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Incorporation of feeding behaviour traits to increase the genetic gain of feed efficiency in Pietrain pigs

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Abstract

Improved feed efficiency is an essential goal for the sustainability of pig production in economic and environmental terms. Traits such as feed conversion rate (FCR), residual feed intake (RFI), residual body weight gain (RG) and feeding behaviour, such as duration (TPV) and feeding rate per visit (FR) can now be measured by automatic feeding systems. The aim of this study was to evaluate the benefits of incorporating feeding behaviour traits into a selection index to improve feed efficiency in a nucleus of purebred Pietrain pigs. Data on body weight, feed intake and duration were recorded at each visit in 1608 animals. The information contained in 843,605 visits was grouped by animal ID to obtain a set of feed efficiency and feeding behaviour traits. These traits were obtained in three periods (first, second and total period). Bayesian models were built to estimate the posterior marginal distribution of the variance components. The heritabilities were between 0.44 and 0.59 for feeding behaviour traits and between 0.31 and 0.49 for feed efficiency traits. The FCR and RFI showed a considerable genetic correlation with daily feed intake (~0.65). FCR showed a genetic correlation with feeding behaviour traits, such as feed intake per visit (FPV) (0.44) and FR (0.33). Furthermore, the fast-eating pigs were less efficient. This was due to the positive genetic correlation found between the FR and the FCR (0.33) and the RFI (0.23), and the negative correlation found with the RG (−0.28). On the other hand, the inclusion of the feeding behaviour traits into a selection index slightly increased the selection response for FCR (4%) and RFI (1.8%). However, there was an increase of up to 19% in the selection response for RG and an improvement in accuracy from 0.59 to 0.70. Therefore, we concluded that it would be interesting to include feeding behaviour traits in a selection index to improve the selection response and accuracy of feed efficiency traits.

KEYWORDS
automatic feeder, feeding behaviour, genetic correlation, heritability, Pietrain line, pigs, selection index

1 | INTRODUCTION

Pig farms' profitability is highly dependent on feed conversion efficiency, with feed accounting for more than 60% of the total cost of pig production (Hoste, 2020). Traditionally, the average daily gain (ADG) has been the most commonly used trait to improve feed efficiency because it is easy to measure. Although selection for ADG has increased the slaughter weight, it has also increased feed intake (Chen et al., 2009; Do et al., 2013). New technologies applied to automatic feeders have made it possible to directly measure individual body weight and consumption, allowing the recording of efficiency traits such as feed conversion ratio (FCR), residual feed intake (RFI) and residual body weight gain (RG). In addition, individual feeding behaviour traits such as duration and rate of feeding and consumption at each visit are recorded (de Haer et al., 1993). In this context, several studies have shown genetic and phenotypic correlations between feeding behaviour traits and feed efficiency in dairy cattle (Cavani et al., 2022), beef cattle (Kelly et al., 2021), and pigs (Chen et al., 2010; de Haer et al., 1993; Do et al., 2013; Herrera-Cáceres et al., 2019; Kavlak & Uimari, 2019; Lu et al., 2017; Santiago et al., 2021). However, these results are inconsistent, due to the different factors that affect feeding traits, which can be related to the individual, the environment or the interaction between them. Do et al. (2013), found phenotypic differences in the feeding behaviour traits of different pig breeds. As the different types of management, housing conditions and diet could also affect the results, it is important to specifically estimate the genetic parameters in the population subjected to selection. Most of the studies related to genetic parameters of feeding behaviour in pigs have been carried out in Duroc (Chen et al., 2009; Do et al., 2013; Herrera-Cáceres et al., 2019; Santiago et al., 2021) or other breeds such as Finish Yorkshire (Kavlak & Uimari, 2019) and Landrace (Do et al., 2013). However, information on the genetic parameters of a growth sire breed such as the Pietrain is lacking. The main objective of this study was to evaluate the benefits of including feeding behaviour traits in an index to improve feed efficiency in a Pietrain nucleus selection. To this end, the genetic parameters of feeding behaviour and feed efficiency traits were estimated. Then, the response to selection in feed efficiency traits was determined by including information from feeding behaviour traits in the selection index.

2 | MATERIALS AND METHODS

Data on the feeding behaviour and feed efficiency traits of purebred Pietrain pigs was collected between June 2019 and October 2022 at the Selección Batallé test station (Riudarenes, Girona, Spain). The animals began the testing period with an initial weight of 51.4 ± 8.4 kg and an age of 95.0 ± 7.5 days and finished at 113.2 ± 9.8 kg and an age of 162.4 ± 6.7 days. The pigs were housed in groups of 12.7 ± 1.8 animals per pen (1.5 m^2 per pig). They were fed ad libitum with a commercial corn-based diet containing 2500 Kcal of net energy, 1.3% of lysine and 18.25% of crude protein according to the Pietrain line's high protein requirements for muscle deposition. The pens were equipped with a single automatic feeder (Nedap, Groenlo, the Netherlands). The animals were identified by electronic tags to allow the recognition and recording of body weight, individual consumption and the duration of each visit. All the visits during the first week were discarded to avoid a high number of outliers when adapting to the automatic feeders. Visits by animals less than 85 days of age (44.2 ± 7.8 kg) were removed because their smaller size allows more than one animal to enter the automatic feeder at a time, increasing the number of outliers in body weight and unassigned visits. All visits from individuals with less than 40 total days in the study (2/3 of the study period) were discarded as not representative. In addition, visits with zero consumption were also removed. The initial database contained 918,749 records from 1688 pigs. After filtering, the 843,605 records of 1608 males were grouped by animal to calculate: mean number of visits per day (NVD, visits/day), mean time spent in feeding per day (TPD, min), daily feed intake (DFI, kg), median time spent per visit (TPV, seconds), median feed intake per visit (FPV, grams), median feeding rate per visit (FR, grams/min), ADG (grams), FCR, RFI (grams), RG (grams) and final body weight (FBW, kg). The ADG was considered as the total weight gain obtained during the test, divided by the total testing days. FCR was calculated as the total consumption during the test period, divided by the total weight gain obtained in the same period. FR (g/min) was calculated as the ratio between feed intake and duration of each visit, and then, the median value for each animal was obtained. All the animals were weighed by a scale at the end of the period to obtain the FBW. RFI was considered as the residual value of the following equation:

$$\mathrm{DFI}_j = \mathrm{b}_1\left(\mathrm{BW}^{0.6}\right)_j + \mathrm{b}_2(\mathrm{ADG})_j + \mathrm{b}_3(\mathrm{BF})_j + \mathrm{e}_j \quad (1)$$

where DFI_j is the daily feed consumption for jth individual (j = 1 to 1608), while b_1, b_2 and b_3 are the regression coefficients of mid-test body weight raised to 0.6 ($BW^{0.6}$) (Noblet et al., 1999), ADG and backfat thickness (BF) for jth individual, respectively. The RG was the residual value of the multiple regression model for ADG on $BW^{0.6}$, DFI and BF. The LT and BF were measured at the end of the test using Piglog® (Frontmatec, Kolding, Denmark) at the last rib level and at a distance of 6.5 cm from the midline.

All the above traits were analysed for the total testing period (85 to 163 days) and also in two periods, except for BF, LT and FBW traits. The first period (85–132 days, $n=1584$) and the second (133–162 days, $n=1576$) were divided by half of the full period as an arbitrary threshold. For the within-period analysis, the animals with less than 15 days of records for each period were discarded to avoid high variability and negative values, especially for feed efficiency traits such as ADG and FCR. Outliers for the feeding behaviour traits were checked following Casey et al. (2005) using the criteria for FPV, TPV and FR. More information about the descriptive statistic of this data can be found in Table S1.

The pedigree information contained 5217 animals composed of 1608 tested animals and their ascendants, with a maximum of five generations. The animals tested were the descendants of 108 sires, and the average number of offspring per sire was 15, ranging from 3 to 92 offspring per sire. The genetic parameters for all traits studied were estimated by univariates and bivariate Bayesian analysis using a classical animal model:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Z_a}\,\mathbf{a} + \mathbf{Z_c}\mathbf{cg} + \mathbf{e}, \quad (2)$$

where $\mathbf{y}$ is the vector of observations; $\mathbf{X}$ is the incidence matrix relating observations for vector $\mathbf{b}$ of systematic effects (initial age and the final age as covariates); $\mathbf{a}$ is the random vector of additive effects with incidence matrix $\mathbf{Z_a}$; $\mathbf{cg}$ is the random vector of the contemporary group (126 levels), consisting in animals that shared the same pen and were slaughtered in the same batch, with an incidence matrix $\mathbf{Z_c}$; while $\mathbf{e}$ is the random vector of residual effects. The model applied for BF, LT and FBW did not include the initial age, as these traits were only measured at the end of the test. Multinomial distributions were assumed for $\mathbf{a}$, $\mathbf{cg}$ and $\mathbf{e}$ effects; $\mathbf{a} \mid \mathbf{G}0 \sim \mathrm{N}(0, \mathbf{G}0 \otimes \mathbf{A})$, $\mathbf{cg} \mid \mathbf{P}0 \sim \mathrm{N}(0, \mathbf{P}0 \otimes \mathbf{I})$, and $\mathbf{e} \mid \mathbf{R}0 \sim \mathrm{N}(0, \mathbf{R}0 \otimes \mathbf{I})$, respectively, where $\mathbf{I}$ represents an identity matrix, $\mathbf{A}$ is the relationship matrix, $\otimes$ refers to a Kronecker product, and $\mathbf{G}0$, $\mathbf{P}0$ and $\mathbf{R}0$ are co(variances) matrices for $\mathbf{a}$, $\mathbf{cg}$ and $\mathbf{e}$, respectively. In the bivariate analysis, $\mathbf{G}0$, $\mathbf{P}0$ and $\mathbf{R}0$ were 2x2 matrices, while they were scalars in the univariate analysis. Flat priors were considered for systematic effects and co(variances). The posterior marginal distributions of all the unknown parameters were obtained by the Gibbs sampling algorithm using the Gibbs1f90 software (Misztal et al., 2002). A single chain of 1 million samples was used for each unknown parameter, and the first 50,000 iterations were discarded. To avoid autocorrelation between the samples, one sample was taken every 100 iterations to calculate statistic parameters from the posterior marginal distribution. Convergence was checked separately for each estimation with Geweke's test and by visual observation.

Once the genetic parameters were obtained, the responses to selection for FCR, RFI and RG were calculated using two different genetic approaches. First, the direct individual response to selection was obtained for FCR, RFI and RG by the classical formula:

$R = h\, i\, \sigma_a$, where h is the square root of the heritability (equivalent to the accuracy for individual selection); i is the selection intensity; and σ_a is the additive standard deviation of the trait of interest. Second, multiple trait breeding indexes were built with the feed efficiency such as target selection trait (FCR, RFI or RG) and feeding behaviour traits. The feeding behaviour traits incorporated in each index were chosen accordingly to the genetic correlations observed with each target trait. No combinations of feed efficiency traits were evaluated in this study, as the objective was to specifically evaluate the benefits of including feeding behaviour traits. The responses for the multi-trait indexes were calculated as $R = i\, \sigma_I$, where σ_I refers to the index standard deviation. The index variance $\left(\sigma_I^2\right)$ was obtained as $\sigma_I^2 = \mathbf{c}'\,\mathbf{V}^{-1}\,\mathbf{c}$ (Mrode, 1996), where $\mathbf{c}$ represents the covariances vector between the additive value of the target trait with the traits used as selection criteria, and $\mathbf{V}$ is the matrix of phenotypic variances and covariances between all the traits included in the index. The accuracy of the response to selection was calculated as σ_I / σ_a. Afterward, we calculated the difference in response to selection between the multi-trait and univariate selection indexes.

3 | RESULTS AND DISCUSSION

3.1 | Phenotypic description

The phenotypic statistics of the analysed traits are shown in Table 1. The distribution of feeding behaviour traits and feed efficiency traits according to the period are in Figures S1 and S2. Some visual differences were found between the feeding behaviour traits. TPV and TPD were higher in the first period than the second, while FPV, FR and DFI were higher in the second. There appear to be similar values in NVD between periods. Feed efficiency traits showed higher values in the second period than in the first, although the standard deviations denote overlapping confidence intervals.

3.2 | Heritability estimates

Posterior means of the heritabilities for feeding behaviour traits and feed efficiency traits are shown in Table 2.

TABLE 1 Phenotypic means and standard deviations of traits evaluated during the different study periods.

		First period		Second period		Total	
Trait	Unit	Mean	SD	Mean	SD	Mean	SD
ADG	g/day	858.2	106.8	970.8	173.4	906.5	101.5
FCR	kg/kg	2.05	0.21	2.13	0.36	2.07	0.19
RG	g/day	1.79	78.31	−0.08	132.4	1.84	73.55
RFI	g/day	−1.12	92.34	−0.51	125.1	−0.40	88.81
BF	mm	–	–	–	–	6.02	1.36
LT	mm	–	–	–	–	65.88	5.17
TPD	min/day	55.25	10.69	46.79	9.6	51.25	9.70
TPV	s/vis	461.9	170.9	381.1	133.0	420.1	140.0
NVD	vis/day	7.76	2.29	8.02	2.06	7.76	2.00
FPV	g/vis	246.9	91.77	283.8	105.0	259.7	89.69
FR	g/m	32.78	7.10	44.14	9.38	36.93	7.84
DFI	kg/day	1.75	0.22	2.02	0.26	1.87	0.21

Abbreviations: ADG, average daily gain; BF, backfat thickness; DFI, daily feed intake; FCR, feed conversion rate; FPV, feed intake per visit; FR, feeding rate per visit; LT, loin depth; RFI, residual feed intake; RG, residual body weight gain; TPD, time spent in feeding per day; TPV, time spent in feeding per visit.

The posterior means of the heritabilities obtained in the first period were similar or higher than those obtained in the second. Greater environmental variability is usually expected in early life due to environmental factors such as weaning, regrouping, dietary changes or establishment of a social hierarchy (Kavlak & Uimari, 2019). However, in this study the animals entered the test at an average of 95 days of age, so the period close to weaning was not included. This could explain why the first period (86–132 days) did not have higher environmental variance than the second. The onset of puberty, which occurs after 150 days (Maignel et al., 1998), might explain the higher environmental variance observed in the second period (over 132 days). Puberty is accompanied by general changes on animal behaviour, including those related to feeding behaviour. Some traits (particularly feed efficiency traits) showed important differences between the estimates by periods and the total estimates. This difference was due to the fact that the total number of records per animal within the period varied due to individuals entering later or being slaughtered earlier. This variation in the number of records within periods may affect feed efficiency traits more than feeding behaviour traits. In general, the estimates for feeding behaviour traits in the whole period were slightly higher than those reported in the literature, ranging from 0.44 to 0.59 (Table 3). These differences could be explained by not taking into account the common litter effect, as animals were preselected before entering the study and in most cases only one pig per litter was included (>50%). Santiago et al. (2021) reported that in Duroc pigs, the common litter effect variance explained a low to moderate proportion (0–14%) of the total variance of feeding behaviour traits, according to the trait analysed.

Feed efficiency traits showed moderate to high heritability estimates (~0.4). These estimates ranged from 0.31 (ADG) to 0.49 (RFI). These estimates were generally in line with those found in the literature. However, there are high variability between studies due to differences in the breeds, housing conditions, length of the testing period, and evaluation models used in each study (Table 4). However, when we compared our results with the study carried out by Dugué et al. (2020), with an analogous model and also in Pietrain pigs, the heritability estimates for FCR were similar. In addition, as the animals belonged to a selection nucleus, environmental variables were more controlled than in commercial farms. This could lead to a reduction of the error variance and a relative increase of the additive variance.

3.3 | Correlation estimates

The posterior means of the estimated genetic and phenotypic correlations between the first and the whole period for feeding behaviour traits are shown in Table 5. Estimated genetic correlations were high for all traits (higher than 0.79). These results indicate that the traits measured in the first period could be good predictors for the whole period. This could lead to a reduction in the testing time and thus a reduction in the feeding cost per animal tested. However, the analysis did not converge properly for feed efficiency traits. These traits could be more sensitive to the number of measures than feed behaviour traits. As some

TABLE 2 Variance components and heritabilities estimates for feeding behaviour traits and feed efficiency traits obtained in both study periods and the total period.

			First period				Second period				Total period			
Trait	**Unit**	σ^2_{cg}	σ^2_a	σ^2_e	h^2	σ^2_{cg}	σ^2_a	σ^2_e	h^2	σ^2_{cg}	σ^2_a	σ^2_e	h^2	**HPD95%**
FR	g/min	6.94	29.27	19.43	0.52	11.80	45.32	40.44	0.46	6.88	33.31	25.3	0.50	[0.37, 0.65]
TPD	min/day	29.57	76.86	38.16	0.53	11.14	58.62	33.03	0.56	12.24	63.89	30.64	0.59	[0.47, 0.72]
TPV	s/vis	5561.15	15,540.06	10,121.63	0.49	3809.11	8807.75	6398.91	0.46	3825.08	9839.02	7134.05	0.47	[0.36, 0.57]
NVD	vis/day	1.53	3.54	0.86	0.59	1.16	1.95	1.56	0.41	1.09	2.68	0.72	0.59	[0.45, 0.73]
FPV	g/vis	1869.71	4214.89	2566.84	0.48	3017.64	4246.22	4535.61	0.35	2119.64	3806.51	2608.81	0.44	[0.32, 0.56]
DFI	kg/day	0.01	0.02	0.01	0.46	0.02	0.03	0.03	0.36	0.01	0.02	0.01	0.46	[0.33, 0.60]
ADG	g/day	7880.24	5629.76	5032.92	0.30	14,247.36	7057	12,810.1	0.20	4590.61	4260.26	4814.71	0.31	[0.18, 0.44]
FCR	kg/kg	0.02	0.02	0.06	0.17	0.05	0.02	0.05	0.15	0.00	0.01	0.01	0.40	[0.25, 0.53]
RG	g/day	2830.41	1645.23	2640.35	0.23	82,610.24	3843	5734	0.21	1718.55	2099.94	2052.76	0.35	[0.22, 0.49]
RFI	g/day	14.28	2700.86	6635.44	0.28	12,673	8821	10,060	0.28	4306.32	7491.48	3183.36	0.49	[0.37, 0.63]
BF	mm	–	–	–	–	–	–	–	–	0.13	0.78	0.92	0.31	[0.24, 0.37]
LT	mm	–	–	–	–	–	–	–	–	8.98	10.68	13.44	0.32	[0.20, 0.44]

Abbreviations: σ^2_{cg}, contemporary group variance; ADG, average daily gain; BF, backfat thickness; DFI, daily feed intake; FCR, feed conversion rate; FPV, feed intake per visit; FR, feeding rate per visit; HPD95%, 95% high posterior density; HPD95%, 95% highest posterior density interval; LT, loin depth; NVD, number of visits per day; RFI, residual feed intake; RG, residual body weight gain; TPD, time spent in feeding per day; TPV, time spent in feeding per visit.

TABLE 3 Comparison of heritability estimates for feeding behaviour traits obtained in different studies.

Trait	Schulze et al. (2003)	Do et al. (2013)	Do et al. (2013)	Herrera-Cáceres et al. (2019)	Santiago et al. (2021)	This study
Breed	LargeWhite × Landrace	Duroc	Landrace	Duroc	Duroc	Pietrain
DFI	0.39 ± 0.03	0.41 ± 0.04	0.48 ± 0.06	0.22 ± 0.08	0.19 ± 0.10	0.46 ± 0.08
FPV	0.41 ± 0.03	0.49 ± 0.04	0.57 ± 0.04	–	0.19 ± 0.10	0.44 ± 0.07
NVD	0.34 ± 0.04	0.44 ± 0.04	0.47 ± 0.05	0.48 ± 0.09	0.27 ± 0.11	0.59 ± 0.08
TPV	0.44 ± 0.03	0.47 ± 0.03	0.49 ± 0.04	0.47 ± 0.08	0.21 ± 0.11	0.47 ± 0.06
TPD	0.46 ± 0.03	0.56 ± 0.04	0.48 ± 0.04	0.23 ± 0.10	0.73 ± 0.12	0.59 ± 0.07
FR	0.44 ± 0.03	0.56 ± 0.01	0.55 ± 0.04	0.30 ± 0.08	0.63 ± 0.11	0.50 ± 0.07
N	5601	7388	4773	1144	602	1608

Abbreviations: DFI, daily feed intake; FPV, feed intake per visit; FR, feeding rate per visit; NVD, number of visits per day; TPD, time spent in feeding per day; TPV, time spent in feeding per visit.

TABLE 4 Comparison of heritability estimates for feed efficiency traits obtained in different studies.

Trait	Schulze et al. (2003)	Do et al. (2013)	Lu et al. (2017)	Kavlak and Uimari (2019)	Dugué et al. (2020)	This study
Breed	Large White × Landrace	Duroc	Duroc	Finnish Yorkshire	Pietrain	Pietrain
FCR	0.28 ± 0.04	0.30 ± 0.04	–	0.28 ± 0.06	0.41 ± 0.07	0.40 ± 0.08
ADG	0.36 ± 0.03	0.32 ± 0.04	0.45 ± 0.04	0.25 ± 0.06	0.36 ± 0.10	0.31 ± 0.07
RFI	–	0.36 ± 0.04	0.55 ± 0.04	0.32 ± 0.06	–	0.49 ± 0.08
RG	–	–	0.45 ± 0.03	–	–	0.35 ± 0.08
N	5601	7388	6464	3235	4773	1608

Abbreviations: ADG, average daily gain; FCR, feed conversion rate; RFI, residual feed intake; RG, residual body weight gain.

TABLE 5 Posterior mean of genetic (r_g) and phenotypic (r_p) correlations between the first period and total period of study of analysed traits with their 95% highest posterior density intervals (HPD95%).

Trait	r_g	HPD95%	r_p	HPD95%
TPD	0.96	[0.88, 1.00]	0.96	[0.95, 0.96]
TPV	0.89	[0.68, 0.99]	0.92	[0.91, 0.93]
NVD	0.94	[0.79, 0.99]	0.95	[0.94, 0.96]
FR	0.93	[0.76, 1.00]	0.93	[0.93, 0.94]
FPV	0.88	[0.57, 0.99]	0.92	[0.91, 0.93]
DFI	0.84	[0.51, 0.99]	0.84	[0.80, 0.90]
FBW	0.79	[0.29, 0.99]	0.79	[0.75, 0.82]

Abbreviations: DFI, daily feed intake; FBW, final body weight; FPV, feed intake per visit; FR, feeding rate per visit; NVD, number of visits per day; TPD, time spent in feeding per day; TPV, time spent in feeding per visit.

animals entered the test at more than 110 days old, they only had 22 days of records in the first period. In addition, the correlation between the first and the second period showed a wide HPD95%, which could be due to a lack of convergence (results not shown) and the high variability for the records within the second period. It is likely that the fewer measurements could affect these traits and their inter-correlations.

The correlations found within feeding behaviour traits (Table 6) indicate that animals that visit the feeder more often have shorter duration with lower feed intake per visit, although total time per day and DFI is higher than animals with a smaller number of visits. These results are in the same direction but of a different magnitude to those obtained in sire lines by Mcsweeny et al. (2003) (0.97 ± 0.02). However, the above-mentioned study was conducted with different housing conditions, in which each pen was occupied by up to 30 animals, which could have affected the behaviour traits due to the higher level of competition. The genetic correlation between TPD and FR was strongly negative (−0.85), which indicates that the animals that spent less time feeding per visit "compensated" by higher FR. The same correlation was reported in Holstein cows (Cavani et al., 2022) (−0.97), beef cattle (Kelly et al., 2021) (−0.65), Duroc pigs (Do et al., 2013; Santiago et al., 2021) (−0.90), and Finnish Yorkshire pigs Kavlak and Uimari (2019) (−0.70). Within the group of feed efficiency traits (Table 7),

TABLE 6 Posterior means of genetic (above) and phenotypic (below) correlations between feeding behaviour traits analysed in the total period with their 95% highest posterior density intervals (in brackets).

Trait	TPD	TPV	FR	NVD	FPV	DFI
TPD		0.52	−0.85	0.21	−0.08	0.38
		[0.34, 0.68]	[−0.92, −0.77]	[0.01, 0.40]	[−0.29, 0.13]	[0.17, 0.57]
TPV	0.44		−0.50	−0.75	0.69	0.01
	[0.37, 0.49]		[−0.67, −0.31]	[−0.84, −0.66]	[0.58, 0.80]	[−0.18, 0.23]
FR	−0.73	−0.29		−0.12	0.24	0.14
	[−0.77, −0.99]	[−0.35, −0.22]		[−0.34, 0.11]	[0.02, 0.45]	[−0.08, 0.36]
NVD	0.24	−0.68	−0.16		−0.90	0.22
	[0.17, 0.30]	[−0.72, −0.65]	[−0.24, −0.09]		[−0.95, −0.85]	[−0.00, 0.43]
FPV	−0.10	0.74	0.33	−0.82		0.23
	[−0.17, −0.03]	[0.71, 0.77]	[0.27, 0.39]	[−0.84, −0.79]		[0.02, 0.45]
DFI	0.23	0.05	0.36	0.13	0.29	
	[0.16, 0.29]	[−0.01, 0.12]	[0.31, 0.43]	[0.05, 0.20]	[0.23, 0.36]	

Abbreviations: DFI, daily feed intake; FPV, feed intake per visit; FR, feeding rate per visit; NVD, number of visits per day; TPD, time spent in feeding per day; TPV, time spent in feeding per visit.

TABLE 7 Posterior means of genetic (above) and phenotypic (below) correlations between feed efficiency traits analysed in the total period with their 95% highest posterior density intervals (in brackets).

Trait	ADG	FCR	RFI	FBW	BF	RG
ADG		−0.09	0.08	0.78	0.16	0.64
		[−0.38, 0.17]	[−0.19, 0.34]	[0.67, 0.88]	[−0.11, 0.42]	[0.47, 0.79]
FCR	−0.29		0.80	0.20	0.35	−0.82
	[−0.36, −0.21]		[0.69, 0.89]	[−0.08, 0.47]	[0.09, 0.60]	[−0.91, −0.7]
RFI	−0.01	0.69		0.06	−0.03	−0.58
	[−0.08, 0.07]	[0.65, 0.73]		[−0.19, 0.32]	[−0.33,0.25]	[−0.75, −0.41]
FBW	0.73	0.02	0.00		0.40	0.29
	[0.69, 0.77]	[−0.05, 0.09]	[−0.07, 0.07]		[0.17, 0.61]	[0.04, 0.53]
BF	0.39	0.17	0.00	0.45		−0.19
	[0.34, 0.44]	[0.11, 0.24]	[−0.11, 0.11]	[0.40, 0.50]		[−0.46, 0.08]
RG	0.76	−0.80	−0.54	0.40	0.08	
	[0.73, 0.79]	[−0.84, −0.7]	[−0.59, −0.5]	[0.34, 0.46]	[0.01, 0.14]	

Abbreviations: ADG, average daily gain; BF, backfat thickness; FBW, final body weight; FCR, feed conversion rate; RFI, residual feed intake; RG, residual body weight gain.

a positive genetic correlation was found between FCR and RFI (0.80), similar to those obtained by Do et al. (2013) and by Kavlak and Uimari (2019). This correlation is important, since FCR and RFI are the most influential efficiency traits. A positive correlation indicates that if one is selected, the other trait will also go in the desired direction. The ADG and RG showed genetic correlations with FBW (0.78 and 0.64, respectively). As FBW was corrected for the final age, these correlations denote that animals with higher ADG and RG reach higher final weights than other animals of the same age. Similar correlations were also found by de Haer et al. (1993) and by Kavlak and Uimari (2019). Contrary to expectations, no genetic correlation was found between ADG and FCR (−0.09). This might be explained by the positive genetic correlation between ADG and DFI (0.71). Similar results were reported in previous studies performed in Large White, Duroc and Yorkshire (Hall et al., 1999; Herrera-Cáceres et al., 2019; Kavlak & Uimari, 2019, respectively).

The DFI was the trait with the highest correlation with feed efficiency (Table 8), showing important genetic correlations with ADG (0.68), FCR (0.62), RFI (0.60), FBW (0.82),

TABLE 8 Genetic (r_g) and phenotypic (r_p) correlations between feeding behaviour traits and feed efficiency traits analysed in the total period with their 95% highest posterior density intervals (in brackets).

Trait	ADG		FCR		RFI		FBW		RG	
	r_g	r_p	r_g	r_p	r_g	r_p	r_g	r_p	r_g	r_p
TPD	0.44	0.30	−0.07	−0.03	0.03	0.09	0.37	0.11	0.24	0.19
	[0.23, 0.64]	[0.24, 0.36]	[−0.30, 0.16]	[−0.10, 0.03]	[−0.18, 0.22]	[0.02, 0.16]	[0.17, 0.58]	[0.04, 0.17]	[0.01, 0.46]	[0.12, 0.25]
TPV	0.09	0.04	0.07	0.08	−0.14	−0.03	0.16	0.09	−0.09	0.00
	[−0.33, 0.15]	[−0.02, 0.11]	[−0.15, 0.29]	[−0.10, 0.14]	[−0.34, 0.04]	[−0.10, 0.03]	[−0.04, 0.38]	[−0.02, 0.15]	[−0.33, 0.13]	[−0.07, 0.06]
NVD	0.49	0.25	−0.24	−0.12	0.14	0.08	0.06	0.00	0.39	0.21
	[0.28, 0.71]	[0.18, 0.32]	[−0.48, −0.01]	[−0.20, −0.05]	[−0.07, 0.34]	[−0.00, 0.16]	[−0.17, 0.29]	[−0.07, 0.06]	[0.17, 0.62]	[0.13, 0.28]
FR	−0.11	0.20	0.33	0.25	0.23	0.17	0.04	0.35	−0.28	−0.04
	[−0.40, 0.14]	[0.14, 0.27]	[0.10, 0.57]	[0.18, 0.31]	[−0.00, 0.44]	[0.10, 0.24]	[−0.20, 0.28]	[0.29, 0.41]	[−0.53, −0.02]	[−0.11, −0.02]
FPV	−0.16	0.11	0.44	0.27	0.09	0.11	0.33	0.33	−0.41	−0.10
	[−0.44, 0.10]	[0.03, 0.19]	[0.22, 0.65]	[0.20, 0.33]	[−0.13, 0.31]	[0.03, 0.18]	[0.10, 0.53]	[0.26, 0.38]	[−0.65, −0.17]	[−0.17, −0.02]
DFI	0.68	0.71	0.62	0.37	0.60	0.53	0.82	0.78	−0.10	0.12
	[0.53, 0.81]	[0.68, 0.75]	[0.41, 0.79]	[0.31, 0.43]	[0.43, 0.76]	[0.47, 0.58]	[0.74, 0.90]	[0.75, 0.81]	[−0.37, 0.16]	[0.05, 0.19]

Abbreviations: ADG, average daily gain; DFI, daily feed intake; FBW, final body weight; FCR, feed conversion rate; FPV, feed intake per visit; FR, feeding rate; NVD, number of visits per day; RFI, residual feed intake; RG, residual body weight gain; TPD, time spent in feeding per day; TPV, time spent in feeding per visit.

TABLE 9 Responses to selection obtained for feed conversion rate (FCR), residual feed intake (RFI), and residual body weight gain (RG) with different selection indices.

Target	Index type	Unit	Selection criteria	Response	Accuracy
FCR	Univariate	Kg/kg	FCR	−0.075i	0.63
RFI	Univariate	g/día	RFI	−60.58i	0.70
RG	Univariate	g/día	RG	27.10i	0.59
FCR	Multi-trait	Kg/kg	FCR+ DFI	−0.076i	0.64
FCR	Multi-trait	Kg/kg	FCR + DFI + FR	−0.077i	0.65
FCR	Multi-trait	Kg/kg	FCR + DFI + FR + FPV	−0.078i	0.66
FCR	Multi-trait	Kg/kg	FCR + FPV + FR	−0.076i	0.64
FCR	Multi-trait	Kg/kg	FCR + FPV + FR + NVD	−0.076i	0.64
RFI	Multi-trait	g/día	RFI + DFI	−61.29i	0.71
RFI	Multi-trait	g/día	RFI + DFI + FR	−61.33i	0.71
RFI	Multi-trait	g/día	RFI + DFI + FR + NVD	−61.53i	0.71
RFI	Multi-trait	g/día	RFI + FR + NVD	−61.51i	0.71
RG	Multi-trait	g/día	RG + FPV	29.02i	0.63
RG	Multi-trait	g/día	RG + FPV + NVD	32.45i	0.70

Abbreviations: DFI, daily feed intake; FPV, feed intake per visit; FR, feeding rate per visit; NVD, number of visits per day; TPD, time spent in feeding per day.

and BF (0.49). Herrera-Cáceres et al. (2019) found similar correlations in Duroc pigs. Kavlak and Uimari (2019) analysed these correlations in five different periods, obtaining similar correlations between DFI and the feed efficiency traits in Finish Yorkshire pigs. The FR was positively correlated with FCR and RFI (0.33 and 0.23) and negatively with RG (−0.28). Positive values between FR and FCR were also found in Duroc (0.40) by Herrera-Cáceres et al. (2019), and Large White (0.15) by Hall et al. (1999). In addition, a negative correlation between FR and RG (−0.41) was found in Duroc by Lu et al. (2017). These results suggest that the fast-eating pigs could be less efficient.

3.4 | Response to selection

The response to the univariate selection was −0.075i for FCR, −60.58i for RFI, and 27.10i for RG (Table 9). The inclusion of feeding behaviour traits in the selection index slightly increased the selection response for FCR (4%) and RFI (1.8%) while a significant increase of 19% was found for RG, with an increase in the accuracy from 0.59 to 0.70. This is explained because RFI (0.49) was the feed efficiency trait with the highest heritability and the lowest genetic and phenotypic correlations with the feeding behaviour traits, while RG had a lower heritability (0.35) and a higher genetic correlation, especially with NVD which had a heritability of 0.59. Although DFI was the most correlated trait with FCR and RFI, its inclusion to improve the responses for FCR and RFI could be redundant because DFI is present in both definitions, leading to 'spurious correlations' (Pearson, 1897). In the case of RG, there was no relevant correlation with DFI because it was corrected by DFI in the lineal regression when it was obtained.

4 | CONCLUSIONS

The heritabilities estimated in the Pietrain line were high for feeding behaviour traits (from 0.44 to 0.59) and moderate to high for feed efficiency traits (from 0.31 to 0.49). Similar estimated values were found between both periods analysed. Relevant genetic correlations were found between feeding behaviour traits measured on an automatic feeder and feed efficiency traits. FCR showed genetic correlations with DFI (0.62), FPV (0.44), FR (0.33), and NVD (−0.24). For RFI, the highest correlation was with DFI (0.60), but the other analysed traits were lower correlated than FCR. In addition, the genetic correlations found between FR and feed efficiency traits may indicate that fast-eating pigs are less efficient. On the other hand, the inclusion of correlated feeding behaviour traits in the selection index did not show much improvement for FCR and RFI, whereas for RG the selection response improved by 19%, with an increase in accuracy from 0.59 to 0.70. This is particularly important in farms that have already introduced automatic feeders, as measuring feeding behaviour traits does not involve an additional cost. However, it is essential to note that the index traits depend on the genetic correlations in the specific population under selection. Furthermore, as the selection indices are susceptible to errors in genetic parameters, a large number of animals are necessary to estimate the genetic parameters accurately and obtain the desired response to selection.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no competing interests.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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