen et al. \(2021\)](#) for reproduction, body composition, and growth traits in LW pigs; [Madsen et al. \(2018\)](#) for growth rate in Danish Duroc pigs; [Shariati et al. \(2007\)](#) for milk production traits in early lactation in Danish Holstein cattle; [Zhang et al. \(2019\)](#) for fertility traits in Danish Holstein cattle; [Oliveira et al. \(2018\)](#) for yearling weight in Nellore cattle; [Silva Neto et al. \(2023\)](#) for efficiency traits in Nellore cattle; and [Carvalho Filho et al. \(2022\)](#) for growth, reproductive, and visual score traits in Nellore cattle.

Variance components

We estimated variance components for increasing the probability of the occurrence of an environmental challenge. Our study revealed an increase in additive genetic variance for environmental sensitivity across the environmental gradient (attributed to the increase of p related to increasing stressful environmental conditions). The change in additive genetic variance along the environmental gradient is evidence of the presence of re-ranking pigs from nonchallenging conditions to challenging conditions. These results are similar to those reported by [Garcia-Baccino et al. \(2021\)](#) for DFI in Romane sheep. [Ravagnolo and Misztal \(2000\)](#) estimated variances of level, environmental sensitivity (heat tolerance) and total additive genetic variance for milk yield, fat, and protein in Holstein cows using temperature-humidity index (THI) as an environmental descriptor and reported similar results. In their study, when there was no heat stress, the additive genetic variance for heat tolerance was 0 but increased as the THI increased. [Madsen et al. \(2018\)](#) studied the genetic variation of macro-environmental sensitivity for average daily gain in Danish Duroc pigs and found increased additive genetic variance when environments became extreme. According to [Mulder \(2017\)](#), the genetic variance across different environments is due to $G \times E$ and can be exploited to select for resilience. In the current study, the maximum genetic variability of the slope

of DFI was highest in highly challenging environments. Therefore, the highly environmentally sensitive pigs will suffer more (less efficient) from challenging environmental conditions than the less sensitive pigs (Madsen et al., 2018).

Selecting for resilience

In our study, we categorized animals into three groups, i.e., animals whose EBV decreased as the probability of the occurrence of an environmental challenge increased, animals whose EBV remained almost constant as the probability of the occurrence of an environmental challenge increased, and animals whose EBV increased as the probability of the occurrence on an environmental challenge increased. The animals whose EBV increased or decreased as the probability of the occurrence of an environmental challenge increased were less resilient, while animals whose EBV remained almost constant were more resilient. Most of the animals for all the lines were in the second group, which suggests that they can maintain production despite the occurrence of environmental challenges. Moreover, the second-group animals have lower CV of DFI, meaning that they have higher levels of within-individual uniformity (less deviations) in the presence of environmental challenges. It is believed that animals can learn from experiences to anticipate their impact through predictive adaptive behavioral and physiological responses (Colditz and Hine, 2016).

Resilient animals will reach their genetic potential under commercial conditions and ensure efficient production (Kavлак and Uimari, 2024). However, even resilient animals have varying rates of response to environmental disturbances, indicated by differences in their slopes of DFI. Less resilient animals will have either a substantial decrease or high day-to-day fluctuations in DFI compared to more resilient animals in the same environment. In this study, it is indicated by the high CV of DFI.

Depending on the circumstances, resistance and flexibility may be involved in different manners in resilience. Resilience is not only about being resistant to stressors but also about how well an animal can sense and adjust to changes depending on the stressor. Therefore, environmental sensitivity can be an adaptive response to manage stress under challenging environments. For example, in more extensive systems where ambient temperatures rise beyond upper critical temperature, animals significantly reduce their internal heat production by decreasing their feed intake, helping them better manage heat stress (Rauw et al., 2017). Therefore, resilient animals can be those that experience a significant drop in production when exposed to stress but quickly recover and return to their pre-stress condition more effectively than less resilient animals (Berghof et al., 2019).

Conclusion

In all the lines, this data-driven method (so far only used in data from an experimental farm) was able to identify unrecorded environmental challenge events in real conditions. As expected, most of the days had a low probability of the occurrence of an environmental challenge. The productive data collected routinely, such as DFI or other measures from automatic devices (e.g., milking robots), can be used to describe environmental challenges and help in selection of resilient animals.

The genetic correlation between the intercept and the slope of the reaction norm of DFI suggests that selecting hypothetically for decreased DFI in nonstressful conditions may lead to increased DFI in challenging environments in LA and PI.

Conversely, the impact of such selection on LW pigs appears marginal, suggesting a breed-specific response to environmental challenges. These results highlight the complex interplay between genetic factors and environmental stressors. A substantial proportion of less environmentally sensitive animals was identified within each breed, emphasizing the feasibility of genetic selection for resilience.

Acknowledgments

We are grateful to SAS NUCLEUS for providing the data analyzed in this study. We are grateful to the genotoul bioinformatics platform Toulouse Occitanie (Bioinfo Genotoul, <https://doi.org/10.15454/1.5572369328961167E12>) for computing resources. This study received financial support from the Institut Carnot France Futur Elevage (SHARP project: Selection for Health and Robustness in Pigs).

Author contributions

Tomasi Tusingwiire (Data curation, Formal analysis, Writing—original draft, Writing—review & editing), Carolina Garcia-Baccino (Investigation, Methodology, Supervision, Validation, Writing—review & editing), Céline Carillier-Jacquin (Conceptualization, Validation, Writing—review & editing), Bruno Ligonesche (Resources, Validation, Writing—review & editing), Catherine Larzul (Conceptualization, Validation, Writing—review & editing), and Zulma Vitezica (Methodology, Supervision, Validation, Writing—review & editing)

Conflict of interest statement

The authors declare no conflicts of interest.

Literature Cited

- Akaike, H. 1974. A new look at the statistical model identification. *IEEE Trans. Automat. Contr.* 19(6):716–723. doi:10.1109/TAC.1974.1100705
- Bai, X., A. M. Putz, Z. Wang, F. Fortin, J. C. S. Harding, M. K. Dyck, J. C. M. Dekkers, C. J. Field, G. S. Plastow, and C. PigGen. 2020. Exploring phenotypes for disease resilience in pigs using complete blood count data from a natural disease challenge model. *Front. Genet.* 11:216. doi:10.3389/fgene.2020.00216
- Baumung, R., G. Lercher, A. Willam, and J. Sölkner. 2006. Feed intake behaviour of different pig breeds during performance testing on station. *Arch. Anim. Breed.* 49:77–88. doi:10.5194/aab-49-77-2006
- Benaglia, T., D. Chauveau, D. R. Hunter, and D. S. Young. 2009. Mixtools: an R package for analyzing finite mixture models. *J. Stat. Softw.* 32:1–29. doi:10.18637/jss.v032.i06
- Berghof, T. V. L., M. Poppe, and H. A. Mulder. 2019. Opportunities to improve resilience in animal breeding programs. *Front. Genet.* 9:1–15. doi:10.3389/fgene.2018.00692
- Carvalho Filho, I., D. A. Silva, C. S. Teixeira, T. L. Silva, L. F. M. Mota, L. G. Albuquerque, and R. Carneiro. 2022. Heteroscedastic reaction norm models improve the assessment of genotype by environment interaction for growth, reproductive, and visual score traits in Nellore cattle. *Animals* 12:2613. doi:10.3390/ani12192613
- Chen, S. Y., P. H. F. Freitas, H. R. Oliveira, S. F. Lázaro, Y. J. Huang, J. T. Howard, Y. Gu, A. P. Schinckel, and L. F. Brito. 2021. Genotype-by-environment interactions for reproduction, body composition, and growth traits in maternal-line pigs based on

- single-step genomic reaction norms. *Genet. Sel. Evol.* 53:51. doi:[10.1186/s12711-021-00645-y](https://doi.org/10.1186/s12711-021-00645-y)
- Cheng, J., K. S. Lim, A. M. Putz, A. Wolc, J. C. S. Harding, M. K. Dyck, F. Fortin, G. S. Plastow, and J. C. M. Dekkers. 2022. Genetic analysis of disease resilience of wean-to-finish pigs under a natural disease challenge model using reaction norms. *Genet. Sel. Evol.* 54:11. doi:[10.1186/s12711-022-00702-0](https://doi.org/10.1186/s12711-022-00702-0)
- Colditz, I. G., and B. C. Hine. 2016. Resilience in farm animals: biology, management, breeding and implications for animal welfare. *Anim. Prod. Sci.* 56:1961–1983. doi:[10.1071/an15297](https://doi.org/10.1071/an15297)
- Dekkers, J. C. M. 2021. Multiple trait breeding programs with genotype-by-environment interactions based on reaction norms, with application to genetic improvement of disease resilience. *Genet. Sel. Evol.* 53:93. doi:[10.1186/s12711-021-00687-2](https://doi.org/10.1186/s12711-021-00687-2)
- Do, D. N., A. B. Strathe, J. Jensen, T. Mark, and H. N. Kadarmideen. 2013. Genetic parameters for different measures of feed efficiency and related traits in boars of three pig breeds. *J. Anim. Sci.* 91:4069–4079. doi:[10.2527/jas.2012-6197](https://doi.org/10.2527/jas.2012-6197)
- Fernández, J., E. Fàbrega, J. Soler, J. Tibau, J. L. Ruiz, X. Puigvert, and X. Manteca. 2011. Feeding strategy in group-housed growing pigs of four different breeds. *Appl. Anim. Behav. Sci.* 134:109–120. doi:[10.1016/j.applanim.2011.06.018](https://doi.org/10.1016/j.applanim.2011.06.018)
- Foury, A., N. A. Geverink, M. Gil, M. Gispert, M. Hortós, M. Font, I. Furnols, D. Carrion, S. C. Blott, G. S. Plastow, et al. 2007. Stress neuroendocrine profiles in five pig breeding lines and the relationship with carcass composition. *Animal* 1:973–982. doi:[10.1017/S1751731107000249](https://doi.org/10.1017/S1751731107000249)
- Friggens, N. C., I. Adriaens, R. Boré, G. Cozzi, J. Jurquet, C. Kamphuis, F. Leiber, I. Lora, T. Sakowski, J. Statham, et al. 2022. Resilience: reference measures based on longer-term consequences are needed to unlock the potential of precision livestock farming technologies for quantifying this trait. *Peer Comm. J.* 2:e38. doi:[10.24072/pjournal.136](https://doi.org/10.24072/pjournal.136)
- Gao, H., G. Su, J. Jensen, P. Madsen, O. F. Christensen, B. Ask, B. G. Poulsen, T. Ostensen, and B. Nielsen. 2021. Genetic parameters and genomic prediction for feed intake recorded at the group and individual level in different production systems for growing pigs. *Genet. Sel. Evol.* 53:33. doi:[10.1186/s12711-021-00624-3](https://doi.org/10.1186/s12711-021-00624-3)
- García-Baccino, C. A., C. Marie-Etancelin, F. Tortereau, D. Marcon, J. L. Weisbecker, and A. Legarra. 2021. Detection of unrecorded environmental challenges in high-frequency recorded traits, and genetic determinism of resilience to challenge, with an application on feed intake in lambs. *Genet. Sel. Evol.* 53:4. doi:[10.1186/s12711-020-00595-x](https://doi.org/10.1186/s12711-020-00595-x)
- Gorssen, W., C. Winters, R. Meyermans, L. Chapard, K. Hooyberghs, S. Janssens, A. Huisman, K. Peeters, H. Mulder, and N. Buys. 2023. A promising resilience parameter for breeding: the use of weight and feed trajectories in growing pigs. *J. Anim. Sci. Biotechnol.* 14:101. doi:[10.1186/s40104-023-00901-9](https://doi.org/10.1186/s40104-023-00901-9)
- Hayes, B. J., H. D. Daetwyler, and M. E. Goddard. 2016. Models for genome \times environment interaction: examples in livestock. *Crop Sci.* 56:2251–2259. doi:[10.2135/cropsci2015.07.0451](https://doi.org/10.2135/cropsci2015.07.0451)
- Hermesch, S., A. E. Huisman, B. G. Luxford, H. U. Graser. 2006. Analysis of genotype by feeding level interaction in pigs applying reaction norm models. In: *Proceedings of the 8th World Congress of Genetics Applied to Livestock Production*; August 13 to 18, 2006; Belo Horizonte.
- Homma, C., K. Hirose, T. Ito, M. Kamikawa, S. Toma, S. Nikaido, M. Satoh, and Y. Uemoto. 2021. Estimation of genetic parameter for feed efficiency and resilience traits in three pig breeds. *Animal* 15:100384. doi:[10.1016/j.animal.2021.100384](https://doi.org/10.1016/j.animal.2021.100384)
- Johnson, Z. B., J. J. Chewning, and R. A. Nugent. 1999. Genetic parameters for production traits and measures of residual feed intake in Large White swine. *J. Anim. Sci.* 77:1679–1685. doi:[10.2527/1999.7771679x](https://doi.org/10.2527/1999.7771679x)
- Kavлак, A. T., and P. Uimari. 2024. Inheritance of feed intake-based resilience traits and their correlation with production traits in Finnish pig breeds. *J. Anim. Sci.* 1:skae037. doi:[10.1093/jas/skae037](https://doi.org/10.1093/jas/skae037)
- Kavлак, A. T., I. Strandén, M. H. Lidauer, and P. Uimari. 2021. Estimation of social genetic effects on feeding behaviour and production traits in pigs. *Animal* 15:100168. doi:[10.1016/j.animal.2020.100168](https://doi.org/10.1016/j.animal.2020.100168)
- Knap, P. W. 2005. Breeding robust pigs. *Aust. J. Exp. Agric.* 45:763–773.
- Knap, P. W. 2020. The scientific development that we need in the animal breeding industry. *J. Anim. Breed. Genet.* 137:343–344. doi:[10.1111/jbg.12485](https://doi.org/10.1111/jbg.12485)
- Labroue, F., R. Guéblez, and P. Sellier. 1997. Genetic parameters of feeding behaviour and performance traits in group-housed Large White and French Landrace growing pigs. *Genet. Sel. Evol.* 29:451–468. doi:[10.1186/1297-9686-29-4-451](https://doi.org/10.1186/1297-9686-29-4-451)
- Labroue, F., R. Guéblez, M.-C. Meunier-Salaün, and P. Sellier. 1999. Feed intake behaviour of group-housed Piétrain and Large White growing pigs. *Ann. Zootech* 48(4):247–261. doi:[10.1051/anim-res:19990402](https://doi.org/10.1051/anim-res:19990402)
- Laghouaouta, H., R. N. Pena, R. Ros-Freixedes, J. Reixach, M. Díaz, J. Estany, R. Armengol, A. Bassols, and L. Fraile. 2021. A methodology to quantify resilience in growing pigs. *Animals* 11:2970. doi:[10.3390/ani11102970](https://doi.org/10.3390/ani11102970)
- Lora, I., F. Gottardo, B. Contiero, A. Zidi, L. Magrin, M. Cassandro, and G. Cozzi. 2020. A survey on sensor systems used in Italian dairy farms and comparison between performances of similar herds equipped or not equipped with sensors. *J. Dairy Sci.* 103:10264–10272. doi:[10.3168/jds.2019-17973](https://doi.org/10.3168/jds.2019-17973)
- Lourenco, D., S. Tsuruta, I. Aguilar, Y. Masuda, M. Bermann, A. Legarra, and I. Misztal. 2022. Recent updates in the BLUPF90 software suite. In: *Proceedings of the 12th World Congress on Genetics Applied to Livestock Production*; July 3 to 8, 2022; Rotterdam.
- Luttman, A. M., B. Lee, J. M. Siegford, J. P. Steibel, N. E. Raney, and C. W. Ernst. 2023. Characterizing resilience to weaning stress and its associations with behavioural differences in finishing gilts. *Appl. Anim. Behav. Sci.* 263:105940. doi:[10.1016/j.applanim.2023.105940](https://doi.org/10.1016/j.applanim.2023.105940)
- Madsen, M. D., P. Madsen, B. Nielsen, T. N. Kristensen, J. Jensen, and M. Shirali. 2018. Macro-environmental sensitivity for growth rate in Danish Duroc pigs is under genetic control. *J. Anim. Sci.* 96:4967–4977. doi:[10.1093/jas/sky376](https://doi.org/10.1093/jas/sky376)
- Malancus, R. N., R. O. Rusu, V. Arsenoiaia, and L. I. Ailincai. 2022. Stress levels of Mangalita, Large White, and Piétrain pigs reared in different housing systems in south eastern Europe. *Arq. Bras. Med. Vet. Zootec.* 74:1161–1165. doi:[10.1590/1678-4162-12819](https://doi.org/10.1590/1678-4162-12819)
- Martínez-Miró, S., F. Tecles, M. Ramón, D. Escribano, F. Hernández, J. Madrid, J. Orengo, S. Martínez-Subiela, X. Manteca, and J. J. Cerón. 2016. Causes, consequences and biomarkers of stress in swine: an update. *BMC Vet. Res.* 12:1–9. doi:[10.1186/s12917-016-0791-8](https://doi.org/10.1186/s12917-016-0791-8)
- Mulder, H. A. 2017. Is G \times E a burden or a blessing? Opportunities for genomic selection and big data. *J. Anim. Breed. Genet.* 134:435–436. doi:[10.1111/jbg.12303](https://doi.org/10.1111/jbg.12303)
- Nguyen-Ba, H., J. Van Milgen, and M. Taghipoor. 2020. A procedure to quantify the feed intake response of growing pigs to perturbations. *Animal* 14:253–260. doi:[10.1017/S1751731119001976](https://doi.org/10.1017/S1751731119001976)
- Núñez, P., S. Gol, J. Reixach, C. Casto-Rebollo, and N. Ibáñez-Escriche. 2023. Incorporation of feeding behaviour traits to increase the genetic gain of feed efficiency in Piétrain pigs. *J. Anim. Breed. Genet.* 140:485–495. doi:[10.1111/jbg.12773](https://doi.org/10.1111/jbg.12773)
- Oliveira, D. P., D. A. L. Lourenco, S. Tsuruta, I. Misztal, D. J. A. Santos, F. R. De Araújo Neto, R. R. Aspilcueta-Borquis, F. Baldi, R. Carvalheiro, G. M. F. De Camargo, et al. 2018. Reaction norm for yearling weight in beef cattle using single-step genomic evaluation. *J. Anim. Sci.* 96:27–34. doi:[10.1093/jas/skx006](https://doi.org/10.1093/jas/skx006)
- Patience, J. F., and A. Ramirez. 2022. Invited review: strategic adoption of antibiotic-free pork production: the importance of a holistic approach. *Transl. Anim. Sci.* 6:3. doi:[10.1093/tas/txac063](https://doi.org/10.1093/tas/txac063)
- Putz, A. M., J. C. S. Harding, M. K. Dyck, F. Fortin, G. S. Plastow, and J. C. M. Dekkers; PigGen Canada. 2019. Novel resilience phenotypes using feed intake data from a natural disease challenge model in wean-to-finish pigs. *Front. Genet.* 9:660. doi:[10.3389/fgene.2018.00660](https://doi.org/10.3389/fgene.2018.00660)

- Rauw, W. M., E. J. Mayorga, S. M. Lei, J. C. M. Dekkers, J. F. Patience, N. K. Gabler, S. M. Lonergan, and L. H. Baumgard. 2017. Effects of diet and genetics on growth performance of pigs in response to repeated exposure to heat stress. *Front. Genet.* 8:155. doi:[10.3389/fgene.2017.00155](https://doi.org/10.3389/fgene.2017.00155)
- Ravagnolo, O., and I. Misztal. 2000. Genetic component of heat stress in dairy cattle, parameter estimation. *J. Dairy Sci.* 83:2126–2130. doi:[10.3168/jds.S0022-0302\(00\)75095-8](https://doi.org/10.3168/jds.S0022-0302(00)75095-8)
- Robertson, A. 1959. The sampling variance of the genetic correlation coefficient. *Biometrics* 15:469–485. doi:[10.2307/2527750](https://doi.org/10.2307/2527750)
- Schnyder, U., A. Hofer, F. Labroue, and N. Künzi. 2001. Genetic parameters of a random regression model for daily feed intake of performance tested French Landrace and Large White growing pigs. *Genet. Sel. Evol.* 33:635–658. doi:[10.1186/1297-9686-33-6-635](https://doi.org/10.1186/1297-9686-33-6-635)
- Shariati, M. M., G. Su, P. Madsen, and D. Sorensen. 2007. Analysis of milk production traits in early lactation using a reaction norm model with unknown covariates. *J. Dairy Sci.* 90:5759–5766. doi:[10.3168/jds.2007-0048](https://doi.org/10.3168/jds.2007-0048)
- Silva Neto, J. B., L. F. M. Mota, S. T. Amorim, E. Peripolli, L. F. Brito, C. U. Magnabosco, and F. Baldi. 2023. Genotype-by-environment interactions for feed efficiency traits in Nellore cattle based on bi-trait reaction norm models. *Genet. Sel. Evol.* 55:93. doi:[10.1186/s12711-023-00867-2](https://doi.org/10.1186/s12711-023-00867-2)
- Waters, D. L., S. A. Clark, N. Moghaddar, and J. H. van der Werf. 2022. Genomic analysis of the slope of the reaction norm for body weight in Australian sheep. *Genet. Sel. Evol.* 54:1–12. doi:[10.1186/s12711-022-00734-6](https://doi.org/10.1186/s12711-022-00734-6)
- Wetten, M., J. Ødegård, O. Vangen, and T. H. E. Meuwissen. 2012. Simultaneous estimation of daily weight and feed intake curves for growing pigs by random regression. *Animal* 6:433–439. doi:[10.1017/S1751731111001832](https://doi.org/10.1017/S1751731111001832)
- Zhang, Z., M. Kargo, A. Liu, J. R. Thomasen, Y. Pan, and G. Su. 2019. Genotype-by-environment interaction of fertility traits in Danish Holstein cattle using a single-step genomic reaction norm model. *Heredity (Edinb.)*. 123:202–214. doi:[10.1038/s41437-019-0192-4](https://doi.org/10.1038/s41437-019-0192-4)