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Genetic parameters of sow feed efficiency during lactation and its underlying traits in a Duroc population

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*As a result of the genetic selection for prolificacy and the improvements in the environment and farms management, litter size has increased in the last few years so that energy requirements of the lactating sow are greater. In addition, selection for feed efficiency of growing pigs is also conducted in maternal lines, and this has led to a decrease in appetite and feed intake that is extended to the lactation period, so the females are not able to obtain the necessary energy and nutrients for milk production and they mobilize their energetic reserves. When this mobilization is excessive, reproductive and health problems occur which ends up in an early sow culling. In this context, it has been suggested to improve feed efficiency at lactation through genetic selection. The aim of this study is to know, in a Duroc population, the genetic determinism of sow feed efficiency during lactation and traits involved in its definition, as well as genetic and environmental associations between them. The studied traits are daily lactation feed intake (**dLFI**), daily sow weight balance (**dSWB**), backfat thickness balance (**BFTB**), daily litter weight gain (**dLWG**), sow residual feed intake (**RFI**) and sow restricted residual feed intake (**RRFI**) during lactation. Data corresponded to 851 parities from 581 Duroc sows. A Bayesian analysis was performed using Gibbs sampling. A four-trait repeatability animal model was implemented including the systematic factors of batch and parity order, the standardized covariates of sow weight (SW_f) and litter weight (LWs) at farrowing for all traits and lactation length for BFTB. The posterior mean (posterior SD) of heritabilities were: 0.09 (0.03) for dLFI, 0.37 (0.07) for dSWB, 0.09 (0.03) for BFTB, 0.22 (0.05) for dLWG, 0.04 (0.02) for RFI and null for RRFI. The genetic correlation between dLFI and dSWB was high and positive (0.74 (0.11)) and null between dLFI and BFTB. Genetic correlation was favourable between RFI and dLFI and BFTB (0.71 (0.16) and −0.69 (0.18)), respectively. The other genetic correlations were not statistically different from zero. The phenotypic correlations were low and positive between dLFI and dSWB (0.27 (0.03), dSWB and BFTB (0.25 (0.04)), and between dLFI and dLWG (0.16 (0.03)). Therefore, in the population under study, the improvement of the lactation feed efficiency would be possible either using RFI, which would not have unfavourable correlated effects, or through an index including its component traits.*

Keywords: pig, selection, genetic parameters, feed efficiency, lactation

Implications

In order to improve feed efficiency of the sow during lactation in a Duroc pig population, a selection index based on its component traits with optimal economic weights or selection for residual feed intake could be effective. However, selection for restricted residual feed intake would not be effective at all because of its null genetic variation. No unfavourable correlated effects on body conditions of the sow at the end of lactation would be expected by selecting for residual feed intake. Daily lactation feed intake seems to be positively correlated with sow weight balance but not significantly correlated with backfat thickness balance.

Introduction

Lactation is one of the most energy demanding processes in the productive life of a sow (Thekkoot *et al.*, 2016). Because litter size has increased as a result of genetic selection in the last years (Silalahi *et al.*, 2016) and is still a main objective of the breeding programs, energy requirements during lactation are also increasing. On the other hand, most of the pig-breeding programs also include among its priority aims the increase of feed efficiency during the growth/finish phase

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of production. This selection has had as correlated effects the reduction of appetite and feed intake capacity at this stage of animal's life but also at reproduction stage, during lactation (Gilbert *et al.*, 2012). In this situation, feed consumed at lactation is not enough to sustain milk production and maintenance of other biological functions of the sow leading to a mobilization of body reserves (Noblet *et al.*, 1990). However, excess mobilization of body reserves impairs sow posterior reproductive performance (Lundgren *et al.*, 2014) and leads to early culling, which in turn affects profitability. Recently, Young *et al.* (2016) have shown that sows selected for low residual feed intake (**RFI**) at growing are also more efficient at converting energy from food and body reserves mobilization into piglet growth, which would be additionally improved by a high piglet feed efficiency. These authors suggest to include in the selection criteria sow feed intake and body condition change at lactation in order to prevent potential negative effects on rebreeding performance due to a negative energy balance (Whittemore and Morgan, 1990; Clowes *et al.*, 2003). This requires having accurate estimates of the genetic parameters of all the traits involved in energy balance of the sow at lactation (Thekkoot *et al.*, 2016) in the population to be selected. However, there is little published information regarding the potential for increasing levels of sow feed efficiency during lactation and its component traits by genetic selection.

Components of feed efficiency during lactation come from energy metabolism in lactating sows which was defined by Bergsma *et al.* (2009), based on studies performed by Noblet *et al.* (1990). Energy inputs are feed intake and mobilized body reserves. This energy is used for growth and maintenance of the sow and for milk production, which in turn is used for piglet growth and maintenance. Lactation feed efficiency results from the combination of all those components, and it has been defined in different ways: (i) as the ratio between the output and the input (Bergsma *et al.*, 2009), (ii) as the difference between actual sow feed intake (**FI**) and that predicted from a phenotypic regression of FI on requirements for production and maintenance of body condition (RFI; Gilbert *et al.*, 2012) and (iii) as the body energy balance (Young *et al.*, 2016) of the sow at lactation. Genetic parameters of all those traits have been previously estimated in few studies in Yorkshire, Large White or Landrace populations (Bergsma *et al.*, 2008; Gilbert *et al.*, 2012; Thekkoot *et al.*, 2016; Young *et al.*, 2016). However, results could be different in a Duroc population, which is characterized for its high content in intramuscular fat (Sánchez *et al.*, 2017), and probably have a different energy metabolism pattern.

Regarding feed efficiency (**FE**) traits, Kennedy *et al.* (1993) showed that despite there is no phenotypic correlation between residuals (RFI) and the explanatory variables representing animal's needs, this does not guarantee null genetic correlations. In fact, unfavourable genetic response on growth has been observed after selection for RFI calculated from phenotypic regressions (Gilbert *et al.*, 2007; Cai *et al.*, 2008; Drouilhet *et al.* 2016). Kennedy *et al.* (1993) proposed estimating RFI from the genetic regression of FI on production traits instead of from the phenotypic regression, and defined restricted residual feed intake (**RRFI**), because of its equivalence to a restricted selection index in which production traits are held constant. This definition of FE guarantees null genetic correlation with performance traits, and thus null correlated response on them. Implementation of this definition of FE has been performed using multiple-trait models (Strathe *et al.*, 2014; Shirali *et al.*, 2018; Piles and Sanchez, 2019) for components of feed efficiency in the growing pigs and rabbits but not during lactation.

The aim of this research was to estimate variance components and genetic parameters of phenotypic and genetic RFI during lactation, as well as of traits involved in their definitions, in a Duroc pig maternal line.

Material and methods

Animals and data

Animals belonged to a Duroc pig population which was bred in a commercial farm placed in Riudarenes, Girona. The purebred Duroc population was established in 1984 and kept reproductively closed since 1991. It has been selected for a genetic index including both reproductive traits, such as number born alive and number of teats (approximately 70% of economic weight), and productive traits, such as BW at 180 days and backfat thickness.

Data from up to 2 farrowings from 677 sows were recorded from May 2015 to May 2016, distributed in 25 batches. Sows were progeny from 68 different boars and 476 different sows. During the trial, sows had on average 734 days of age and 3.4 parities. Culling criteria were the same throughout the experiment. Sows were culled due to poor fertility (24%), old age (28%), low productivity (12%), lameness (13%), mortality (9%) and other not specified causes (14%). For example, a sow was culled due to low fertility after failing to cycle twice consecutively. After the third and subsequent weanings, sows with an average litter size less than 7.5 piglets weaned were culled due to low productivity. Sows with signs of lameness were culled after weaning.

During gestation, sows were housed in groups and fed once a day 2.16 kg on average of a standard diet containing 2085 kcal net energy, a minimum of 125 g CP, 70 g crude fibre and 6.6 g total lysine/kg. On average, a week before parturition, sows were transferred to the farrowing house. At that time, they were weighed (**SW**$_E$) and backfat thickness (**BFT**$_E$) was measured at last rib level using an ultrasound system (PIGLOG 105.MB45). Feed intake was limited to a maximum of 2.2 kg before farrowing and no food was provided at farrowing day. Within a maximum of 2 days after farrowing, the number of piglets born alive and stillborn was recorded and adoptions were made to equalize the number of piglets per litter. The number of total born, litter size (i.e. the final number of piglets in the litter; **LS**$_S$) and litter weight (**LW**$_S$) at the start of lactation were recorded and average piglet weight (**PIW**$_S$) at this time was computed as $PIW_S = LW_S/LS_S$.

Records from litters weighed later than 2 days after farrowing were not included in the analysis. During the first week of lactation, sows were fed twice a day a standard food containing 2325 kcal net energy, 166 g CP, 9 g total lysine, and a minimum of 49.1 g of crude fibre per kilogram. The amount of food supplied was fixed for all sows increasing daily from 1 kg twice a day at day 1 to 3 kg twice a day at day 10 of lactation. Then, the amount of food provided to each sow was established based on sow feed intake during the previous day. Thus, it was increased 0.5 kg every 2 days when the sow finished the whole food the day before, and was kept constant or reduced otherwise. Food refusals occurred in less than 3% of the meals. The amount of food rejected was not recorded. Daily feed intake was recorded every 3 to 5 days during lactation. The minimum and maximum amount of feed supplied daily were 2.22 and 9.62 kg/day, respectively. Data from sows with less than five daily feed intake records or from sows which rejected to eat more than 2 consecutive days were removed for the analysis. Then, after comparing different polynomial models, a quadratic function was fitted to the individual daily feed intake data according to the goodness of fit (i.e. Bayesian information criterion) with 'lm' function from the 'stats' R package (R Core Team) assuming that the error variance was constant through lactation. The adjusted R^2 was on average 0.997. Total feed intake was estimated as the sum of daily predicted feed intake for the period from farrowing to 27 days after that. Finally, daily lactation feed intake (**dLFI**) was calculated dividing total feed intake by lactation length (27 days). Around mid-lactation (12 ± 6 days after birth), litter size (**LS$_\mathbf{i}$**) and weight (**LW$_\mathbf{i}$**) were recorded in 2 of the 25 batches. At weaning, litter size (**LS$_\mathbf{W}$**) and weight (**LW$_\mathbf{W}$**) were recorded again in all batches. Average piglet weight at mid-lactation (**PIW$_\mathbf{i}$**) was obtained as $\mathrm{PIW_i(kg)} = \frac{\mathrm{LW_i}}{\mathrm{LS_i}}$.

At weaning, sow BW (**SW$_\mathbf{W}$**) and backfat thickness (**BFT$_\mathbf{W}$**) were also recorded in the same way as before. Sow weight at farrowing (**SW$_\mathbf{f}$**) was estimated as in Bersgma *et al.* (2009) (deduced from Noblet *et al.*, 1985 and described in Supplementary Material S1).

Daily sow weight balance (**dSWB**) (gain/loss) was computed as follows:

$$\mathrm{dSWB}\left(\frac{\mathrm{kg}}{\mathrm{day}}\right) = \frac{\mathrm{SW_w} - \mathrm{SW_f}}{\mathrm{DL}}$$

where DL was the number of days between $\mathrm{SW_W}$ and $\mathrm{SW_f}$ recordings (i.e. lactation length).

Backfat thickness balance (**BFTB**) was defined as: $\mathrm{BFTB} = \mathrm{BFT_W} - \mathrm{BFT_E}$.

Sow weight at weaning (**SW$_\mathbf{W}$**) was computed as Bergsma *et al.* (2009); based on Kim *et al.* (1999, 2000) and described in Supplementary Material S1.

Finally, daily litter weight gain (**dLWG**) was computed: $\mathrm{dLWG}\left(\frac{\mathrm{kg}}{\mathrm{day}}\right) = \frac{\mathrm{LW_w} - \mathrm{LW_s}}{\mathrm{DL}}$.

After removing records with missing values and outliers (i.e. observations that lie outside 1.5 * IQR, where IQR, the 'Inter Quartile Range' is the difference between 75th and 25th quartiles), the data set consisted of 851 farrowings from 581 sows distributed in 90, 208, 176, 136, 120 and 121 l for parity order classes 1 to 6, respectively.

Statistical analysis

Daily lactation feed intake, dSWB, BFTB and dLWG were considered to be the main components of feed efficiency during lactation. Backfat thickness balance corrected for lactation length was used as a measure of energy sink instead of daily BFTB because of numerical errors associated with the low variation of the last trait. Component traits of feed efficiency were jointly analysed in a four-trait repeatability model. Piles *et al.* (2006) showed that this approach can be considered appropriate for selection because the accuracies of predicted breeding values obtained under the repeatability and multi-trait models are practically equal, despite those traits at different parities could be considered as different traits because of heterogeneity of heritabilities and correlations lower than 1 as it happens for litter size (Noguera *et al.*, 2002). The model was defined as follows:

$$\begin{aligned}\mathbf{dLFI} = {} & \mathbf{Xb}_{\mathrm{dLFI}} + \beta_{1,1}\mathbf{SW}_{\mathrm{f}} + \beta_{1,2}\mathbf{LW}_{\mathrm{s}} + \mathbf{Za}_{\mathrm{dLFI}} + \mathbf{Sp}_{\mathrm{dLFI}} \\ & + \mathbf{e}_{\mathrm{dLFI}}\end{aligned}$$

$$\begin{aligned}\mathbf{dSWB} = {} & \mathbf{Xb}_{\mathrm{dSWB}} + \beta_{2,1}\mathbf{SW}_{\mathrm{f}} + \beta_{2,2}\mathbf{LW}_{\mathrm{s}} + \mathbf{Za}_{\mathrm{dSWB}} + \mathbf{Sp}_{\mathrm{dSWB}} \\ & + \mathbf{e}_{\mathrm{dSWB}}\end{aligned}$$

$$\begin{aligned}\mathbf{BFTB} = {} & \mathbf{Xb}_{\mathrm{BFTB}} + \beta_{3,1}\mathbf{SW}_{\mathrm{f}} + \beta_{3,2}\mathbf{LW}_{\mathrm{s}} + \beta_{3,3}\mathbf{DL} + \mathbf{Za}_{\mathrm{BFTB}} \\ & + \mathbf{Sp}_{\mathrm{BFTB}} + \mathbf{e}_{\mathrm{BFTB}}\end{aligned}$$

$$\begin{aligned}\mathbf{dLWG} = {} & +\mathbf{Xb}_{\mathrm{dLWG}} + \beta_{4,1}\mathbf{SW}_{\mathrm{f}} + \beta_{4,2}\mathbf{LW}_{\mathrm{s}} + \mathbf{Za}_{\mathrm{dLWG}} \\ & + \mathbf{Sp}_{\mathrm{dLWG}} + \mathbf{e}_{\mathrm{dLWG}}\end{aligned}$$

where **dLFI**, **dSWB**, **BFTB** and **dLWG** denote the vectors of phenotypic records for the respective traits. The systematic effects of batch and parity order were included in the vectors: $\mathrm{b_{dLFI}}$ for dLFI, $\mathrm{b_{dSWB}}$ for dSWB, $\mathrm{b_{BFTB}}$ for BFTB and $\mathrm{b_{dLWG}}$ for dLWG. Batch (i.e. reproduction groups) effect had 25 levels, with 6 to 45 records each (average equal to 34). Parity order had 6 levels (1, 2, 3, 4, 5, >5 parities) with 116 to 245 records each (average equal to 190). In order to focus on lactation period, covariates defining initial conditions of the females and litter at lactation were introduced in the models. Thus, **SW$_\mathbf{f}$** and **LW$_\mathbf{s}$** are vectors of standardized covariates of $\mathrm{SW_f}$ and $\mathrm{LW_s}$, respectively, which were computed subtracting the mean from the original variable and dividing by the SD; $\beta_{1,1,}$ and $\beta_{1,2}$ are partial coefficients of regression of dLFI on $\mathrm{SW_f}$ and $\mathrm{LW_s}$, respectively; $\beta_{2,1,}$ and $\beta_{2,2}$ are partial coefficients of regression of dSWB on $\mathrm{SW_f}$ and $\mathrm{LW_s}$, respectively; $\beta_{3,1,}$ and $\beta_{3,2}$ are partial coefficients of regression of BFTB on $\mathrm{SW_f}$ and $\mathrm{LW_s}$, respectively; $\beta_{4,1}$ and $\beta_{4,2}$ are partial coefficients of regression of dLWG on $\mathrm{SW_f}$ and $\mathrm{LW_s}$, respectively. $\mathbf{a}_{\mathrm{dLFI}}$, $\mathbf{a}_{\mathrm{dSWB}}$, $\mathbf{a}_{\mathrm{BFTB}}$ and $\mathbf{a}_{\mathrm{dLWG}}$ are vectors of additive genetic effects for dLFI, dSWB, $\mathrm{BFT_W}$ and dLWG, respectively. Similarly, $\mathbf{p}_{\mathrm{dLFI}}$, $\mathbf{p}_{\mathrm{dSWB}}$, $\mathbf{p}_{\mathrm{BFTB}}$, $\mathbf{p}_{\mathrm{dLWG}}$, and $\mathbf{e}_{\mathrm{dLFI}}$, $\mathbf{e}_{\mathrm{dSWB}}$, $\mathbf{e}_{\mathrm{BFTB}}$, $\mathbf{e}_{\mathrm{dLWG}}$ are the vectors of permanent effects and residuals for the four traits, respectively. **X**, **Z** and **S** are design matrices for systematic, additive genetic and permanent effects, respectively.

Marginal posterior distributions of variance components and all other unknowns were estimated applying Gibbs sampling algorithm using gibbs1f90 program (Misztal *et al.*, 2002). Prior distributions for all random effects were multivariate normal distributions with a mean of zero and variances:

$$\mathrm{var}\begin{pmatrix}\mathbf{e}_{\mathrm{dLFI}}\\ \mathbf{e}_{\mathrm{dSWB}}\\ \mathbf{e}_{\mathrm{BFTB}}\\ \mathbf{e}_{\mathrm{dLWG}}\end{pmatrix} = \mathbf{I}\otimes\mathbf{R}_0,\ \mathrm{var}\begin{pmatrix}\mathbf{a}_{\mathrm{dLFI}}\\ \mathbf{a}_{\mathrm{dSWB}}\\ \mathbf{a}_{\mathrm{BFTB}}\\ \mathbf{a}_{\mathrm{dLWG}}\end{pmatrix} = \mathbf{A}\otimes\mathbf{G}_0\ and$$

$$\mathrm{var}\begin{pmatrix}\mathbf{p}_{\mathrm{dLFI}}\\ \mathbf{p}_{\mathrm{dSWB}}\\ \mathbf{p}_{\mathrm{BFTB}}\\ \mathbf{p}_{\mathrm{dLWG}}\end{pmatrix} = \mathbf{I}\otimes\mathbf{P}_0$$

where $\mathbf{R_0}$, $\mathbf{G_0}$ and $\mathbf{P_0}$ are 4×4 matrices of residual, additive genetic and permanent environmental (co)variances, respectively, and **A** is the additive genetic relationship matrix. To construct this matrix, the pedigree file comprised 1659 individuals including 3 generations of ancestors.

Random effects **e**, **a** and **p** were considered independent of each other. Prior distributions for the covariance matrices $\mathbf{R_0}$, $\mathbf{G_0}$ and $\mathbf{P_0}$ were inverse Wishart distributions, and priors for systematic effects of the model were assumed to be flat priors.

The Gibbs sampler was run for 1 000 000 rounds with a burn-in of 200 000 rounds. For the posterior analysis, 1 of each 100 samples was saved. Thus, a total of 8000 samples from the joint posterior distribution of all location and (co) variance parameters were saved for post-Gibbs analysis. The 'boa' R package (Smith, 2007) was used for convergence diagnostics and to obtain summary statistics of marginal posterior distributions of model parameters.

Definitions of RFI and RRFI are equivalent to selection indexes based on the component traits with weights equal to the corresponding partial regression coefficients at a negative value (Kennedy *et al.*, 1993). Phenotypic and genetic variance–covariance matrices for those selection indexes and FE components were defined as was shown by Kennedy *et al.* (1993) and recently implemented by Shirali *et al.* (2018):

$$\mathbf{I_G} = \mathbf{B}'\mathbf{G}_0\mathbf{B}\ \text{and}\ \mathbf{I_P} = \mathbf{B}'\mathbf{P}_0\mathbf{B}.$$

Being ***b*** matrix defined as:

$$\mathbf{B} = \begin{bmatrix} 1 & 0 & 0 & 0\\ 0 & 1 & 0 & 0\\ 0 & 0 & 1 & 0\\ 0 & 0 & 0 & 0\\ 1 & \mathrm{b_{P,dSWB}} & \mathrm{b_{P,BFTB}} & \mathrm{b_{P,dLWG}}\\ 1 & \mathrm{b_{G,dSWB}} & \mathrm{b_{G,BFTB}} & \mathrm{b_{G,dLWG}} \end{bmatrix}$$

where $\mathrm{b_{P,dSWB}}$, $\mathrm{b_{P,BFTB}}$ and $\mathrm{b_{P,dLWG}}$ are phenotypic regression coefficients from the 3×1 vector: $\boldsymbol{b_P} = \boldsymbol{P_p^{-1} P_{p,dLFI}}$ and $\mathrm{b_{G,dSWB}}$, $\mathrm{b_{G,BFTB}}$ and $\mathrm{b_{G,dLWG}}$ are genetic regression coefficients from the vector $\boldsymbol{b_G} = \boldsymbol{G_p^{-1} G_{p,dLFI}}$ being $\boldsymbol{P_p^{-1}}$ and $\boldsymbol{G_p^{-1}}$ 3×3 matrices of phenotypic and genetic variance–covariance of dSWB, BFTB and dLWG obtained from $\mathbf{P_0}$ and $\mathbf{G_0}$, respectively. $\boldsymbol{P_{p,dLFI}}$ and $\boldsymbol{G_{p,dLFI}}$ are the 3×1 vector of phenotypic and genetic covariances of dSWB, BFTB and dLWG with dLFI also obtained from $\mathbf{P_0}$ and $\mathbf{G_0}$.

Results

Descriptive statistics

Descriptive statistics of the traits analysed in this study are given in Table 1. Sow weighed around 200 kg at farrowing and had 19 mm of backfat. They consumed 153 kg during lactation (27 days) and lost 2.9 mm of backfat thickness (15% the initial amount) whereas they gained 1 kg of BW (0.04 kg/day) on average, being this amount highly variable (CV = 18) with an interquartile range of (−8.6, 12.6) (up to 6.2% the initial value). Litter weight at farrowing was around 16 kg on average, growing at a rate of 2.09 kg/day (0.19 kg/day per piglet, being litter size at the start of lactation 11 piglets).

Impact of pre-farrow traits on feed efficiency during lactation and its component traits

Partial regression coefficients of pre-farrow traits on dLFI, dSWB, BFTB and dLWG are shown in Table 2. Body weight at farrowing ($\mathrm{SW_f}$) had a significant but small effect on feed intake during lactation. A greater $\mathrm{SW_f}$ resulted in a smaller feed intake 0.072 kg/day per SD unit of increase in $\mathrm{SW_f}$. This corresponds to −0.003 kg/day per kg of increase in $\mathrm{SW_f}$. Note that in Table 2 regression coefficients are referred to SD units of the covariates, so the numbers reported here are transformations from those in Table 2, using the variation indicated in Table 1. Litter weight at the beginning of lactation had also a small effect: Sows eat 13 g/day more per 1 kg of increment in $\mathrm{LW_s}$. Sow weight at farrowing also had a significant effect on mobilization of body reserves (i.e. dSWB and BFTB). Heavier sows at farrowing tend to have a greater mobilization of body reserves (i.e. to lose more BW and backfat) than lighter sows (i.e. dSWB and BFTB decreased 14 g/day and 0.06 mm, respectively, during

Table 1 *Summary statistics*

Trait	Abbreviation	Units	Mean	SD	Interquartile range
Sow weight at farrowing	SW_f	kg	201.8	22.4	185.8, 217.1
Backfat at farrowing	BF_f	mm	19.18	3.78	17, 21
Litter weight at start of lactation	LW_s	kg	15.8	2.8	13.7, 17.8
Litter size at start of lactation	LS_s	units	10.93	1.02	10, 12
Litter size at weaning	LS_w	units	9.38	1.35	9, 10
Daily lactation feed intake	dLFI	kg/day	5.68	0.54	5.32, 6.03
Daily sow weight balance	dSWB	kg/day	0.04	0.72	−0.41, 0.51
Back fat thickness balance	BFTB	mm	−2.94	1.79	−3.94, −1.94
Daily litter weight gain	dLWG	kg/day	2.09	0.30	1.8, 2.3
Lactation length	DL	day	26.4	1.8	25, 28

Phenotypic means, SD and interquartile range of traits involved in sow lactation feed efficiency.

Table 2 *Regression coefficients (standard error) of dLFI, dSWB, BFTB and dLWG on standardized pre-farrow traits (SW_f and LW_s) and DL*

Covariate	**dLFI** (kg/day)	**dSWB** (kg/day)	**BFTB** (mm)	**dLWG** (kg/day)
SW_f (SD units)	−0.072 (0.019)	−0.304 (0.022)	−0.370 (0.083)	0.0059 (0.013)
LW_s (SD units)	0.037 (0.015)	−0.177 (0.017)	−0.209 (0.065)	0.054 (0.010)
DL (day)	–	–	−0.077 (0.047)	–

dLFI = daily lactation feed intake; dSWB = daily sow weight balance; BFTB = backfat thickness balance; dLWG = daily litter weight gain; SWf = standardized sow weight at farrowing; LW_s = standardized litter weight at start of lactation; DL = lactation length.

Table 3 *Posterior means (posterior SD) of variance components and ratios of phenotypic variance of sow lactation feed efficiency and its component traits*

	Trait					
Parameter	dLFI	dSWB	BFTB	dLWG	RFI	RRFI
σ_a^2	0.014 (0.005)	0.079 (0.018)	0.242 (0.098)	0.015 (0.004)	0.0053 (0.0024)	0.000 (0.000)
σ_p^2	0.013 (0.005)	0.025 (0.010)	0.518 (0.151)	0.009 (0.003)	0.015 (0.006)	0.039 (0.013)
σ_e^2	0.131 (0.009)	0.109 (0.010)	2.084 (0.155)	0.046 (0.003)	0.116 (0.008)	0.170 (0.016)
h^2	0.085 (0.028)	0.368 (0.070)	0.085 (0.033)	0.217 (0.052)	0.039 (0.017)	0.000 (0.000)
p^2	0.084 (0.031)	0.117 (0.045)	0.182 (0.050)	0.126 (0.048)	0.111 (0.039)	0.186 (0.056)

dLFI = daily lactation feed intake (kg/day); dSWB = daily sow weight balance (kg/day); BFTB = back fat thickness balance (mm); dLWG = daily litter weight gain (kg/day); RFI = sow residual feed intake (kg/day); RRFI = sow restricted residual feed intake (kg/day); σ_a^2 = additive variance; σ_p^2 = permanent variance; σ_e^2 = residual variance; h^2 = heritability; p^2 = permanent environmental variation relative to phenotypic variation.

lactation per kg of SW_f). Litter weight at the beginning of lactation affects litter growth mainly due to a scale effect but also to body reserves mobilization decreasing the balance of sow weight and backfat thickness. An increase of 1 kg in litter weight at the beginning of lactation means a loss of 63 g/day in sow weight and 0.07 mm of backfat thickness.

Heritability and proportion of the phenotypic variance due permanent effects

Heritability was very low for RFI during lactation (posterior mean (posterior SD) = 0.039 (0.017)) and null for RRFI (Table 3). The highest values were found for daily changes in BW of the sow (0.37 (0.07)) and the litter (0.22 (0.05)). Both, dLFI and BFTB had a low heritability. The proportion of the phenotypic variance due to permanent effects ranged from 0.08 to 0.18 for components of FE. It was low for RFI (0.11 (0.04)) but larger for RRFI (0.19 (0.06)).

Genetic and environmental correlations

Genetic and phenotypic correlations are shown in Figure 1, and permanent effects and residual correlations are shown in Figure 2. Residual correlations had the same sign and magnitude than phenotypic correlations. As it was expected, RFI was not phenotypically correlated with dSWB, BFTB and dLWG. Residual feed intake and RRFI were highly correlated

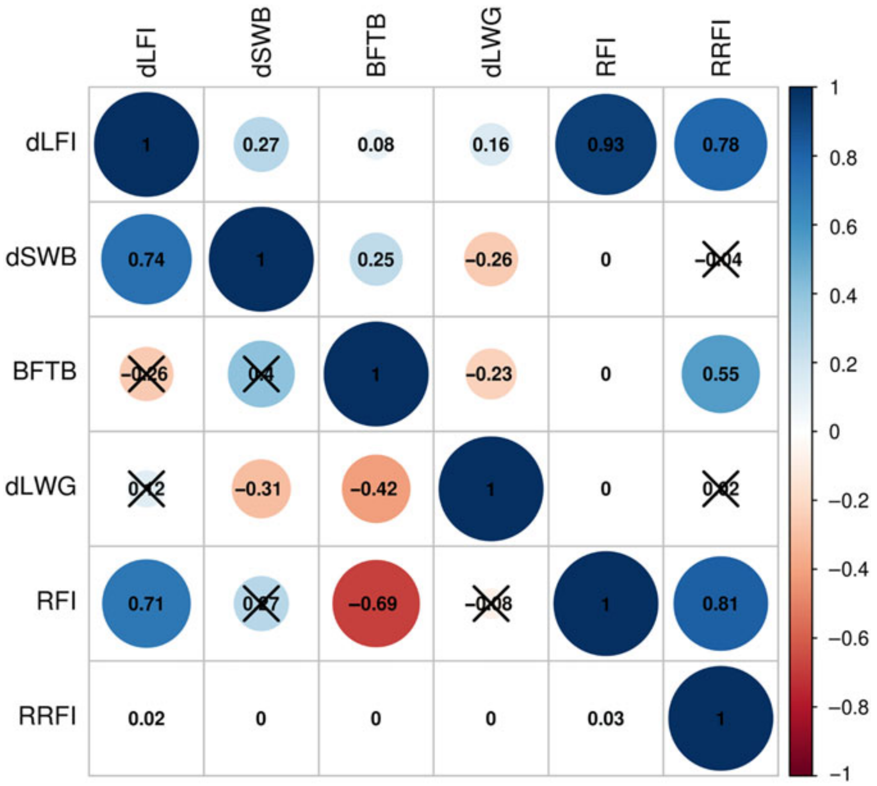

Figure 1 (colour online) Phenotypic (upper triangular) and genetic (lower triangular) correlations between dLFI, dSWB, BFTB, dLWG, RFI and RRFI. Cells with a cross have a posterior probability of being greater or smaller than zero lower than 0.95. dLFI = daily lactation feed intake; dSWB = daily sow weight balance, BFTB = backfat thickness balance, dLWG = daily litter weight gain, RFI = residual feed intake; RRFI = restricted residual feed intake.

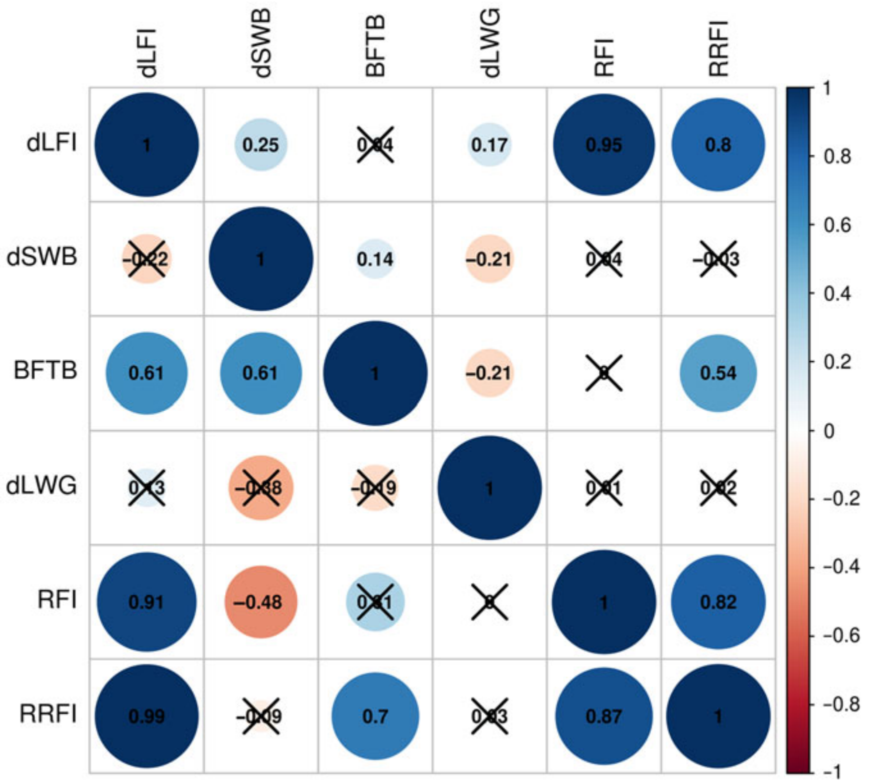

Figure 2 (colour online) Residual (upper triangular) and permanent effects (lower triangular) correlations between dLFI, dSWB, BFTB, dLWG, RFI and RRFI. Cells with a cross have a posterior probability of being greater or smaller than zero lower than 0.95. dLFI = daily lactation feed intake; dSWB = daily sow weight balance, BFTB = backfat thickness balance, dLWG = daily litter weight gain, RFI = residual feed intake; RRFI = restricted residual feed intake.

between them (0.81 (0.03)) and both with dLFI, especially RFI (0.93 (0.01) and 0.78 (0.02), respectively). Restricted RFI was moderately correlated with BFTB (0.55 (0.04)). Phenotypically, dLFI was positively but lightly associated with energy and nutrient balances (0.27 (0.03) with dSWB and 0.08 (0.04) with BFTB) and litter weight gain (0.16 (0.03)). Therefore, the more a sow eats the more it increases its BW, backfat reserves and its litter weight. An increase in dSWB was associated with an increase in BFTB (0.25 (0.04)) but to a decrease in dLWG (−0.26 (0.04)). In the same way, an increase in backfat thickness corresponded to a decrease in litter weigh (−0.23 (0.04)).

Because of the null genetic variation of RRFI, genetic correlation with any other trait was also null. However, genetically, RFI was highly and positively correlated with dLFI (0.71 (0.16)) and highly and negatively correlated with BFTB (−0.69 (0.18)) and not significantly correlated with dSWB, whereas dLFI was highly correlated with dSWB (0.74 (0.11)).

Regarding permanent environmental effects, RFI and RRFI and both of them with dLFI were highly correlated, ranging this correlation from 0.87 to 0.99. The correlation between RRFI and BFTB was moderate to high (0.70 (0.14)). Daily lactation feed intake was moderately correlated with BFTB. All other phenotypic, genetic and permanent environmental correlations were not statistically different from zero.

Discussion

Traits involved in feed efficiency can be divided into two groups: energy input and energy output related traits. Energy sources for a lactating sow are feed intake and body reserves mobilization during lactation (i.e. sow BW and backfat loss). Available energy is used for growth (sow BW and backfat gain) and maintenance of the sow and for milk production, quantified by piglet growth and maintenance. Therefore, dSWB and BFTB are variables that quantify the balance of body reserves during lactation, which is negative whenever sow losses weight and/or fat, and positive otherwise. Other traits involved in the definition of lactation feed efficiency are pre-farrow traits which are those measured before farrowing (i.e. SW_f and LWs) that may have an impact on sow lactation performance and are included as covariates in the analysis of all other traits.

In this study, all those components of feed efficiency during lactation were analysed to gather relevant information for the design of a breeding program to improve this trait. Data come from a Duroc population selected for prolificacy and backfat thickness at the end of the fattening period. Because of selection for prolificacy, sows are required to have an increased milk production, and this performance is expected to be maintained throughout consecutive parities. Litter size at the start of lactation was around 11 piglets in this population. In order to meet all the energy and nutrient requirements during this period, sows ate 5.7 kg/day of food (2.8% of their weight at farrowing), mobilize 2.7 mm of backfat, which means a 14% of the initial amount of this tissue, and a negligible part of other body tissues (i.e. sow weight loss was very small). Compared with other populations of pigs, sows in our population eat more and mobilize less energy and nutrient reserves. For example, in the two lines divergently selected for RFI in the growing pigs Gilbert *et al.* (2012) observed that on average, during lactation (28 days), sows eat daily 1.8% of its initial weight, and lost 20% of their initial backfat reserves and 13% of their initial BW to produce milk for 11.6 piglets. Similar figures are found by Thekkoot *et al.* (2016) and Bergsma *et al.* (2008). Therefore, increasing levels of feed intake during lactation are associated with reduced mobilization of body reserves, as it was found by Dourmad (1991).

The potential for increasing levels of sow feed efficiency during lactation through direct selection has been previously reported in a limited number of studies and populations (Bergsma *et al.*, 2008; Gilbert *et al.*, 2012; Thekkoot *et al.*, 2016; Young *et al.*, 2016). In agreement with those studies, results show that this trait is heritable. However, heritability was very low in our Duroc population (posterior mean = 0.04 (posterior SD = 0.02)) limiting the possibilities of effective selection. Sow RFI during lactation was studied by Gilbert *et al.* (2012), Young *et al.* (2016) and Thekkoot *et al.* (2016). Heritability reported by Gilbert *et al.* (2012) was also low (0.14 ± 0.06). However, Thekkoot *et al.* (2016) obtained higher values in two different populations: 0.26 ± 0.05 in a Yorkshire line and 0.30 ± 0.06 in a Landrace population. Young *et al.* (2016) also found a large heritability estimate (0.32 ± 0.05) in two lines divergently selected for RFI coming from a common Yorkshire population. Bergsma *et al.* (2008), Young *et al.* (2016) and Thekkoot *et al.* (2016) reported estimates of heritability for other measures of feed efficiency during lactation such as: (i) lactation efficiency (Bergsma *et al.*, 2008), defined as the ratio of energy output (measured from piglet growth) to energy input (energy from feed and body tissue mobilization above maintenance requirements of the sow); (ii) energy balance (Young *et al.*, 2016), defined as the difference between energy retained by the sow at weaning and at farrowing. Heritability estimates of lactation efficiency were in general low ranging from 0.05 to 0.12 (Bergsma *et al.*, 2008; Thekkoot *et al.*, 2016; Young *et al.*, 2016) whereas energy balance showed low to moderate values of this parameter ranging from 0.12 to 0.36 (Thekkoot *et al.*, 2016; Young *et al.*, 2016). However, lactation energy balance cannot be considered as a feed efficiency trait by itself because it does not directly account for the productive effort of the sow, as it is the case of energy balance obtained by Young *et al.* (2016).

Because of the moderate to high genetic correlation, selection for RFI would lead to a decrease in dLFI and an increase in energy balance (i.e. BFTB) at the end of lactation, which are favourable correlated effects. Because of the definition of RRFI, genetic variance is smaller for this trait than for RFI. In our population, selection for RRFI would not have any correlated effect on production traits because genetic variance for this trait is null.

Regarding feed efficiency components, our heritability estimate for dLFI was low (0.09 (0.03)). It is known that heritability increases with the length of the period measured because the residual variance is reduced by averaging the observations over a longer time period (Wetten *et al*., 2012). However, Gilbert *et al*. (2012) found higher values of heritability (0.26 ± 0.07) for this trait in two lines divergently selected for RFI obtained from a unique Large White population. Also, greater heritability estimates (from 0.23 to 0.30) were found for sow feed intake during the whole lactation period by Bergsma *et al*. (2008), Young *et al*. (2016) and Thekkoot *et al*. (2016) in Yorkshire and Landrace pig populations or crossbred sows. As in the aforementioned studies, heritability of dLFI was in our population higher than that of RFI. The low value found in our study compared with previously reported values is probably due, among other reasons, to the inaccuracy of our measurement conditioned by the way feed was supplied to the sows and data were recorded.

Feed intake and mobilization of body reserves are important traits to consider for the improvement of sow lactation performance (Eissen *et al*., 2000; Grandinson *et al*., 2005; Lundgren *et al*., 2014). Phenotypically, increasing levels of feed intake during lactation are associated with significant slightly higher litter weaning weights in agreement with results found by Schinckel *et al*. (2010) and Bergsma *et al*. (2008). On the other hand, dLFI was positively correlated with dSWB, which means that a high level of dLFI is associated with a positive balance of body tissue reserves (i.e. reduced BW loss) in agreement with Bergsma *et al*. (2008), Lundgren *et al*. (2014) and Thekkoot *et al*. (2016). In our experiment, significant but very low phenotypic correlation was found between dLFI and BFTB in agreement with Bergsma *et al*. (2008) who also found a positive relationship between these two traits (negative relationship between lactation feed intake and back fat losses).

At the genetic level, dLFI was highly and positively correlated with dSWB (0.71) and not significantly correlated with BFTB. This result is in agreement with results found by Bergsma *et al*. (2008) and Thekkoot *et al*. (2016) who found a negative correlation between lactation feed intake and weight and backfat losses. Lundgren *et al*. (2014) also found that genetic correlations between feed intake in 1 day of lactation and body condition at weaning (measured by the farmers with a visual nine levels scale) was 0.52, indicating that sows with a higher feed intake were able to maintain a better body condition during lactation. Genetic correlation between dLFI and dLWG was null in our experiment in agreement with Thekkoot *et al*. (2016) but unlike Bergsma *et al*. (2008) who obtain a low to moderate and positive (0.37) genetic relationship between these two traits. Differences in results among studies could be explained, among other factors, by: (i) the genetic origin of the populations; (ii) the implicit definition of the traits based on the covariates that are fitted or not to account for initial conditions regarding body condition of the sow and litter weight (e.g. Thekkoot *et al*. (2016) and Young *et al*. (2016), included in the model covariates referring to those initial conditions but Gilbert *et al*. (2012) and Bergsma *et al*. (2008) did not); (iii) differences in management, environment and feeding strategy; in our study, sows were fed on the basis of previous day consumption (i.e. quasi *ad libitum*) while in other studies sows were fed *ad libitum*; (iv) the lower backfat losses of sows in our experiment; and (v) the precision of feed intake measurements. Bergsma *et al*. (2008), Thekkoot *et al*. (2016) and Young *et al*. (2016) used electronic feeders while in our study, as well as in Gilbert *et al*. (2012), feed intake was recorded manually. In addition, in our study feed intake data were predicted from a nonlinear model fitted to twice a week recorded data after removing outliers. In order to improve the efficacy of selection for lactation feed efficiency effort should be made into recording dLFI on complete *ad libitum* feeding.

Traits related with body tissue mobilization seem to be heritable and therefore genetic selection for these traits could be successful especially for dSWB. We found a moderate to high heritability for dSWB (0.37 (0.07)) and a low heritability for BFTB (0.09 (0.03)). Estimates for BFTB are in agreement with those obtained by Grandinson *et al*. (2005) and Gilbert *et al*. (2012) (0.10 and 0.14, respectively) but not with Bergsma *et al*. (2008) who obtained a null heritability for backfat loss. The low heritability estimates for this trait could be explained by the lack of accuracy in the measurement of the backfat thickness, which is particularly problematic in furry animals, as it is our Duroc population. To overcome this issue, sows were shaved in the area where backfat thickness was recorded; nevertheless, the measurement error of backfat thickness could be around 1 to 1.5 mm, which is around 40% to 60% the average total BFTB during the whole lactation (from Table b1: 0.1 (mm/day)*27 day = 2.7 (mm/lactation)). Heritability estimated for dSWB was in agreement with those obtained by Bergsma *et al*. (2008), Grandinson *et al*. (2005) and Gilbert *et al*. (2012). Smaller values were found by Young *et al*. (2016) in their divergently selected lines for RFI of growing pigs (0.13).

Daily sow weight balance and BFTB were phenotypically but not significantly genetically correlated. The precision of our estimates of genetic correlation was low because of the limited amount of records and high variability in dSWB. Bergsma *et al*. (2008) found strong genetic correlations between sow weight loss and protein loss (0.99) and between sow weight loss and fat loss (0.86), whereas Thekkoot *et al*. (2016) found a lower but also positive genetic correlation in a Yorkshire population and a null correlation in a Landrace population. Body reserves balances were both phenotypically correlated with dLWG being those correlations low and negative (−0.26 and −0.23 for correlations between dLWG with dSWB and BFTB, respectively). This means that increasing levels of body reserves mobilization led to increasing levels of litter growth, and sows that gain fat and weight during lactation are probably producing less milk. At the genetic level, both dSWB and BFTB were negatively and moderately correlated with dLWG. Bergsma *et al*. (2008) also found a positive phenotypic correlation of LWG. with BW, backfat and protein losses (negative correlation with balances) but no significant correlations between any of those pairs of traits. Thekkoot *et al.* (2016) obtained moderate positive and significant correlations between LWG and BW and backfat losses in a Landrace population and null and moderate and positive correlations between LWG and BW lose and between LWG and backfat losses, respectively, in a Yorkshire population. Therefore, the genetic association between dLWG and body reserves mobilization depends on the genetic origin of the population. Finally, heritability for dLWG. was moderate (0.22 (0.05)) as the one reported by Young *et al.* (2016) for their high RFI group, and very similar to the heritabilities estimated in other studies: 0.16 (Grandinson *et al.*, 2005) and 0.18 (Bergsma *et al.*, 2008).

As a conclusion, it could be stated that selection for improving lactation feed efficiency would be more effective by selecting for an index based on FE component traits with optimal economic weights than by selecting for RFI because of the low heritability of the last trait. However, the last strategy would not have unfavourable correlated effects on production traits. Selection for RRFI would not be effective at all in our population under the current feeding strategy and data recording system because of its null genetic variation.

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Declaration of interest

The authors declare that they have no competing interests.

Ethics statement

Animal Care and Use Committee approval was not obtained for this study because data come from a commercial farm belonging to a private company (Batallé S.A., Spain) which strictly operates in line with the regulations of the Spanish law on animal protection.

Software and data repository resources

The data sets used and analysed during the current study are available from the corresponding author on reasonable request.

Supplementary material

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