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R. Saintilan, R. Saintilan, Isabelle Merour, L. Brossard ...+11 more authors

Institutions: Institut national de la recherche agronomique, Agro ParisTech, Agrocampus Ouest

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Romain Saintilan, Isabelle Merour, Ludovic Brossard, Thierry Tribout, Jean-Yves Dourmad, Pierre Sellier, Jean Pierre Bidanel, Jaap van Milgen, Hélène Gilbert

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Genetics of residual feed intake in growing pigs: Relationships with production traits, and nitrogen and phosphorus excretion traits[1]

R. Saintilan,*†[2] I. Mérour,‡[3] L. Brossard,§# T. Tribout,*† J. Y. Dourmad,§# P. Sellier,*† J. Bidanel,‡ J. van Milgen,§# and H. Gilbert*†‖¶

*INRA, UMR1313, GABI, F-78352 Jouy-en-Josas Cedex, France; †AgroParisTech, UMR1313, GABI, F-75231 Paris Cedex, France; ‡IFIP- Institut du porc, F-35651 Le Rheu Cedex, France; §INRA, UMR1348, PEGASE, F-35590 Saint Gilles Cedex, France; #Agrocampus Ouest, UMR1348, PEGASE, F-35000 Rennes Cedex, France; ‖INRA, UMR444, LGC, F-31326 Castanet-Tolosan Cedex, France; and ¶INP, UMR444, LGC, F-31029 Toulouse Cedex, France

ABSTRACT: Residual feed intake (RFI) is defined as the difference between the observed ADFI and the ADFI predicted from production and maintenance requirements. The objectives of this study were to evaluate RFI as a selection criterion to improve feed efficiency and its potential to reduce N and P excretion in 4 pig breeds. Data were collected between 2000 and 2009 in French central test stations for 2 dam breeds [French Landrace (LR) and Large White (LWD)], and 2 sire breeds [Large White (LWS) and Piétrain (PP)]. Numbers of recorded pigs were 6407, 10,694, 2342, and 2448 for the LR, LWD, LWS, and PP breeds, respectively. All PP animals were genotyped for the halothane mutation. This data set was used to calculate RFI equations for each of the 4 breeds, and to estimate genetic parameters for RFI together with growth, carcass, and meat quality traits, and N and P excretion during the test period (35 to 110 kg BW). The RFI explained 20.1% in PP, 26.5% in LWS, 27.6% in LWD, and 29.5% in LR of the phenotypic variability of ADFI. The PP breed differed from the others in this respect, probably due to a lower impact of the variation of body composition on ADFI. Heritability estimates of RFI ranged from 0.21 ± 0.03 (LWD) to 0.33 ± 0.06 (PP) depending on the breed. Heritabilities of N and P excretion traits ranged from 0.29 ± 0.06 to 0.40 ± 0.06. The RFI showed positive genetic correlations with feed conversion ratio (FCR) and excretion traits, these correlations being greater in the sire breeds (from 0.57 to 0.86) than in the dam breeds (from 0.38 to 0.53). Compared with FCR, RFI had weaker genetic correlations with carcass composition, growth rate, and excretion traits. Estimates of genetic correlations between FCR and excretion traits were very close to 1 for all breeds. Finally, excretion traits were, at the genetic level, correlated positively with ADFI, negatively with growth rate and carcass leanness, whereas the halothane *n* mutation in PP was shown to reduce N and P excretion levels. To conclude, new selection indexes including RFI can be envisaged to efficiently disentangle the responses to selection on growth rate and body composition from those on feed efficiency, with favorable impacts on N and P excretions, particularly in sire pig breeds. However, the switch from FCR to RFI in selection indexes should not resolve the genetic antagonism between feed efficiency and meat quality.

Key words: excretion traits, genetic parameters, pig, production traits, residual feed intake

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INTRODUCTION

Improving feed efficiency of the growing animal has been, for several decades, a major goal in pig breeding. This trait is currently gaining more importance due to the increase in feed costs, the greater attention paid to the environmental footprint of the pig industry, and the enlarged competition between human food, feed for animals, and biofuel in the use of agricultural land. In

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[2]Corresponding author: romain.saintilan@jouy.inra.fr
[3]Present address: COBIPORC- Le Val- F-35590 Saint Gilles, France.

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France, feed efficiency has been improved either by direct selection for lower feed conversion ratio (**FCR**), when individual feed intake records were available, or, most often, by indirect selection for greater lean growth rate. However, a decrease in FCR does not necessarily relate to an improvement in feed efficiency (Crews, 2005), and different sources of variability in feed intake have to be taken into account. Variability in feed intake is due to differences in nutrient requirements for maintenance (including physical activity and thermoregulation) and growth (digestion, metabolism, and protein and lipid deposition; Herd and Arthur, 2009). The residual feed intake (**RFI**) is defined as the difference between actual feed intake and feed intake predicted from production and maintenance requirements (Koch et al., 1963; Kennedy et al., 1993). It is proposed as an alternative trait to FCR to improve feed efficiency and specifically target the variation of feed intake. Heritability of RFI and genetic relationships of RFI with production traits usually taken into account in pig breeding have been investigated in a variety of genetic backgrounds, for example, in experimental Yorkshire and Large White lines (Gilbert et al., 2007; Caï et al., 2008) and in Duroc and Landrace populations (Hoque and Suzuki, 2008; Hoque et al., 2009). Crocker and Robison (2002) have found significant differences between various pig crosses for quantity and composition of excreta. However, to our knowledge, no information exists on the heritabilities of excretion traits and genetic correlations between production and excretion traits for pigs. The objectives of our study were to compute RFI for 4 pig breeds with different selection objectives and performance levels, and to estimate genetic parameters for RFI, together with N and P excretion and production traits.

MATERIALS AND METHODS

Data were collected within the framework of the French national pig breeding scheme, and were obtained in accordance with the national regulations of humane care and use of animals in research.

Source of Data

Data were collected between 2000 and 2009 in the 3 French central test stations (Le Rheu, Ille-et-Vilaine; Argentré, Mayenne; Mauron, Morbihan) for 4 pig breeds: Landrace dam breed (**LR**), Large White dam breed (**LWD**), Large White sire breed (**LWS**), and Piétrain sire breed (**PP**). Animals were either castrated full-brothers (LWD, LWS, and LR) or full-sisters (PP) of on-farm tested male and female candidates for selection. Only PP pigs with available halothane genotype and tested in batches comprising at least 2 halothane genotypes were kept for analysis. A total of 6470 LR, 10,694 LWD, 2342 LWS, and 2448 PP were included in the present study.

In the 4 breeds, each herd contributing to a given central testing batch provided 8 to 12 piglets homogenous in BW and age, with a recommendation of 2 piglets per litter. For the Le Rheu and Argentré stations, piglets entered the station between 25 and 30 d of age, with a minimum BW of 7.0 kg, or between 31 and 37 d of age with a minimum BW of 8.5 kg. For the Mauron station, piglets arrived between 9 and 14 d of age, with a minimum BW of 3.5 kg, and were raised in a nursery until they reached 8.5 kg BW. Pigs arriving in a test station over a period of 2 wk formed a batch, which consisted of at least 2 herds of origin per breed. Whatever the station, animals were raised in a postweaning unit from 8.5 kg to 28 kg BW. Pigs were then moved to a fattening unit consisting of pens of 12 animals equipped with single-place electronic Acema 48 feeders (before 2005) or Acema 64 feeders (2005 and later; Acemo, Pontivy, France; Labroue et al., 1994). The test began at 35 kg (**BW_1**) and ended at approximately 110 kg (**BW_2**). Pigs were slaughtered in 2 commercial abattoirs (Socopa in Evron, for the Argentré station and Cooperl in Montfort-sur-Meu, for the other 2 stations) on the week they reached the intended BW_2. Transport time for both abattoirs was approximately 35 min. During the test period, animals were offered a pelleted diet based on cereals and soybean meal and provided 9.5 MJ NE and 156 g CP and 4.8 g of total phosphorus per kilogram of feed, with a minimum of 0.87 g of digestible lysine per megajoule NE.

Traits Recorded during the Test Period

Average daily gain between BW_1 and BW_2 was computed, and ADFI and FCR were calculated from data collected from the electronic feeders. The average metabolic body weight during the test period (**AMW**) was estimated for each animal using this formula established from various genetic types and sexes (Noblet et al., 1999):

$$AMW = (BW_2^{1.6} - BW_1^{1.6})/[1.6\,(BW_2 - BW_1)].$$

Traits Recorded at the Abattoir

Carcasses with head and feet and without kidney fat were chilled in a cooling room at 4°C for 24 h, and right half-carcasses were cut using the standard procedures described by Métayer and Daumas (1998). Dressing percentage (**DP**) was defined as the ratio of cold carcass weight to slaughter BW measured after a fasting period of 16 h minimum the day pigs were slaughtered. Carcass backfat thickness (**BFT**, average of 3 measurements

taken at the shoulder, midback, and loin sites on the middorsal line), and weights of primal cuts (shoulder, ham, loin, belly, and backfat) were recorded for the right half-carcass without head. Lean meat content (**LMC**) was estimated from a linear combination of cut weights expressed in percentage of the cold half-carcass weight for ham, loin, and backfat (Daumas 2008):

LMC (%) = 25.08 —1.23 backfat (%) + 0.87 loin (%) + 0.73 ham (%).

Meat quality traits were recorded 24 h post mortem. Water holding capacity (**WHC**) of the *gluteus superficialis* muscle was measured as the time required by a filter paper (1 cm^2) placed on the fresh meat to become saturated with water (1 point = 10 s, maximum 20). Ultimate pH ($\mathbf{pH_u}$) of the *semimembranosus* muscle was measured using a Xerolyt electrode (ref: 10 406 3123) and a Sydel pH meter (Sydel, Lorient, France). The lightness (**L***, scale 0 to 100 points, a lower value being associated with darker meat) of the *gluteus superficialis* muscle was measured using a Minolta CR-300 spectrophotometer (Minolta, Carrieres sur Seine, France). A global meat quality index (**MQI**), defined as a predictor of the technological yield of cured-cooked ham processing, was calculated as reported by Tribout et al. (2004): MQI (point) = – 41 + 11.01 pH_u (point) + 0.105 WHC (10 s) – 0.231 L* (point).

Computation of Residual Feed Intake

Residual feed intake was computed separately for each breed. For each animal, the deviation between recorded ADFI and ADFI predicted from requirements for maintenance and production was calculated. The predicted ADFI was estimated by a multiple phenotypic linear regression of ADFI on ADG, to account for growth; BFT, LMC, and DP to account for composition of BW gain; and AMW to account for maintenance requirements (GLM procedure; SAS Inst. Inc., Cary, NC). Two fixed effects were included in the model: the contemporary group (batch), and the pen size defined as the number of pigs in the pen when the first pig ended the test (3 classes: <8 pigs, 8 to 11 pigs, and >11 pigs). All traits used in the multiple regression models for the 4 breeds contributed significantly ($P < 0.05$) to the variability of RFI for at least 1 breed, to compare the equations between breeds. Despite the segregation of the halothane gene in the PP breed, no fixed effect was included in the model to account for this, because it has been previously shown that the halothane genotype does not influence RFI (Saintilan et al., 2011). The percentages of variability of ADFI explained by each factor or trait included in the multiple linear regression model were obtained as the difference between the R^2 of the full model and the R^2 of the reduced model obtained by deleting this trait or factor from the full model (SAS). The percentage of variability of ADFI due to RFI was obtained as $1 - R^2$ of the full model.

Estimation of N and P Excretion during the Test Period

The N and P excretions ($\mathbf{N_e}$ and $\mathbf{P_e}$) during the test period were estimated as the difference between the intake and the retention of N and P. The N and P intakes were estimated from the total feed intake during the test period and the chemical composition of feed.

The N and P contents (N_{cBW} and P_{cBW} respectively) in the body were estimated using these formulas obtained from variety of genetic types and sexes:

$$N_{cBW} = \frac{e^{(-0.9892 - 0.0145 \times LMC)} \times \left(0.915 \times BW^{1.009}\right)^{(0.7518 + 0.0044 \times LMC)}}{6.25}$$

[Guillou et al. (1993) adapted in CORPEN, 2003], and

$$P_{cBW} = \frac{5.36335 \times e^{\left(\frac{\ln(BW)}{0.986} + \ln(0.89)\right)} - 0.00227 \times e^{\left(\frac{\ln(BW)}{0.986} + \ln(0.89)\right)^2}}{1000}$$

[Dourmad et al. (2002), adapted in CORPEN, 2003].

The N (P) retention was thus computed as the differences between N_{cBW2} (P_{cBW2}) and N_{cBW1} (P_{cBW1}). The N (P) excretion during the test period was also expressed as a proportion of N (P) intake ($\mathbf{N_r}$ and $\mathbf{P_r}$ respectively).

The distribution of all traits was validated before further analyses as being gaussian (Proc Univariate, SAS). Only WHC deviated significantly from normality. The consistency of the genetic parameter estimations obtained with the trait itself or after a log-transformation of the trait was confirmed.

Estimation of Genetic Parameters

Variance-covariance components of a mixed animal model were estimated for each breed separately using the REML methodology (Patterson and Thompson, 1971) with the WOMBAT software (Meyer, 2007, v. 19/05/2012). Heritabilities were estimated in single-trait analyses and genetic correlations in 2-trait analyses. The models included the fixed effect of the contemporary group (133 levels in LF, 148 levels in LWD, 89 levels in LWS, and 77 levels in PP), except for meat quality traits. An additional fixed effect of the halothane genotype of the animal (3 levels: *NN*, *Nn*, and *nn*) was included in the model pertaining to the PP breed. The additive genetic value of the animal and the common environment of the litter were retained as random effects for all traits. The

Table 1. Percentage of variability of ADFI explained by the factors or traits included in the multiple linear regression model used for ADFI prediction for each breed

	Breed[1]			
Factor or trait[2]	LR	LWD	LWS	PP
Contemporary group + pen size	24.84	23.91	28.30	25.48
ADG	28.97	35.09	33.40	47.08
LMC	15.71	12.13	10.58	5.81
BFT	0.03	0.05	0.04	0.04
DP	0.16	0.15	0.09	0.07
AMW	0.84	1.14	1.06	1.38
RFI	29.46	27.54	26.52	20.12

[1]LR = Landrace dam breed; LWD = Large White dam breed; LWS = Large White sire breed; PP = Piétrain sire breed.

[2]LMC = lean meat content; BFT = backfat thickness; DP = dressing percentage; AMW = average metabolic weight; RFI = residual feed intake.

pen-group was retained as an additional random effect for ADFI, RFI, ADG, FCR, N_e, P_e, N_r, and P_r, and the slaughter day was retained as an additional random effect for meat quality traits. The variance covariance structure of the animal random effect was given by the pedigree kinship matrix, whereas the other random effects were distributed according to a normal distribution with mean 0 and variance covariance $\sigma^2\mathbf{I}$, where σ^2 was the variance of the given random effect to be estimated and **I** is the identity matrix of size depending on the population and traits. The model included these covariates: BW_1 for ADG, RFI, FCR, N_r and P_r, BW_1 and BW_2 for N_e and P_e, and cold carcass weight for LMC, BFT, and meat quality traits. Because the piglets arrived at an early age in the test station, the herd of origin was not significantly affecting the traits, and this effect was not included in the models. The pedigree files (16,581, 27,497, 6535, and 7223 animals in LF, LWD, LWS, and PP, respectively) included 6 generations of ancestors in addition to the animals with phenotypic records.

RESULTS

Computation of Residual Feed Intake

Percentages of variability of ADFI explained by each factor or trait included in the multiple linear regression model are presented in Table 1. In our testing conditions, nuisance parameters (contemporary group and pen size, plus halothane genotype for the PP pigs), ADG, carcass composition and maintenance requirements accounted for 70.5% (LF) to 79.9% (PP) of the phenotypic variance of ADFI. Average daily gain, carcass composition, and maintenance requirements accounted for 45.2 to 54.4% of the variability of ADFI. The RFI was the residual term of this multiple regression model (i.e., RFI represented 20.1% in PP, 26.5% in LWS, 27.6% in LWD, and 29.5% in LR of the phenotypic variability of ADFI). All explicative traits were significant at $P < 0.05$, except BFT in LWS ($P < 0.10$). The PP breed exhibited the greatest contribution of ADG and the lowest contribution of body composition traits (LMC, BFT, DP) to the variability of ADFI. For all breeds, maintenance requirements accounted for 0.84 to 1.38% of this variance. This low proportion is partly because animals were tested between essentially fixed on-test and off-test BW, so that variability of AMW was small.

Equations obtained for the calculation of RFI by multiple regression in each breed, taking into account the fixed effects of contemporary group and pen size, were:

$$\text{LR: RFI} = \text{ADFI} - 1.46\,\text{ADG} - 8.16\,\text{DP} - 2.03\,\text{BFT} + 33.7\,\text{LMC} - 94.1\,\text{AMW}$$

$$\text{LWD: RFI} = \text{ADFI} - 1.41\,\text{ADG} - 7.84\,\text{DP} - 2.83\,\text{BFT} + 31.8\,\text{LMC} - 110.9\,\text{AMW}$$

$$\text{LWS: RFI} = \text{ADFI} - 1.36\,\text{ADG} - 6.70\,\text{DP} - 2.87\,\text{BFT} + 36.0\,\text{LMC} - 113.8\,\text{AMW}$$

$$\text{PP: RFI} = \text{ADFI} - 1.38\,\text{ADG} - 5.36\,\text{DP} - 1.91\,\text{BFT} + 28.3\,\text{LMC} - 105.3\,\text{AMW}$$

with RFI, ADFI, and ADG in g/d, LMC and DP in %, BFT in mm, and AMW in $kg^{0.60}$.

Phenotypic Means

Phenotypic means and SD of all the traits investigated are presented for each breed in Table 2. Means of BW_1 and BW_2 were close to the intended values of 35 kg and 110 kg, respectively. However, average BW_2 of PP pigs was slightly lighter than that of other breeds, in relation to their lower ADG. As expected, means of RFI were 0 for all the breeds, with SD ranging from 149 to 158 g/d for LF, LWS, and LWD, and being markedly lower for PP (109 g/d). Breed means for N_e and P_e during the test period ranged from 2.61 to 3.36 kg and 0.51 to 0.63 kg, respectively. Breed means for N_r and P_r ranged from 57.9 to 64.9% and 59.3 to 63.6%, respectively. Piétrain pigs exhibited the lowest average values compared with other breeds for all excretion traits.

Variance–Covariance Components

Estimates of heritability and proportion of phenotypic variance due to litter effect are given in Table 3. Heritabilities for RFI were moderate for all breeds, ranging

Table 2. Summary statistics of traits for each breed

	Breed[1]							
	LR (n = 6470)		LWD (n = 10,694)		LWS (n = 2342)		PP (n = 2448)	
Trait[2]	Mean	SD[3]	Mean	SD	Mean	SD	Mean	SD
BW_1, kg	34.8	1.8	34.8	1.8	34.9	1.9	34.8	2.1
BW_2, kg	108.8	6.1	109.5	6.4	110.1	6.8	107.1	6.7
RFI, g/d	0	149	0	150	0	158	0	109
FCR, kg feed/kg BW gain	2.79	0.23	2.69	0.21	2.62	0.21	2.49	0.17
ADFI, kg/d	2.58	0.24	2.57	0.25	2.55	0.26	2.08	0.20
ADG, g/d	928	86	958	93	978	94	839	86
N_e, kg	3.36	0.43	3.18	0.40	3.03	0.40	2.61	0.31
P_e, kg	0.63	0.08	0.60	0.07	0.58	0.07	0.51	0.06
N_r, %	64.9	3.3	62.9	3.2	61.3	3.3	57.9	2.9
P_r, %	63.6	3.0	62.3	2.9	61.2	3.0	59.3	2.7
LMC, %	54.0	3.0	56.1	2.8	58.3	2.6	65.3	1.9
BFT, mm	24.1	3.3	23.8	3.2	21.8	3.2	18.1	2.8
DP, %	78.0	1.3	78.6	1.3	79.3	1.2	82.2	1.1
L*, point	50.6	3.7	51.0	3.6	50.8	3.7	52.8	3.8
pH_u, point	5.70	0.19	5.71	0.18	5.74	0.19	5.63	0.15
WHC, point	9.8	6.5	10.3	6.4	10.3	6.4	2.6	3.3
MQI, point	11.1	2.9	11.1	2.8	11.5	3.0	9.1	2.2

[1]LR = Landrace dam breed; LWD = Large White dam breed; LWS = Large White sire breed; PP = Piétrain sire breed.

[2]BW_1 = BWat the beginning of the test; BW_2 = BW at the end of the test; RFI: residual feed intake; FCR = feed conversion ratio; N_e = N excreted during the test period; P_e = P excreted during the test period; N_r = ratio of N excreted over N intake during the test period; P_r = ratio of P excreted over P intake during the test period; LMC = lean meat content; BFT = backfat thickness; DP = dressing percentage; L* = lightness of the meat of the gluteus superficialis muscle; pH_u = ultimate pH measurement of the semimembranosus muscle; WHC = water holding capacity of the gluteus superficialis muscle; MQI = meat quality index.

[3]SD = phenotypic SD of traits, corrected for the fixed effects and covariates included in the model used for genetic parameters calculation.

from 0.21 (LWD) to 0.33 (PP). Estimates for FCR were slightly greater and ranged from 0.30 (LWD and LWS) to 0.40 (PP). Heritability estimates for excretion traits ranged from 0.29 to 0.43, and were slightly greater for N_r than for P_r. These estimates were also systematically greater for PP than for the other breeds. In general, heritability estimates were moderate for ADFI, ADG, and meat quality traits, and greater for body composition traits. Unexpectedly, the heritability estimate for ADG in LWS was quite low (0.05).

Phenotypic correlations ($\boldsymbol{r_p}$) of RFI and FCR with the other traits are given in Table 4. As expected, RFI was phenotypically independent from the traits used to predict ADFI (ADG, LMC, BFT and DP) for all breeds studied. Phenotypic correlations between RFI and excretion traits were positive and high (~0.70) whereas phenotypic correlations between FCR and excretion traits were very close to 1. The RFI was phenotypically positively correlated with FCR (r_p values between 0.71 and 0.80) and ADFI (r_p values between 0.51 and 0.62). Phenotypic correlations between FCR and ADFI (r_p values between 0.21 and 0.43) were lower than those between RFI and ADFI (r_p values between 0.51 and 0.62). The FCR was phenotypically correlated (except for DP) with traits used to estimate RFI, negatively with ADG and LMC, and positively with BFT. Absolute values of phenotypic correlations between FCR or RFI and meat quality traits were lower than 0.12.

Genetic correlations ($\boldsymbol{r_A}$) of all recorded traits with RFI and FCR are given in Table 5.

The RFI was positively correlated with both ADFI (r_A ranging from 0.48 to 0.72) and FCR (r_A ranging from 0.52 to 0.85). Genetic correlations between RFI and FCR were greater in sire breeds (0.69 and 0.85) than in dam breeds (0.52 and 0.53). Absolute values of genetic correlations between RFI and the traits used to compute the predicted ADFI were less than 0.16 and did not differ significantly from 0. Corresponding genetic correlations for FCR were negative with ADG and LMC, positive with BFT, and low to null with DP. The RFI showed moderate to high positive genetic correlations with excretion traits, with greater values for P than for N. These correlations were greater in sire breeds (from 0.57 to 0.86) than in dam breeds (from 0.38 to 0.52). For excretion traits, the closest genetic relationships with RFI were systematically found for PP. Genetic correlations between excretion traits and FCR were very close to 1 for all breeds. Genetic correlations with meat color (L*) tended to be more favorable for FCR than for RFI in the dam breeds.

Phenotypic and genetic correlations of excretion traits with the 5 traits used to compute RFI are presented in Tables 6 and 7, respectively. Phenotypic correlations of excretion traits with ADFI were positive in all breeds, with slightly lower values for N_r and P_r than for N_e and P_e. Corresponding correlations were negative with ADG and LMC, positive with BFT and not greater than 0.10

Table 3. Estimates of h^2 and proportions of variance due to litter effect (c^2) for each breed[2] (SE in parentheses)

	h^2				c^2			
Trait[1]	LR	LWD	LWS	PP	LR	LWD	LWS	PP
RFI	0.23 (0.03)	0.21 (0.03)	0.26 (0.06)	0.33 (0.06)	0.04 (0.03)	0.13 (0.02)	0.05 (0.05)	0.05 (0.04)
FCR	0.35 (0.04)	0.30 (0.03)	0.30 (0.06)	0.40 (0.06)	0.07 (0.03)	0.13 (0.02)	0.10 (0.05)	0.02 (0.04)
ADFI	0.27 (0.04)	0.34 (0.03)	0.21 (0.06)	0.48 (0.06)	0.05 (0.03)	0.10 (0.02)	0.11 (0.05)	0.00 (0.04)
ADG	0.26 (0.04)	0.33 (0.03)	0.05 (0.04)	0.48 (0.06)	0.06 (0.03)	0.07 (0.02)	0.12 (0.05)	0.00 (0.04)
N_e	0.37 (0.04)	0.33 (0.03)	0.31 (0.06)	0.40 (0.06)	0.05 (0.03)	0.13 (0.02)	0.08 (0.04)	0.03 (0.04)
P_e	0.34 (0.04)	0.30 (0.03)	0.29 (0.06)	0.40 (0.06)	0.06 (0.03)	0.13 (0.02)	0.09 (0.04)	0.03 (0.04)
N_r	0.43 (0.04)	0.37 (0.03)	0.36 (0.07)	0.41 (0.06)	0.05 (0.03)	0.12 (0.02)	0.07 (0.04)	0.00 (0.04)
P_r	0.34 (0.04)	0.30 (0.03)	0.30 (0.06)	0.41 (0.06)	0.07 (0.03)	0.13 (0.02)	0.09 (0.04)	0.00 (0.04)
LMC	0.66 (0.04)	0.60 (0.03)	0.55 (0.07)	0.49 (0.06)	0.04 (0.02)	0.07 (0.02)	0.06 (0.04)	0.00 (0.04)
BFT	0.61 (0.04)	0.51 (0.03)	0.53 (0.07)	0.38 (0.06)	0.00 (0.03)	0.08 (0.02)	0.04 (0.04)	0.03 (0.05)
DP	0.32 (0.04)	0.40 (0.03)	0.31 (0.06)	0.44 (0.06)	0.13 (0.03)	0.08 (0.02)	0.12 (0.04)	0.09 (0.05)
L*	0.31 (0.04)	0.27 (0.03)	0.18 (0.05)	0.21 (0.05)	0.07 (0.03)	0.03 (0.02)	0.03 (0.05)	0.06 (0.04)
pH_u	0.22 (0.03)	0.21 (0.02)	0.09 (0.04)	0.23 (0.05)	0.03 (0.02)	0.06 (0.02)	0.03 (0.05)	0.04 (0.04)
WHC	0.23 (0.03)	0.15 (0.02)	0.16 (0.05)	0.08 (0.04)	0.02 (0.03)	0.03 (0.02)	0.02 (0.05)	0.00 (0.04)
MQI	0.29 (0.03)	0.24 (0.02)	0.14 (0.05)	0.27 (0.05)	0.03 (0.03)	0.06 (0.02)	0.03 (0.05)	0.05 (0.04)

[1]RFI = residual feed intake; FCR = feed conversion ratio; N_e = N excreted during the test period; P_e = P excreted during the test period; N_r = ratio of N excreted over N intake during the test period; P_r = ratio of P excreted over P intake during the test period; LMC = lean meat content; BFT = backfat thickness; DP = dressing percentage; L* = lightness of the meat of the gluteus superficialis muscle; pH_u = ultimate pH measurement of the semimembranosus muscle; WHC = water holding capacity of the gluteus superficialis muscle; MQI = meat quality index.

[2]LR = French Landrace dam breed; LWD = Large White dam breed; LWS = Large White sire breed; PP = Piétrain sire breed.

with DP. Genetic correlations between excretion traits and other traits were moderately to highly negative for ADG and LMC, positive and of similar magnitude for ADFI and BFT, and low to null for DP. However, the genetic relationships of excretion traits with LMC or BFT were weaker in PP than in LF, LWD, and LWS (~0.30 vs. ~0.70 in absolute values).

Effect of Halothane Genotype on Excretion Traits

The contrasts between halothane genotypes (*nn* to *NN* and *Nn* to *NN*) for excretion traits in PP are reported in Table 8. Excretion levels were lower in *nn* than in *NN* animals (average difference of 0.50 and 0.36 phenotypic standard deviation unit for N and P traits, respectively). The *Nn* animals showed intermediate levels of excretion compared with the 2 homozygous genotypes.

Table 4. Phenotypic correlations of residual feed intake and feed conversion ratio with all recorded traits for each breed (SE in parentheses)

	RFI				FCR			
Trait[1]	LR[2]	LWD[2]	LWS[2]	PP[2]	LR	LWD	LWS	PP
FCR	0.71 (0.01)	0.74 (0.01)	0.77 (0.01)	0.80 (0.01)	–	–	–	–
ADFI	0.62 (0.01)	0.60 (0.01)	0.61 (0.02)	0.51 (0.02)	0.42 (0.01)	0.37 (0.01)	0.43 (0.02)	0.21 (0.02)
ADG	0.00 (0.01)	0.00 (0.01)	0.00 (0.02)	–0.06 (0.03)	–0.45 (0.01)	–0.42 (0.01)	–0.35 (0.02)	–0.45 (0.02)
N_e	0.67 (0.01)	0.71 (0.01)	0.75 (0.01)	0.79 (0.01)	0.99 (0.00)	0.99 (0.00)	0.99 (0.00)	0.99 (0.00)
P_e	0.71 (0.01)	0.74 (0.01)	0.77 (0.01)	0.80 (0.01)	0.99 (0.00)	0.99 (0.00)	0.99 (0.00)	0.99 (0.00)
N_r	0.62 (0.01)	0.66 (0.01)	0.70 (0.01)	0.77 (0.01)	0.96 (0.00)	0.97 (0.01)	0.97 (0.01)	0.98 (0.00)
P_r	0.71 (0.01)	0.74 (0.01)	0.77 (0.01)	0.80 (0.01)	0.99 (0.01)	0.99 (0.01)	0.99 (0.01)	0.99 (0.01)
LMC	0.00 (0.02)	0.01 (0.01)	0.00 (0.02)	–0.01 (0.02)	–0.50 (0.01)	–0.40 (0.01)	–0.39 (0.02)	–0.21 (0.02)
BFT	–0.01 (0.02)	0.00 (0.01)	0.00 (0.02)	0.01 (0.02)	0.37 (0.01)	0.30 (0.01)	0.31 (0.02)	0.14 (0.02)
DP	0.00 (0.01)	0.01 (0.01)	0.00 (0.02)	–0.02 (0.02)	0.05 (0.02)	0.09 (0.01)	0.01 (0.02)	0.06 (0.02)
L*	–0.03 (0.01)	–0.03 (0.01)	–0.09 (0.02)	–0.10 (0.02)	–0.12 (0.01)	–0.09 (0.01)	–0.10 (0.02)	–0.12 (0.02)
pH_u	0.01 (0.01)	0.01 (0.01)	0.04 (0.02)	0.09 (0.02)	0.00 (0.01)	0.04 (0.01)	0.07 (0.02)	0.08 (0.02)
WHC	–0.01 (0.01)	–0.01 (0.01)	0.00 (0.02)	0.01 (0.02)	–0.10 (0.01)	–0.06 (0.01)	–0.06 (0.02)	0.01 (0.02)
MQI	0.01 (0.01)	0.02 (0.01)	0.05 (0.02)	0.10 (0.02)	0.01 (0.01)	0.04 (0.01)	0.06 (0.02)	0.11 (0.02)

[1]RFI = residual feed intake; FCR = feed conversion ratio; N_e = N excreted during the test period; P_e = P excreted during the test period; N_r = ratio of N excreted over N intake during the test period; P_r = ratio of P excreted over P intake during the test period; LMC = lean meat content; BFT = backfat thickness; DP = dressing percentage; L* = lightness of the meat of the gluteus superficialis muscle; pH_u = ultimate pH measurement of the semimembranosus muscle; WHC = water holding capacity of the gluteus superficialis muscle; MQI = meat quality index.

[2]LR = French Landrace dam breed; LWD = Large White dam breed; LWS = Large White sire breed; PP = Piétrain sire breed.

Table 5. Genetic correlations of residual feed intake and feed conversion ratio with all recorded traits for each breed (SE in parentheses)

	RFI				FCR			
Trait[1]	LR[2]	LWD[2]	LWS[2]	PP[2]	LR	LWD	LWS	PP
FCR	0.53 (0.07)	0.52 (0.05)	0.69 (0.08)	0.85 (0.04)	–	–	–	–
ADFI	0.61 (0.06)	0.55 (0.05)	0.72 (0.09)	0.48 (0.09)	0.51 (0.07)	0.37 (0.06)	0.88 (0.08)	0.20 (0.11)
ADG	0.07 (0.11)	0.16 (0.08)	0.09 (0.30)	–0.05 (0.12)	–0.51 (0.07)	–0.39 (0.06)	–0.09 (0.28)	–0.42 (0.09)
N_e	0.48 (0.07)	0.46 (0.06)	0.64 (0.09)	0.84 (0.04)	0.99 (0.00)	0.99 (0.00)	0.99 (0.00)	0.99 (0.00)
P_e	0.52 (0.07)	0.51 (0.05)	0.70 (0.08)	0.85 (0.04)	0.99 (0.00)	0.99 (0.00)	0.99 (0.02)	0.99 (0.00)
N_r	0.41 (0.07)	0.38 (0.06)	0.57 (0.10)	0.83 (0.04)	0.97 (0.01)	0.97 (0.01)	0.98 (0.01)	0.98 (0.01)
P_r	0.52 (0.07)	0.52 (0.05)	0.69 (0.08)	0.86 (0.04)	0.99 (0.01)	0.99 (0.01)	0.99 (0.01)	0.99 (0.01)
LMC	0.03 (0.08)	0.08 (0.07)	–0.04 (0.13)	–0.15 (0.12)	–0.74 (0.04)	–0.64 (0.04)	–0.71 (0.08)	–0.25 (0.11)
BFT	–0.11 (0.08)	–0.06 (0.07)	0.04 (0.14)	0.07 (0.13)	0.56 (0.05)	0.54 (0.05)	0.63 (0.10)	0.21 (0.12)
DP	0.03 (0.10)	0.01 (0.08)	–0.09 (0.16)	–0.11 (0.12)	–0.02 (0.09)	0.18 (0.07)	–0.06 (0.15)	0.07 (0.12)
L*	–0.08 (0.10)	–0.17 (0.08)	–0.19 (0.17)	–0.42 (0.14)	–0.32 (0.08)	–0.35 (0.07)	–0.20 (0.17)	–0.34 (0.14)
pH_u	0.11 (0.11)	0.14 (0.08)	–0.05 (0.23)	0.22 (0.14)	0.01 (0.09)	0.18 (0.07)	0.08 (0.21)	0.13 (0.13)
WHC	–0.13 (0.11)	0.14 (0.09)	–0.36 (0.18)	0.30 (0.22)	–0.34 (0.09)	–0.12 (0.08)	–0.50 (0.17)	0.25 (0.23)
MQI	0.07 (0.10)	0.17 (0.08)	–0.06 (0.20)	0.31 (0.13)	0.03 (0.09)	0.21 (0.07)	–0.01 (0.19)	0.21 (0.13)

[1]RFI = residual feed intake; FCR = feed conversion ratio; N_e = N excreted during the test period; P_e = P excreted during the test period; N_r = ratio of N excreted over N intake during the test period; P_r = ratio of P excreted over P intake during the test period; LMC = lean meat content; BFT = backfat thickness; DP = dressing percentage; L* = lightness of the meat of the gluteus superficialis muscle; pH_u = ultimate pH measurement of the semimembranosus muscle; WHC = water holding capacity of the gluteus superficialis muscle; MQI = meat quality index.

[2]LR = French Landrace dam breed; LWD = Large White dam breed; LWS = Large White sire breed; PP = Piétrain sire breed.

DISCUSSION

The objective of our study, conducted in 4 French major pig breeds, was to estimate genetic parameters for RFI with emphasis on the genetic relationships with production traits and N and P excretion. Means and SD for the usual production traits (e.g., ADG, FCR, ADFI, and LMC) were in agreement with the results previously found for these breeds (Labroue et al., 1997, 1999). It should be pointed out that differences between PP and the other breeds were accentuated because PP animals in this study were females, known to eat less, be leaner, and have a lower FCR and ADG than castrated males (Morales et al., 2011). However, for the purpose of the present genetic study, the most important feature is not the relative magnitude of the phenotypic differences caused by the breed or the sex of the animals, but that the genetic correlations between the sexes for any trait

Table 6. Phenotypic correlations of excretion traits with consumption, growth, and carcass traits for each breed (SE in parentheses)

Breed[1]	Trait[2]	ADFI	ADG	LMC	BFT	DP
LR	N_e	0.56 (0.01)	–0.50 (0.01)	–0.57 (0.01)	0.42 (0.01)	0.05 (0.02)
	P_e	0.55 (0.01)	–0.52 (0.01)	–0.51 (0.01)	0.38 (0.01)	0.06 (0.02)
	N_r	0.47 (0.01)	–0.38 (0.01)	–0.64 (0.01)	0.48 (0.01)	0.04 (0.02)
	P_r	0.44 (0.01)	–0.43 (0.01)	–0.51 (0.01)	0.38 (0.01)	0.05 (0.02)
LWD	N_e	0.53 (0.01)	–0.48 (0.01)	–0.47 (0.01)	0.36 (0.01)	0.10 (0.01)
	P_e	0.51 (0.01)	–0.50 (0.01)	–0.41 (0.01)	0.31 (0.01)	0.10 (0.01)
	N_r	0.44 (0.01)	–0.33 (0.01)	–0.55 (0.01)	0.43 (0.01)	0.10 (0.01)
	P_r	0.39 (0.01)	–0.40 (0.01)	–0.41 (0.01)	0.31 (0.01)	0.10 (0.01)
LWS	N_e	0.62 (0.02)	–0.41 (0.02)	–0.46 (0.02)	0.36 (0.02)	0.02 (0.02)
	P_e	0.60 (0.02)	–0.44 (0.02)	–0.41 (0.02)	0.31 (0.02)	0.02 (0.02)
	N_r	0.50 (0.02)	–0.26 (0.02)	–0.53 (0.02)	0.42 (0.02)	0.01 (0.02)
	P_r	0.45 (0.02)	–0.33 (0.02)	–0.40 (0.02)	0.31 (0.02)	0.02 (0.02)
PP	N_e	0.40 (0.02)	–0.53 (0.02)	–0.27 (0.02)	0.18 (0.02)	0.05 (0.02)
	P_e	0.37 (0.02)	–0.56 (0.02)	–0.22 (0.02)	0.15 (0.02)	0.07 (0.02)
	N_r	0.28 (0.02)	–0.38 (0.02)	–0.32 (0.02)	0.22 (0.02)	0.04 (0.02)
	P_r	0.23 (0.02)	–0.43 (0.02)	–0.21 (0.02)	0.15 (0.02)	0.07 (0.02)

[1]LR = French Landrace dam breed; LWD = Large White dam breed; LWS = Large White sire breed; PP = Piétrain sire breed.

[2]LMC = lean meat content; BFT = backfat thickness; DP = dressing percentage; N_e = N excreted during the test period; P_e = P excreted during the test period; N_r = ratio of N excreted over N intake during the test period; P_r = ratio of P excreted over P intake during the test period.

Table 7. Genetic correlations of excretion traits with consumption, growth, and carcass traits for each breed (SE in parentheses)

Breed[1]	Trait[2]	ADFI	ADG	LMC	BFT	DP
LR	N_e	0.59 (0.06)	–0.55 (0.07)	–0.80 (0.03)	0.62 (0.05)	–0.06 (0.09)
	P_e	0.59 (0.06)	–0.55 (0.07)	–0.75 (0.04)	0.57 (0.05)	–0.04 (0.09)
	N_r	0.54 (0.06)	–0.46 (0.07)	–0.85 (0.03)	0.68 (0.04)	–0.06 (0.04)
	P_r	0.53 (0.07)	–0.49 (0.07)	–0.75 (0.04)	0.59 (0.05)	–0.03 (0.09)
LWD	N_e	0.55 (0.05)	–0.46 (0.06)	–0.72 (0.04)	0.62 (0.04)	0.18 (0.06)
	P_e	0.54 (0.05)	–0.50 (0.05)	–0.66 (0.04)	0.56 (0.05)	0.18 (0.07)
	N_r	0.44 (0.05)	–0.29 (0.06)	–0.80 (0.03)	0.69 (0.04)	0.17 (0.06)
	P_r	0.40 (0.06)	–0.36 (0.06)	–0.66 (0.04)	0.56 (0.05)	0.18 (0.07)
LWS	N_e	0.95 (0.05)	–0.19 (0.28)	–0.76 (0.07)	0.68 (0.09)	–0.09 (0.15)
	P_e	0.95 (0.05)	–0.21 (0.28)	–0.71 (0.08)	0.64 (0.10)	–0.06 (0.15)
	N_r	0.89 (0.07)	–0.05 (0.28)	–0.82 (0.06)	0.74 (0.07)	–0.11 (0.14)
	P_r	0.88 (0.08)	–0.09 (0.28)	–0.71 (0.08)	0.65 (0.09)	–0.07 (0.15)
PP	N_e	0.46 (0.09)	–0.51 (0.08)	–0.36 (0.10)	0.27 (0.12)	0.05 (.012)
	P_e	0.40 (0.10)	–0.56 (0.08)	–0.29 (0.10)	0.23 (0.12)	0.06 (0.12)
	N_r	0.31 (0.10)	–0.32 (0.10)	–0.40 (0.10)	0.31 (0.11)	0.05 (0.12)
	P_r	0.22 (0.10)	–0.40 (0.10)	–0.26 (0.10)	0.22 (0.12)	0.07 (0.12)

[1]LR = French Landrace dam breed; LWD = Large White dam breed; LWS = Large White sire breed; PP = Piétrain sire breed

[2]LMC = lean meat content; BFT = backfat thickness; DP = dressing percentage; N_e = N excreted during the test period; P_e = P excreted during the test period; N_r = ratio of N excreted over N intake during the test period; P_r = ratio of P excreted over P intake during the test period.

does not differ from unity, which has been confirmed at a reasonable extend in an earlier study (Saintilan et al., 2012).

Computation of Residual Feed Intake

It has been hypothesized that selection to reduce RFI diminishes the portion of feed used for activity, metabolism, thermoregulation, and nutrient digestion (Herd et al., 2004). The proportion of phenotypic variability of ADFI accounted for by RFI in the present study was in agreement than those reported by Gilbert et al. (2007) and Caï et al. (2008) in Large White and Yorkshire pigs (24 and 34%, respectively). The better prediction of ADFI in PP is possibly due to the lower variability of body composition in this breed, as body composition contributed to only 7% of ADFI variability in this breed, compared with more than 12% in the other breeds. Regarding RFI, the effects of sex and breed were partly confounded in the current study, the tested pigs being females in PP breed and castrated males in the 3 other breeds. However, differences in genetic parameters involving RFI are likely to be mainly due to the breed, because genetic correlations between females and castrated males have been shown to be very close to 1 for RFI (Saintilan et al., 2012).

Table 8. Estimated contrasts between halothane genotypes (*Nn*-*NN* and *nn*-*NN*)[1] for N and P excretion traits in the Piétrain breed

Trait[2]	*Nn*-*NN*	*nn*-*NN*
N_e, kg	—0.076 (0.030)	—0.145 (0.032)
P_e, kg	—0.012 (0.006)	—0.022 (0.006)
N_r, %	—0.81 (0.28)	—1.65 (0.30)
P_r, %	—0.54 (0.26)	—0.98 (0.28)

[1]Numbers of *NN*, *Nn*, and *nn* pigs = 195, 520, and 1729, respectively.

[2]N_e = N excreted during the test period; P_e = P excreted during the test period; N_r = ratio of N excreted over N intake during the test period; P_r = ratio of P excreted over P intake during the test period.

Estimation of Nitrogen and Phosphorus Excretions

To our knowledge, this study is the first to report on the genetics of N and P estimated excretion in purebred pigs. The lowest excretion levels were found for PP in connection with decreased ADFI and FCR. Values previously reported in the literature have been obtained in crossbred pigs. Dourmad et al. (1999), Fernández et al. (1999) and van der Peet-Schwering et al. (1999) estimated N and P excretion for growing pigs in France, Denmark, and the Netherlands, respectively. These estimates were greater than those of our study for both total quantities (from 3.38 to 4.26 kg/pig for N_e, and from 0.72 to 0.92 kg/pig for P_e) and excretion expressed as percentage of N and P intakes (from 63.2 to 67.2% for N_r and from 62.9 to 65.7% for P_r). However, when estimated on a daily basis (results not shown), the excretion levels reported by the above-cited studies were not different from our estimates except for PP. Potential explanations for these differences could be the longer growing period than in our dataset (110 d and 28 to 108 kg, 94 d and 30 to 110 kg, and 119 d and 26 to 113 kg, respectively, in the 3 above-cited studies, vs. 77 to 86 d in our study), associated with lower ADG (from 729 to 744 g/d) and greater FCR (from 2.74 kg/kg to 2.89 kg/kg).

In addition, there were differences in feed composition compared with our study: feeds were richer in CP (16.5 to 17.4% vs. 15.6% in our study) and in total P (0.48 to 0.60% vs.0.48% in our study). Similarly, Shirali et al. (2012) reported estimates for N excretion in a crossbred Piétrain population, with average values of 5.35 kg for total N excreted per pig, 72.0% for N_r, and 52.7 g for daily N excretion; pigs had been tested from 60 to 140 kg BW, with a diet containing a minimum of 16.5% CP. In a meta-analysis on P balance, Schulin-Zeuthen et al. (2007) found that, on average, 64% of total P intake was excreted by pigs, which is of the same order as our values, ranging from 57.9 to 64.9%, according to the breed.

In chickens tested from 17 to 23 d of age and divergently selected for the digestibility of a poor quality wheat, de Verdal et al. (2011) found N_r and P_r of, respectively, 41 and 47% for "good-digesters," and of 63 and 58% for "bad digesters." On average, these values are lower than our estimates in pigs, but the differences in animal metabolic stages between the studies (1 wk early in the growing period in the chicken study compared with the whole growing-finishing period for our study) make these gross values difficult to compare. In a review, Kyriazakis (2011) actually suggested a systematic greater nutrient efficiency in pigs than in poultry, essentially due to differences in the digestive tract and digestion processes.

Heritabilities

Our estimates of heritability for RFI are within the range of the literature values for growing pigs having ad libitum and semi ad libitum access to feed (Clutter, 2011). The estimates for LWD and LWS breeds are close to the values of 0.24 and 0.29 reported by Gilbert et al. (2007) and Caï et al. (2008), respectively, in Large White and Yorkshire growing pigs. The slightly greater heritability found in PP can be related to the better accuracy of prediction of feed intake in this breed, and the greater heritability for ADFI in this breed compared with the others. Our estimate for LR was slightly less than the value of 0.29 reported by Hoque and Suzuki (2008) for this breed. However, these authors included only BFT as predictor of the BW gain composition in the prediction of ADF. Inclusion of body composition in the equation used to compute RFI has been consistently reported to reduce estimates of RFI heritability in pigs, as reviewed by Hoque and Suzuki (2009). The noninclusion of body composition for the calculation of RFI in certain studies has 2 main reasons. The first is that the variability in body composition in the targeted species was low enough to be ignored as a source of variability in feed intake, as in animals tested at early stages of growth (Lancaster et al., 2010; de Verdal et al., 2011). The second reason is that estimating correlations between RFI and body composition was the target of the analyses (Arthur et al., 2001).

To our knowledge, very few heritability estimates exist for N and P excretion traits. In growing chickens, de Verdal (2011) estimated heritabilities for these traits, with N excretion and P excretion measured directly by near infrared spectroscopy and by a colorimetric method, respectively. They also found that N_e, N_r, P_e, and P_r are moderately heritable (0.40, 0.29, 0.32, and 0.22, respectively).

Heritability estimates for growth and carcass composition traits were in the range of values reported by Clutter (2011). We have, however, no explanation for the low heritability estimate for ADG in LWS (0.05), which is much lower than expected. Our heritability estimates for meat quality traits were of the same order as those reported by Gilbert et al. (2007) for pH_u, L*, and WHC in Large White pigs, and in the range of values reviewed by Clutter (2011) for MQI.

Correlations

Genetic correlations between traits were of similar magnitude across breeds, except some correlations in PP. The positive and relatively high estimates for genetic correlations between RFI and ADFI or FCR were consistent with the values previously reported for growing pigs (Nguyen Hong et al., 2004; Gilbert et al., 2007; Caï et al., 2008; Hoque and Suzuki, 2009). Our estimates of genetic correlations between RFI and the traits included in the phenotypic multiple regression used for predicting ADFI did not differ from 0, whereas estimates reported by Hoque and Suzuki (2009) and Nguyen Hong et al. (2004) for genetic correlations of RFI with ADG, BFT, and LMC were low and positive, positive, and negative, respectively. Genetic correlations pertaining to FCR were reported to be moderately negative with ADG and LMC and moderately positive with BFT by Clutter (2011). Genetic correlations between RFI and meat quality traits showed that low-RFI animals would have a smaller MQI, with a paler and more acid meat in LWD and PP, as reported by Gilbert et al. (2007) in Large White pigs. Genetic correlations between RFI and excretion traits were positive and moderate to high in our study, with generally slightly greater correlations for P excretion than for N excretion. Positive genetic correlations between RFI and excretion traits were also found by de Verdal et al. (2011) in broilers, but with lower magnitude for ratio traits (0.37 for N_r and 0.08 for P_r) and greater magnitude for total amounts excreted (0.87 for N_e and 0.84 for P_e) than in our study. Differences in estimates of genetic correlations in LWS between excretion traits and ADFI and between excretion traits and ADG could be due to the greater genetic correlation between FCR and ADFI estimated in this breed, and due to the very low unexplained heritability of ADG. However, in this poultry study, ADFI was only predicted from ADG and

metabolic weight ($BW^{0.5}$), without considering carcass composition. Genetic correlations between FCR and excretion traits were also found to be highly positive by de Verdal (2011), with values of 0.95, 0.89, 0.66, and 0.76 for N_r, N_e, P_r, and P_e, respectively.

In the study of Shirali et al. (2012), total N excretion from 60 to 140 kg BW had a strong positive phenotypic correlation with FCR (r_p = 0.91) and a negative phenotypic correlation with ADG (r_p = —0.48), which is consistent with our estimates for all breeds. To our knowledge, no estimates have been reported for the correlations dealing with P excretion traits, and for those between N excretion traits and body composition.

Effect of the Halothane Genotype on Excretion Traits

The estimated contrasts between halothane genotypes for excretion traits in PP breed showed a significant effect of the *n* mutation on N and P excretion. Heterozygotes were found intermediate between the 2 homozygotes, and the effect of the halothane mutation on N and P excretion traits appears to be additive. Thus, heterozygous *Nn* pigs have reduced excretion levels compared with *NN* pigs. Considering the strong positive relationship between FCR and excretion traits, these results are in line with the effect of halothane genotype on FCR reported in purebred (Saintilan et al., 2011) or crossbred Piétrain pigs (Larzul et al., 1997; Gilbert et al., 2010). However, our results are not consistent with the differences between halothane genotypes reported by Shirali et al. (2012) for FCR and total N excretion in crossbred PP pigs. In that study, FCR and total N excretion were similar in *Nn* and *nn* pigs, but significantly lower in *NN* pigs. This suggests dominance of the *n* allele over the *N* allele, rather than additivity, as observed in our study.

Using Residual Feed Intake for Selection

It is quite expensive to measure RFI accurately, because it requires accurate recording of individual feed intake and estimation of body composition. Some early indicators, such as IGF-1 (Bunter et al., 2010), have been suggested to carry out a first step of selection for RFI and thus reduce the number of candidates for actual measurement of RFI. Genomic information could also be a tool to improve RFI, but only a small number of significant associations between this trait and genetic polymorphisms at individual loci have been reported so far (Fan et al., 2010; Gilbert et al., 2010).

The correlated responses to selection suggested by the genetic correlations found in the 4 breeds studied here are in general agreement with those reported by Dekkers and Gilbert (2010) on the basis of 2 selection experiments for RFI in Large White pigs (INRA, France) and Yorkshire pigs [Iowa State University (**ISU**), Ames]. These projects aimed at characterizing genetic and biological bases of RFI, such as physical activity, feeding behavior, nutrient digestion, maintenance requirements, stress, and energy homeostasis and partitioning (Luiting, 1999; Dekkers and Gilbert, 2010).

Compared with high-RFI or control pigs, low-RFI pigs have been reported to be less active both for feed consumption and for social interactions (Gilbert et al., 2009; Dekkers and Gilbert, 2010; Meunier-Salaün et al., 2011), to have a lower heat production in relation to a reduced basal metabolism (Barea et al., 2010), a reduced activity of enzymes implicated in oxidative and glycolytic metabolisms (Le Naou et al., 2012), and reduced viscera size (Dekkers and Gilbert, 2010). All these elements are associated to energy costs, which seem to be less in low-RFI pigs. It has been suggested that low-RFI pigs have lower energy requirements for maintenance (Nguyen Hong et al., 2005; Boddicker et al., 2011). However, to maintain a similar level of production as high-RFI pigs, with no difference in feed digestibility (Barea et al., 2010), low-RFI pigs have been reported to have greater requirements in AA, expressed in grams of digestible lysine per megajoule of NE (Brossard et al., 2012). This suggests that selection for improved RFI, like that for improved FCR, should only be conducted jointly with a reformulation of feed composition to cover nutritional requirements.

Selection for enhanced feed efficiency based on RFI led to leaner pigs (Gilbert et al., 2007; Caï et al., 2008); which is not concordant with our weak genetic correlations found between RFI with BFT and between RFI with LMC. Selection also led to less intramuscular fat and a hypertrophy of muscle fibers of the type IIBW (Lefaucheur et al., 2011). This muscular hypertrophy was associated with greater muscle glycogen content, in relation with a reduced technological quality of meat (lower pH_u, paler color, and greater drip loss; Lefaucheur et al., 2011) also found here for L* and pH_u (except for LWS), but this was not observed by others (Dekkers and Gilbert, 2010). However, no evidence of major meat defects has been reported in low-RFI lines, and only limited correlated impacts on eating quality of pork were found by Faure et al. (2013). In the ISU selection experiment, a switch to short-term energy storage in the low-RFI pigs compared with control pigs was associated with a downregulation of expression of genes involved in lipogenesis in both liver and adipose tissue (Lkhagvadorj et al., 2010). The lack of long-term energy storage could be a problem to face stresses, for example when ambient temperature decreases. Despite the reduction of RFI intake, which allegedly limits the ability of animals to cope with stress (Rauw et al., 1998),

low-RFI ruminants have been reported to better resist to stress, as shown by blood cell parameters in divergently selected steers for RFI (Richardson et al., 2002) or by cortisol measures in rams after an ACTH challenge (Knott et al., 2008). In pigs, no results are currently available on this aspect.

Finally, selection based on RFI in growing pigs has been reported not to impair reproductive performance of sows and boars. Selection for reduced RFI in growing pigs has been found to improve sow performance at farrowing, as well as number of piglets and litter growth (Young et al., 2010; Gilbert et al., 2012). Low-RFI sows have even been shown to have a reduced feed intake in lactation in combination with a greater mobilization of body reserves during lactation (Gilbert et al., 2012). No negative impact on rebreeding performance has been found in response to selection for RFI during growth in sows (Gilbert et al., 2012) and in cows (Herd, 2008).

Altogether, these features suggest that, despite early reservations about the use of RFI in breeding programs (Rauw et al., 1998), RFI is a good candidate to select efficient growing animals and specifically target the feed intake unrelated to production traits.

Compared with FCR, RFI is less heritable, particularly in dam breeds, and shows weaker genetic correlations with excretion traits. Residual feed intake has genetic correlations of the same magnitude as FCR with meat quality traits, so switching to this trait as a selection criterion to improve feed efficiency is not a solution to resolve the genetic antagonism between feed efficiency and meat quality. The most interesting feature of RFI is that it specifically quantifies the amount of feed intake not explained by production and maintenance requirements. As a consequence, it is nearly genetically uncorrelated to the traits used to estimate it. Using RFI as a selection criterion to improve feed efficiency would thus allow specific targeting of this fraction of feed intake and disentangling of responses to selection obtained on feed efficiency from responses obtained on growth rate or body composition, so that growth rate and body composition would not be modified. Of course, in such extreme strategy, because RFI represents only about a third of ADFI variability, the expected responses to selection would certainly be reduced for feed efficiency itself. However, it is reasonable to assume that using adequate weights of the traits in the selection indices, similar responses to selection can be obtained using either RFI or FCR as a selection criterion to improve feed efficiency. The major advantage of RFI compared with FCR as a selection criterion to improve feed efficiency is certainly in some intermediate strategy, such as, for example, to lower the selection pressure on body composition in a maternal line and maintain a large selection intensity on feed efficiency.

Implications

Residual feed intake represents a proportion of feed use not directly selected up to now in pig commercial populations. The RFI is a heritable trait in all pig breeds used in the current study. The PP breed shows reduced variability of feed requirements for growth compared with the other breeds. Positive genetic correlations between RFI and FCR and between RFI and excretion traits, unfavorable genetic correlations between RFI and meat quality traits, and a relative genetic independence of RFI with growth and carcass composition traits are confirmed in the 4 breeds studied. Compared with FCR, RFI had weaker genetic correlations with carcass composition, growth rate, and excretion traits. Estimates of genetic correlations between FCR and excretion traits were very close to 1 for all breeds. Traits related to N and P excretion are genetically more closely related to RFI in leaner sire breeds than in fatter dam breeds, in connection with greater genetic correlations between FCR and RFI in sire than in dam breeds. Differences between dam and sire breeds in terms of expected correlated responses to selection for RFI could be explained by the past integration of reproductive traits and maternal abilities in addition to production traits in the aggregate objective of selection of dam breeds. In conclusion, new selection indexes including RFI can be proposed to continue improving feed efficiency, with a favorable impact on N and P excretion, particularly sire pig breeds. However, the unfavorable genetic relationship between feed efficiency and meat quality traits remains a matter of concern when RFI is used in place of FCR, which needs to be accounted for in selection strategies.

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