Genetic correlations between feed efficiency traits, and growth performance and carcass traits in purebred and crossbred pigs

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ABSTRACT: Selection for feed efficiency (FE) is a strategy to reduce the production costs per unit of animal product, which is one of the major objectives of current animal breeding programs. In pig breeding, selection for FE and other traits traditionally takes place based on purebred pig (PB) performance at the nucleus level, while pork production typically makes use of crossbred animals (CB). The success of this selection, therefore, depends on the genetic correlation between the performance of PB and CB (r_{pc}) and on the genetic correlation (r_g) between FE and the other traits that are currently under selection. Different traits are being used to account for FE, but the r_{pc} has been reported only for feed conversion rate. Therefore, this study aimed 1) to estimate the r_{pc} for growth performance, carcass, and FE traits; 2) to estimate r_g between traits within PB and CB populations; and 3) to compare three different traits representing FE: feed conversion rate, residual energy intake (REI), and residual feed intake (RFI). Phenotypes of 194,445 PB animals from 23 nucleus farms, and 46,328 CB animals from three farms where research is conducted under near commercial production conditions were

available for this study. From these, 22,984 PB and 8,657 CB presented records for feed intake. The PB population consisted of five sire and four dam lines, and the CB population consisted of terminal cross-progeny generated by crossing sires from one of the five PB sire lines with commercially available two-way maternal sow crosses. Estimates of r_{pc} ranged from 0.61 to 0.71 for growth performance traits, from 0.75 to 0.82 for carcass traits, and from 0.62 to 0.67 for FE traits. Estimates of r_g between growth performance, carcass, and FE traits differed within PB and CB. REI and RFI showed substantial positive r_g estimates in PB (0.84) and CB (0.90) populations. The magnitudes of r_{pc} estimates indicate that genetic progress is being realized in CB at the production level from selection on PB performance at nucleus level. However, including CB phenotypes recorded on production farms, when predicting breeding values, has the potential to increase genetic progress for these traits in CB. Given the genetic correlations with growth performance traits and the genetic correlation between the performance of PB and CB, REI is an attractive FE parameter for a breeding program.

Key words: breeding program, carcass traits, feed efficiency, growth, genetic correlations, growing–finishing pigs

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INTRODUCTION

In an international scenario of increasing demand for animal protein and decreasing availability of natural resources, animal production systems have the challenge to increase productivity

Table 1. Number of animals with phenotypes of each line (sire, dam, or three-way cross) by farm

Line	Farms	Male	Females	Total
Sire 1	1,2,3,4,5	36,472	33,988	70,460
Sire 2	1,2,4,6,7	23,674	21,792	45,466
Sire 3	1,2,3,4	20,841	17,977	38,818
Sire 4	1,3	860	918	1,778
Sire 5	12	356	1,150	1,506
Dam 1	4,8,9,11,12,14,15,17	5,749	9,237	14,986
Dam 2	11,13,18,19,20,21,22	3,034	8,037	11,071
Dam 3	10,12,23	1,540	3,604	5,144
Dam 4	1,2,4,5,7,11,16,23	1,522	1,694	3,216
CB1	24,25,26	11,609	10,958	22,567
CB2	24,25	4,121	3,990	8,111
CB3	24,25	4,254	3,943	8,197
CB4	24,25	1,846	1,702	3,548
CB5	24,25	2,040	1,865	3,905

CB: three-way cross between the numbered sire line and a crossbred female of two dam lines.

and to reduce environmental load (Neeteson-van Nieuwenhoven et al., 2013). Furthermore, continuous growth of human population and increased demand for grains by biofuel industry press animal producers to use diet inputs in a more effective way. Therefore, the future of pork production is centered on pigs that efficiently convert feed into lean meat. Feed efficiency (FE) covers a broad spectrum of factors that in brief means to produce more output using less input (Patience, 2012). Thus, selection based on FE is a strategy to minimize the production cost per unit of animal product, which is one of the major objectives of current animal breeding programs. In pig breeding, selection for FE and other traits traditionally takes place based on purebred pig (PB) performance at the nucleus level, whereas pork production typically makes use of crossbred animals (CB). Thus, the success of this selection depends on the genetic correlation between the performance of PB and CB (r_{pc}) (Zumbach et al., 2007) and on the genetic correlation (r_g) between FE and the other traits that are currently under selection. For traits presenting low values of r_{pc} , the use of CB information has the potential to maximize genetic progress for crossbreeding schemes (Wei and van der Werf, 1994; Bijma and van Arendonk, 1998). The r_{pc} of FE was reported only for the trait feed conversion rate (Nakavisut et al., 2005; Habier et al., 2007; Tusell et al., 2016). Therefore, this study aimed 1) to estimate the r_{pc} for growth performance, carcass, and FE traits; 2) to estimate the r_g between traits within PB and CB populations; and 3) to compare three different traits representing FE: feed conversion rate (FCR), residual energy intake (REI), and residual feed intake (RFI).

MATERIALS AND METHODS

The data used for this study were collected as part of routine data recording in a commercial breeding program. Observations from 26 farms located in different countries (the Netherlands, France, Spain, Hungary, and Canada) were used in this study. All these farms are operating in line with the regulations on protection of animals of their countries.

Dataset

Phenotypic records of 194,445 PB and 46,328 CB were available for this study. Individual feed intake records were available on 22,984 PB and 8,657 CB. The PB population consisted of five sire and four dam lines, which were located in 23 nucleus farms (Table 1). Sire lines were located in eight of these farms. Dam lines were located in 21 of these farms. The CB population consisted of terminal cross-progeny generated by crossing sires from one of the five PB sire lines with commercially available two-way maternal sow crosses and were located in three farms where research is conducted under near commercial production conditions: Schothorst Feed Research (SFR) (Lelystad, the Netherlands), Experimental Farm of Institute for Pig Genetics (IPG) (Beilen, the Netherlands), and Varkens Innovatie Centrum (VIC) (Sterkel, the Netherlands). All pigs had a space allowance of at least 1 m² as this is part of the guidelines for the nucleus farms worldwide, and this rule also applies for commercial farms in the Netherlands. Group size (animals grouped together in the same pen) varied from 6 to 16 with an average of 10.6 and 10.2

Table 2. Number of observations, mean, standard deviation, minimum and maximum for covariates¹ and traits used to estimate heritabilities and genetic correlations

	No.	μ	SD	Min	Max
I. Purebred traits					
BW _{birth} [†] , g		1,441	318.70	400	3,150
BW _{ontest} [†] , kg		30.47	6.79	15	50
BW _{offtest} [†] , kg		114.9	13.97	70	194
ADG, g/d	182,988	902	150.54	443	1,562
ALDG, g/d	187,325	673.2	97.22	305	1,057
ADFI, g/d	22,984	2,077	236.66	1,301	2,700
LD, g/d	181,633	157.3	62.82	9	446
PD, g/d	181,633	156.8	27.17	59	281
MD, mm	180,003	57.96	7.72	23.3	90.5
BF, mm	186,905	10.18	2.74	2.5	24.3
FCR	22,984	2.2	0.25	1.23	3.53
REI, g/d	22,822	32.07	195.28	-769	775
RFI, g/d	22,727	-11.56	182.86	-803	659
II. Crossbred traits					
BW _{birth} [†] , g		1,396	321.92	320	3,160
BW _{ontest} [†] , kg		25.98	4.87	15	49.9
HCW, kg		91.16	6.57	52	130.8
CBW, kg		116.55	6.91	71.63	154.41
ADG, g/d	41,632	848.7	93.49	466	1,182
ALDG, g/d	41,976	521.1	51.59	213	810
ADFI, g/d	8,657	2,262	240.80	1,330	2,700
LD, g/d	10,464	197.1	54.91	47	429
PD, g/d	10,464	143.4	17.38	81	210
MD, mm	41,644	60.45	7.11	34.8	88.4
BF, mm	41,644	14.9	3.20	4.6	28.8
FCR	8,657	2.48	0.24	1.51	3.43
REI, g/d	8,381	113.3	187.99	-694	850
RFI, g/d	8,388	34.5	178.07	-741	739

[†]BW_{birth}[†], body weight at birth; BW_{ontest}[†], body weight ontest; BW_{offtest}[†], body weight offtest; CBW, calculated body weight.

pigs per pen for PB and CB, respectively. Pedigree records were available for all animals, up to a maximum of 21 generations. A total of 272,825 animals were included in the pedigree file with 7,257 different sires and 31,166 different dams. Average number of offspring was 32.9 per sire and 7.7 per dam. The degree of connectedness of contemporary groups (CGs) estimated using the AMC Program (Roso and Schenkel, 2006) based on the number of genetic ties to the main population group was high (98.45% of the CG and 99.9% of the animals connected).

Traits

Corresponding traits were identified in both PB and CB populations (Table 2). All animals were weighed individually at start of the growing–finishing period (ontest), around 25 kg. All PB had their BW (kg) recorded, and back fat thickness (BF, mm) and muscle depth (MD, mm) ultrasonically

measured at the end of the growing–finishing period (offtest). CB animals had their HCW recorded along with BF and MD using the Hennessy Grading Probe (Hennessy Grading Systems, Auckland, New Zealand) or the Capteur Gras Maigre (CGM, Sydel, France) at slaughter. Average daily gain on test (ADG, g/d) was obtained in PB as the BW at the end of the growing–finishing period (BW_{offtest}) minus penning BW (BW_{ontest}), divided by the length of the period. ADG was obtained in CB as the calculated BW (CBW) minus BW_{ontest}, divided by the length of the growing–finishing period. For average lifetime daily gain (ALDG, g/d) the BW at birth (BW_{birth}) instead of BW_{ontest} was considered. The formula used to obtain the CBW based on the HCW (Handboek varkenshouderij, 2004) was the following:

$$\text{CBW} = 1.3 \times \text{HCW} - 0.0025 \times \text{HCW}^2 + 0.2075 \times \text{HCW}$$

Animals were fed ad libitum in both populations (PB and CB). Individual feed intake was recorded using IVOG-stations (Insentec, Marknesse, the Netherlands). Average daily feed intake (ADFI, g/d) was calculated as cumulative feed intake during the total growing–finishing period divided by the length of the period. Lipid deposition (LD, g/d) and protein deposition (PD, g/d) were estimated as the increment in lipid and protein mass content during the phase based on BW and back fat measurements (de Greef et al., 1994):

$$\%fat_{\text{offtest}} = \frac{BF, \text{mm} - 1.87}{53.3},$$

$$\%fat_{\text{ontest}} = \%fat_{\text{offtest}} \times \frac{(-0.000005(BW_{\text{ontest}})^2 + 0.0019(BW_{\text{ontest}}) + 0.0665)}{(-0.000005(BW_{\text{offtest}})^2 + 0.0019(BW_{\text{offtest}}) + 0.0665)},$$

$$\text{Protein} - \text{water ratio} = 5.39(BW \times 0.14)^{-0.145},$$

$$\text{Ash} = 0.03 \times BW,$$

$$\text{Lipid mass (LM)} = \%fat \times 0.95 \times BW,$$

$$\text{Protein mass(PM)} = \frac{0.95 \times BW - LM - \text{Ash}}{\text{Protein} - \text{water ratio} + 1},$$

$$LD = \frac{(LM_{\text{offtest}} - LM_{\text{ontest}}) \times 1000}{\text{Test length}, d},$$

$$PD = \frac{(PM_{\text{offtest}} - PM_{\text{ontest}}) \times 1000}{\text{Test length}, d},$$

FE was calculated as FCR, REI (g/d), and RFI (g/d). FCR was calculated as the ADFI divided by the ADG. REI represents the efficiency of the energy metabolism, and was calculated as a linear function of energy intake, energy required for maintenance of live BW and energy required for lipid and protein accretion (Bergsma et al., 2013):

$$REI = \frac{ADFI \times 13.5 - ME_m - (LD + PD) \times 53}{13.5},$$

in which ME_m is the metabolizable energy required for maintenance of BW calculated from the metabolic BW (de Haer et al., 1993):

$$ME_m = \frac{(BW_{\text{offtest}}^{1.75} - BW_{\text{ontest}}^{1.75}) \times 420}{(BW_{\text{offtest}} - BW_{\text{ontest}}) \times 1.75}.$$

RFI was obtained as the difference between the observed and predicted ADFI (Cai et al., 2008):

$$ADFI = \mu + b_1 BW_{\text{ontest}} + b_2 BW_{\text{offtest}} + b_3 BF + b_4 ADG + b_5 Age_{\text{ontest}} + e,$$

in which Age_{ontest} is the age at which the animal was put on test; b_1 , b_2 , b_3 , b_4 , and b_5 are the linear coefficients of the regression on covariates; and e is the RFI.

Genetic Parameters Estimation

Genetic parameters were estimated under different approaches. Firstly, univariate analyses were performed to estimate the variance components and heritabilities of all traits. Secondly, correlations were estimated using bivariate analyses. Genetic correlation between the performance of PB and CB (r_{pc}) were estimated using corresponding traits together (e.g., ADG in PB and ADG in CB). Genetic (r_g) and phenotypic (r_p) correlations between different traits were estimated within populations (PB or CB). The fixed effects included for each trait are presented in Table 3. Only significant effects were included in the models for estimating variance components. BF and MD were preadjusted for the covariate weight prior to the bivariate analysis.

A linear mixed model implemented in ASReml (Gilmour et al., 2009) was used for the analyses as follows:

$$y = Xb + Za + Wc + Vg + Uf + e, \quad (1)$$

in which y is the vector of observations; X , Z , W , V , and U are known incidence matrices; b is a vector of fixed effects (Table 3); a is a vector of random additive genetic effects (breeding values),

Table 3. Fixed effects¹ included in the vector b for different traits

Model	Dependent trait(s)
	Fixed effects ¹
A	ADG; ALDG; LD; PD; FCR $\mu + SEX_j + LINE_k + HYS_l + COMP_m + b_1 \times BW_{\text{birth}}$
B	ADFI; REI; RFI $\mu + SEX_j + LINE_k + HYS_l + COMP_m + b_1 \times BW_{\text{ontest}}$
C	BF and MD in purebreds $\mu + SEX_j + LINE_k + HYS_l + COMP_m + b_1 \times BW_{\text{offtest}}$
D	BF and MD in crossbreds $\mu + SEX_j + LINE_k + HYS_l + COMP_m + b_1 \times HCW$

¹SEX, the sex of the animal; LINE, the line of the animal; HYS, Herd-Year-Season = farm $\times$ year of birth; COMP, compartment within barn $\times$ farm; BW_{birth} , body weight at birth; BW_{ontest} , body weight ontest; BW_{offtest} , body weight offtest.

$\mathbf{a} \sim N(0, \mathbf{A} \otimes \sum_a)$; $\mathbf{c}$ is a vector of random nongenetic effects common to individuals born in the same litter, $\mathbf{c} \sim N(0, \mathbf{I}_c \otimes \sum_c)$; $\mathbf{g}$ is the vector of random pen effects (animals grouped together in the same pen) $\mathbf{g} \sim N(0, \mathbf{I}_g \otimes \sum_g)$; $\mathbf{f}$ is the vector of random effects common to individuals performance tested in the same compartment of the barn within the same CG, $\mathbf{f} \sim N(0, \mathbf{I}_f \otimes \sum_f)$; and $\mathbf{e}$ is a vector of residuals, $\mathbf{e} \sim N(0, \mathbf{I}_e \otimes \sum_e)$. $\mathbf{A}$ is a matrix of additive genetic relationships among all individuals; $\mathbf{I}_c$, $\mathbf{I}_g$, $\mathbf{I}_f$, and $\mathbf{I}_e$ are identity matrices of the appropriate dimensions; and $\sum_a$, $\sum_c$, $\sum_g$, $\sum_f$, and $\sum_e$ are covariance matrices related to each effect. In the case of univariate analyses, the covariance matrix $\sum_i$ is scalar with the variance component σ_i associated to the respective effect.

Response to Selection

The response to direct selection on CB performance (R_{CB}) and the correlated response for CB performance (CR_{CB}) to indirect selection on

PB performance were calculated as (Falconer and Mackay, 1996):

$$R_{CB} = i_{CB} \times h_{CB} \times \sigma_{A_{CB}}$$

in which i_{CB} is the intensity of selection on CB (assumed to be 1 in this study), h_{CB} is the square root of the heritability of the trait on CB, and $\sigma_{A_{CB}}$ is the genetic standard deviation of the trait on CB.

$$CR_{CB} = i_{PB} \times h_{PB} \times r_{pc} \times \sigma_{A_{CB}}$$

in which i_{PB} is the intensity of selection on PB (assumed to be 1 in this study), h_{PB} is the square root of the heritability of the trait on PB, r_{pc} is the genetic correlation between the performance of PB and CB, and $\sigma_{A_{CB}}$ is the genetic standard deviation of the trait on CB.

RESULTS

Variance Components

Heritability estimates (Table 4) were larger for carcass traits (0.35–0.47 for PB and 0.24–0.43 for CB) than for growth performance traits (0.22–0.36 for PB and 0.26–0.36 for CB) and for FE traits

Table 4. Contribution (SE) of different random effects¹ to the estimation of the traits² in PB (I) and CB (II)

	h^2	$\frac{\sigma_{lr}^2}{\sigma_P^2}$	$\frac{\sigma_{pen}^2}{\sigma_P^2}$	$\frac{\sigma_{co}^2}{\sigma_P^2}$
I. Purebred				
ADG	0.23 (0.01)	0.06 (0.01)	0.12 (0.01)	0.11 (0.01)
ALDG	0.23 (0.01)	0.08 (0.01)	0.14 (0.01)	0.08 (0.01)
ADFI	0.23 (0.02)	0.05 (0.01)	0.14 (0.01)	0.16 (0.01)
LD	0.36 (0.01)	0.05 (0.01)	0.09 (0.01)	0.08 (0.01)
PD	0.22 (0.01)	0.06 (0.01)	0.11 (0.01)	0.13 (0.01)
MD	0.35 (0.01)	0.03 (0.01)	0.06 (0.01)	0.10 (0.01)
BF	0.47 (0.01)	0.04 (0.01)	0.05 (0.01)	0.06 (0.01)
FCR	0.17 (0.01)	0.04 (0.01)	0.18 (0.01)	0.12 (0.01)
REI	0.16 (0.01)	0.04 (0.01)	0.17 (0.01)	0.15 (0.01)
RFI	0.15 (0.01)	0.04 (0.01)	0.18 (0.01)	0.18 (0.01)
II. Crossbred				
ADG	0.26 (0.01)	0.05 (0.01)	0.08 (0.01)	0.10 (0.01)
ALDG	0.28 (0.01)	0.05 (0.01)	0.08 (0.01)	0.10 (0.01)
ADFI	0.28 (0.03)	0.05 (0.01)	0.19 (0.01)	0.11 (0.02)
LD	0.36 (0.03)	0.03 (0.01)	0.07 (0.01)	0.10 (0.01)
PD	0.33 (0.03)	0.05 (0.01)	0.07 (0.01)	0.12 (0.02)
MD	0.24 (0.02)	0.01 (0.01)	0.01 (0.01)	0.03 (0.01)
BF	0.43 (0.02)	0.03 (0.01)	0.02 (0.01)	0.02 (0.01)
FCR	0.15 (0.02)	0.04 (0.01)	0.22 (0.01)	0.18 (0.03)
REI	0.16 (0.02)	0.02 (0.01)	0.21 (0.01)	0.17 (0.02)
RFI	0.19 (0.02)	0.02 (0.01)	0.23 (0.01)	0.18 (0.03)

¹ h^2 is the heritability; σ_{lr}^2 is the variance of the common litter; σ_{pen}^2 is the variance of the contemporary pen; σ_{co}^2 is the variance of the contemporary compartment; σ_P^2 is the phenotypic variance.

(0.15–0.17 for PB and 0.15–0.19 for CB). The phenotypic variance explained by the common environment among litter mates was larger for growth performance traits (5–8% for PB and 3–5% for CB) than for FE traits (4% for PB and 2–4% for CB) and carcass traits (3–4% for PB and 1–3% for CB). The phenotypic variance explained by the contemporary pen effect was larger for FE traits (17–18% for PB and 21–23% for CB) than for growth performance traits (9–14% for PB and 7–19% for CB) and carcass traits (5–6% for PB and 1–2% for CB). The pattern of phenotypic variance explained by the contemporary compartment effect follows that of the contemporary pen effect, being larger for FE traits (12–18% for PB and 17–18% for CB) than for growth performance traits (8–16% for PB and 10–12% for CB) and carcass traits (6–10% for PB and 2–3% for CB).

Purebred–Crossbred Genetic Correlations

Estimates of r_{pc} are presented in Table 5. The range of estimated values was similar for the three groups of traits, with somewhat higher values for carcass traits. The r_{pc} ranged from 0.61 to 0.71 for growth performance traits, from 0.75 to 0.82 in carcass traits and from 0.62 to 0.67 for FE traits.

Genetic Correlations Between Traits Within PB and CB

Estimates of r_g within PB and within CB are given in Table 6. High growth was genetically associated with a high ADFI, LD and PD in PB and in CB. The r_g of growth with LD was stronger in PB than in CB. The r_g of growth with carcass traits was moderate in PB and low in CB, and these correlations were different in direction being unfavorable in PB but favorable in CB. Like growth, high ADFI is also genetically associated with high LD in PB and in CB. The r_g between ADFI and PD was moderate in PB as well as in CB; between ADFI and carcass traits it was moderate in CB; and between ADFI and MD it was low in PB. All r_g between the three traits LD, PD, and MD were low. BF was strongly negative associated (–0.84) with PD in PB, while this association was moderate in CB (–0.47). The r_g between LD and BF was almost unity in PB and high in CB.

Between FE traits and growth performance and carcass traits, we observed that the r_g of FCR with LD, MD, and BF were moderate in both PB and CB. In PB, FCR had high r_g with ADFI, and low r_g with growth and PD. In contrast, FCR in CB presented a high r_g with PD, and moderate r_g with growth and ADFI. REI presented moderate r_g with ADFI, LD, PD, and BF, low r_g with MD, and was not genetically associated with growth in PB and CB. The r_g of RFI was high with ADFI, moderate with growth, PD and MD, and low with LD and BF. Among FE traits, we observed that FCR in PB had high r_g with REI and RFI. In contrast, FCR in CB presented moderate r_g with REI and RFI. The r_g between REI and RFI was 0.84 in PB and 0.90 in CB.

Response to Selection

The expected response to direct selection on CB performance (R_{CB}), the expected correlated response for CB performance (CR_{CB}) to indirect selection on PB performance, and the ratio between them (R_{CB}/CR_{CB}) are presented in Table 8. The R_{CB} compared with the CR_{CB} were between 41% and 91% larger for growth performance traits, 10% and 17% larger for carcass traits, and between 40% and 82% larger for FE traits.

DISCUSSION

Variance Components

The random effects related to the grouping of animals (pen and contemporary compartment) were shown to be important, especially for ADFI and FE traits. For FE traits, the amount of the total phenotypic variance that could be attributed to the variance of common group (30–41%) was much higher than the amount accounted for by the additive variance (15–19%). The variation of these phenotypes was highly influenced by the housing and animal interactions. For FE, the proportion of the variance due to group was higher in CB (~40%) than in PB (~33%). These results are in agreement with Bergsma et al. (2013) who reported 46% of the phenotypic variance of REI being accounted for by group effect in a CB population and Cai et al. (2008) who reported 30% of the phenotypic variance of RFI explained by the effect of group in PB.

Table 5. Genetic correlations (SEs) between purebred and crossbred traits

	ADG	ALDG	ADFI	LD	PD	MD	BF	FCR	REI	RFI
r_{pc}	0.61 (0.06)	0.63 (0.06)	0.65 (0.15)	0.71 (0.07)	0.64 (0.08)	0.75 (0.04)	0.82 (0.03)	0.67 (0.18)	0.67 (0.18)	0.62 (0.18)

Table 6. Genetic correlations¹ (SEs) among purebred and crossbred traits

	ADG	ALDG	ADFI	LD	PD	MD	BF	FCR	REI	RFI
ADG										
ALDG	0.96 (0.01)		0.66 (0.04)	0.57 (0.04)	0.78 (0.02)	0.10 (0.04)	-0.05 (0.04)	-0.29 (0.07)	0.04 (0.07)	0.27 (0.07)
ADFI	0.71 (0.03)	0.72 (0.03)	0.67 (0.04)	0.58 (0.04)	0.73 (0.03)	0.07 (0.04)	-0.04 (0.04)	NC	-0.05 (0.07)	0.20 (0.07)
LD	0.69 (0.01)	0.70 (0.01)	0.76 (0.02)	0.75 (0.03)	0.28 (0.07)	-0.32 (0.06)	0.48 (0.05)	0.49 (0.06)	0.33 (0.07)	<u>0.65</u> (0.05)
PD	0.79 (0.01)	0.74 (0.01)	0.36 (0.04)	0.09 (0.02)	-0.02 (0.06)	-0.11 (0.05)	0.80 (0.02)	0.25 (0.08)	-0.54 (0.03)	<u>0.05</u> (0.08)
MD	-0.22 (0.02)	-0.24 (0.02)	-0.17 (0.04)	0.09 (0.02)		0.07 (0.06)	-0.49 (0.03)	-0.69 (0.03)	0.31 (0.08)	0.41 (0.07)
BF	0.24 (0.02)	0.27 (0.02)	NC	-0.15 (0.02)	-0.14 (0.02)		-0.07 (0.04)	-0.33 (0.07)	-0.18 (0.04)	-0.32 (0.06)
FCR	0.08 (0.05)	0.19 (0.05)	0.71 (0.03)	0.99 (0.01)	-0.84 (0.01)	-0.07 (0.01)	0.37 (0.04)	0.49 (0.06)	-0.29 (0.06)	-0.06 (0.06)
REI	0.02 (0.05)	-0.04 (0.05)	0.37 (0.05)	-0.32 (0.04)	0.24 (0.05)	-0.12 (0.04)	-0.45 (0.04)	0.70 (0.03)	0.53 (0.07)	0.55 (0.06)
RFI	<u>0.34</u> (0.05)	<u>0.32</u> (0.05)	<u>0.73</u> (0.03)	<u>0.20</u> (0.05)	0.32 (0.05)	-0.21 (0.04)	-0.03 (0.05)	<u>0.82</u> (0.02)	0.84 (0.02)	0.90 (0.02)

¹Genetic correlations among purebred traits below and among crossbred traits above diagonal.NC = analysis has not converged. Correlations in *italic* do not differ significantly from zero, in **bold** do differ in PB and CB, and underlined do differ in both REI and RFI ($P < 0.01$).

Comparisons between models that include or exclude the effect of group were presented for traits in growing pigs. If a nongenetic covariance among group mates exists, the group effect should be included in the model to avoid biased genetic parameters estimates (Bijma et al., 2007). Lu et al. (2017) reported around 72% of the phenotypic variance of six different measures of RFI being accounted for by group effect in a PB population. They concluded that the inclusion of a group effect in mixed animal models is necessary to improve the estimation of genetic parameters in growing pigs. By accounting for the group effect, the amount of the total phenotypic variance of RFI that could be attributed to the additive variance was reduced from around 54% to around 6%. This reduction was lower for ADG (from 35% to 23%) and for ADFI (from 18% to 14%). The group effect accounted for 55% and 59% of the phenotypic variance in ADG and ADFI, respectively. The inclusion of a group effect in the model was also shown to be necessary by Bergsma et al. (2008), to avoid biased estimates of genetic parameters in a population of CB growing pigs. They reported 27.5% and 42% of the phenotypic variance accounted for by the group effect in ADG and ADFI, respectively. By accounting for this group effect, the amount of the total phenotypic variance that could be attributed to the additive variance was reduced from 36% to 25% for ADG, and from 41% to 18% for ADFI.

Genetic Correlation Between the Performance of PB and CB

The values estimated for r_{pc} (Table 5) indicate that genetic progress is being realized in CB at the production level from selection on PB performance at nucleus level. When the goal is to improve CB performance, the value of having CB information increases when the r_{pc} decreases (Wei and van der Werf, 1994; Bijma and van Arendonk, 1998). Combined CB and PB selection (CCPS) for CB improved performance was suggested to be worthwhile over PB selection when the r_{pc} is lower than 0.8 (Wei and van der Werf, 1994). Estimate of r_{pc} for BF (0.82) indicate that we should expect less benefit from having CB information combined with PB information for the improvement of the CB performance for BF. For all other traits, the values of r_{pc} estimates are 0.75 or lower. Including CB phenotypes recorded on production farms, when predicting breeding values, has the potential to lead to higher genetic progress on these traits in CB.

Besides ADFI, all other traits are corresponding traits, meaning that they were obtained in different ways in PB or CB. To calculate ADG and ALDG, and thus also FCR, the BW_{offtest} is recorded in PB but in CB it is estimated from the HCW. The traits BF and MD are measured ultrasonically in live PB but estimated with a probe in the carcass of CB. The traits LD, PD, REI, and RFI are calculated using BW, ADG, and BF, traits that are measured differently in PB and CB. The use of corresponding traits to estimate correlations may have lowered the values of the r_{pc} estimates because they may not fully behave as the same trait. The impact of this is expected to be small.

The values of r_{pc} estimates for growth performance and carcass traits presented in this study are in the range of literature. For the trait FCR, high values (0.66–0.92) have also been obtained in other studies (Nakavisut et al., 2005; Habier et al., 2007; Tusell et al., 2016). To the best of our knowledge, this is the first report of r_{pc} for ADFI, REI, and RFI in pigs. The limited number of studies is due to the fact that feed intake, and thus FE, are expensive to measure and therefore not broadly available. Especially in CB, the availability of feed intake data is very low. In this study, estimation of r_{pc} for these traits was possible given the high number of records on ADFI of crossbreds.

Although records on feed intake are not broadly available in pigs, the expectation was that r_{pc} for ADFI, REI, and RFI would not be high given differences concerning health status and housing between nucleus and production farms, among other differences between PB and CB. Knap and Wang (2012) concluded that ADFI as it is recorded in nucleus conditions is not very useful for breeding value estimation of FE in a system that aims to produce commercially fattened pigs. They reported correlations between univariate EBVs of two lines of PB in nucleus farm and their halfsib CB in production conditions. They found moderate correlations between EBV for ADFI (0.55 for line S1 and 0.54 for line S2) and extremely low EBV correlations for RFI (−0.06 for line S1 and 0.06 for line S2). Because these values are based on EBV, they could have been higher depending on the EBV accuracies. Also, no information about the production environment for CB was provided. Large differences from nucleus conditions could have lowered the correlation values. In the current data, management on the current CB farms was better than the average production farm. Our estimates of r_{pc} for ADFI and FE traits are all between 0.62 and 0.67 (Table 5), in the same range as other production

traits. Part of genetic progress from selection in PB for ADFI, FCR, REI, and RFI is therefore being realized in CB performance.

Reduction of r_{pc} below 1 may not purely be attributable to genetic factors but also to genotype by environment interaction ($G \times E$), given the usual differences between environments where PB and CB are raised (Wei and van der Werf, 1994; Bijma and van Arendonk, 1998; Zumbach et al., 2007; Tusell et al., 2016). When considering estimates of genetic correlations between the performance of PB and CB, it is important to remark that this methodology also detects genotype by environment interaction ($G \times E$) considering the same trait as different traits in both environments. In this study, the reduction of r_{pc} estimates below 1 may also be caused by $G \times E$, given the differences between the nucleus environment where PB are maintained and production farms where CB were raised. Production farms have lower levels of hygiene status and may have different housing systems compared with nucleus farms. These factors affect performance and therefore lower the r_{pc} estimate. Besides the fact that PB and CB are not in the same environment, the limited number of CB farms may give rise to $G \times E$ by chance.

Tusell et al. (2016) reported r_{pc} estimates for PB and CB raised at the same time and in the same test station facility. They obtained higher r_{pc} estimated values for ADG (0.79) and FCR (0.89). Habier et al. (2007) also presented r_{pc} estimates of PB and CB raised in the same two stations over a 5-year period with values of 0.88 for ADG and 0.74 for FCR. Stamer et al. (2007) presented r_g estimates for 17 growth performance, carcass and meat quality traits of PB and CB pigs raised in two housing systems, either in groups of 2 (g2) or in groups of 10 pigs (g10). Average r_g estimates were 0.87 between the performance of CB(g2) and CB(g10), 0.72 between the performance of PB(g2) and CB(g2), and 0.63 between the performance of PB(g2) and CB(g10). The value of 0.63 represents the r_g between traits measured on PB in one environment (g2) and measured on CB in another environment (g10). Effects of $r_{pc} < 1$ as well as $G \times E$ are possible contributors to the r_g of 0.63 being smaller than unity. Indeed, when only r_{pc} was expected to contribute (PB(g2) vs. CB(g2)) or when only $G \times E$ is expected to contribute (CB(g2) vs. CB(g10)) the genetic correlation was higher than 0.63. The situation where the performance of PB(g2) and CB(g10) was compared approximates the reality where selection takes place in PB performance in improved environment and the CB are raised in larger groups in production

farms. In this comparison, an r_{pc} estimate of 0.65 was reported for the trait ADG, which is close to our value for the same trait (0.61). In our r_{pc} estimates, the effects of $G \times E$ are likely to be present as shown in Stamer et al. (2007).

Moreover, a distinction between effects due to $G \times E$ or a truly lowered r_{pc} is not necessary in CCPS since optimal breeding decisions in both cases are taken based on the same model (Wei and van der Werf, 1994). In our data, we cannot disentangle the effects of r_{pc} and $G \times E$. However, because in practical pork production the environments typically vary together with the breed composition, PB or CB, our estimates of r_{pc} are relevant measures, even without knowing which part is caused by the different genetic background of the growing animal and which part by the environmental differences between the PB and CB growing environment.

Genetic Correlation Between Growth Performance and Carcass Traits Within PB and CB

Depending on the genetic background of the animals (PB or CB), the genetic association between traits changes between favorable and unfavorable or values are changing (Table 6). The differences in signs and magnitudes of r_g in PB and CB are relevant for a breeding program aiming at CB performance. Less BF is genetic associated with more PD with the estimate being higher in PB than in CB. On the other hand, more growth was associated with more LD with the estimate being higher in PB than in CB. Differences in the sign of r_g were found between gain and MD, gain and BF, and MD and PD with the favorable values in CB. In a multitrait breeding program, these favorable correlations could lead to a larger overall genetic response with data collection in CB compared with the same program in PB.

Comparison Between FE Traits

The high r_g between REI and RFI indicate that they largely explain the same genetic variance, in both PB and CB (Table 6). In addition, the high r_g found between these traits and FCR indicates that genetic progress based on any one of them will improve the other traits. However, we observe differences between the FE traits when it comes to their r_g with growth performance and carcass traits. Thus, the total genetic gain on the breeding goal can be influenced by the choice of trait that is used to measure FE.

In contrast with FCR and REI, RFI was phenotypically independent from growth performance and carcass traits, both in PB and CB (Table 7). This independency has been reported as an advantage of RFI over FCR (de Haer et al., 1993; Kennedy et al., 1993) because it captures variance on FE not accounted for by its component traits. FCR presented a favorable genetic correlation with all other traits in PB and CB with moderate or high values. The favorable correlations with all other production traits mean that selection on production traits will result in progress for FCR. Therefore, FCR is of limited interest to breeders because the trait has low potential to capture variance in FE due to other effects rather than its components traits (Patience, 2012).

The pattern of r_g estimates of REI with the other studied traits in PB and CB is preferable over the pattern of r_g estimates of RFI with those other traits for several reasons. First, REI shows no r_g with growth, while RFI has an unfavorable moderate r_g . Second, values of r_g between REI and the traits MD, PD, and ADFI were lower than between these traits and RFI. Lower values of r_g with production traits imply that REI captures other sources of variance. It is remarkable that the r_g between REI and ADFI is only half the size of r_g between RFI and ADFI. Finally, we note that r_g of PD with RFI as well as PD with REI were unfavorable with higher values for the correlation with RFI. On the other hand, RFI shows no genetic association with BF and LD in CB, and with BF in PB. The r_g between RFI and LD in PB was favorable and of low magnitude. In contrast, unfavorable r_g were found between REI and BF and between REI and LD in both PB and CB with moderate values. Phenotypic correlations between these traits were also unfavorable with moderate values. Except for the unfavorable correlations with BF and LD, our findings indicate that REI is an attractive trait since it is genetically independent from growth and present lower correlations with ADFI and thus has a great potential to capture other sources of variation in FE that is not explained by ADFI.

In grower–finishers, energy usage is divided into energy used for growth (lipid and protein deposition) and for maintenance. One-third of the total daily supply of energy is devoted to maintenance (Patience, 2012), which makes variation in energy required for animal maintenance a major factor in the variation in FE. From this point of view, energy for maintenance should be in the equation of FE. Henken et al. (1991) showed the presence of genetic variation in maintenance requirements in

pigs being due to differences in physical activity and heat production. This fits with our results that leaner animals have higher REI. A possible explanation is that leaner animals are more active and thus have a higher energy requirement for maintenance. This hypothesis is supported by Boddicker et al. (2011), who also indicated maintenance requirement as one of the main factors contributing for variation in RFI. Low RFI pigs spent less time in feeders and have reduced numbers of meals and high consumption rate when in feeders (De Haer et al., 1993). Selection on RFI has been shown to be associated with animal characteristics that are related to energy cost (Shirali, 2014). Reduced maintenance energy requirements reduced physical activity and thus reduced heat production of pigs selected downward for RFI has shown to greatly contributed to the gain in energy efficiency (Gilbert et al., 2017). Low RFI pigs are therefore desired because of the advantages of spending less energy on feed consumption, interacting with others, heat production, and maintenance requirements.

Response to Selection

Differences between the additive genetic variance (not shown) and the heritability estimates in PB and CB (Table 4), the intensity of selection applied in PB and CB, and the r_{pc} (Table 5) will impact the genetic gain (Table 8) that can be achieved in CB performance when selecting based on PB or CB performance. When the goal is the CB performance, the benefit of direct selection on CB performance (R_{CB}) over the indirect selection on PB performance (CR_{CB}) can be assessed by the ratio between them (R_{CB}/CR_{CB}). When the intensity of selection is equal in PB and CB, this ratio is assessed by h_{CB} divided by $h_{PB} \times r_{pc}$ (Falconer and Mackay, 1996). Thus, with higher h_{CB} , relative to h_{PB} , and with lower r_{pc} , the benefit of direct selecting based on CB performance increases. R_{CB} was higher than CR_{CB} for all traits meaning that direct selection on CB performance would lead to higher response to selection for all traits.

Carcass traits presented lower heritability estimates in CB than in PB. Also the r_{pc} were higher compared with growth performance and FE traits. Therefore, while R_{CB} was still superior, it was lower for these traits (10–17%). Traditionally, data recording for breeding programs in pigs is organized at the nucleus level on PB animals. Given the limited benefit in response from direct selection on CB performance, the extra cost of data recording on CB may not be worthwhile for carcass traits. Because

Table 7. Phenotypic correlations¹ (SEs) among purebred and crossbred traits²

	ADG	ALDG	ADFI	LD	PD	MD	BF	FCR	REI	RFI
ADG		0.85 (0.01)	0.52 (0.01)	0.63 (0.01)	0.78 (0.01)	0.05 (0.01)	0.12 (0.01)	-0.32 (0.02)	NC	0.05 (0.02)
ALDG	0.92 (0.01)		0.50 (0.02)	0.63 (0.01)	0.69 (0.01)	0.04 (0.01)	0.09 (0.01)	NC	-0.20 (0.02)	0.02 (0.02)
ADFI	0.47 (0.01)	0.47 (0.01)		0.56 (0.01)	0.25 (0.02)	-0.08 (0.01)	0.30 (0.01)	0.54 (0.01)	0.51 (0.01)	0.70 (0.01)
LD	0.72 (0.01)	0.70 (0.01)	0.54 (0.01)		0.09 (0.02)	-0.13 (0.01)	0.59 (0.01)	0.05 (0.02)	-0.44 (0.01)	-0.09 (0.02)
PD	0.87 (0.01)	0.79 (0.01)	0.29 (0.01)	0.33 (0.01)		-0.02 (0.01)	-0.30 (0.01)	-0.47 (0.01)	0.04 (0.02)	0.13 (0.02)
MD	-0.08 (0.01)	-0.09 (0.01)	-0.06 (0.01)	-0.01 (0.01)	-0.07 (0.01)		-0.03 (0.01)	-0.07 (0.01)	-0.08 (0.01)	-0.08 (0.01)
BF	0.20 (0.01)	0.18 (0.01)	NC	0.98 (0.01)	-0.77 (0.01)	0.01 (0.01)		0.16 (0.01)	-0.17 (0.01)	-0.04 (0.01)
FCR	-0.23 (0.01)	-0.11 (0.01)	0.64 (0.01)	0.03 (0.01)	-0.29 (0.01)	-0.03 (0.01)	0.19 (0.01)		0.77 (0.01)	0.77 (0.01)
REI	-0.25 (0.01)	-0.28 (0.01)	0.57 (0.01)	-0.36 (0.01)	-0.09 (0.01)	-0.05 (0.01)	-0.28 (0.01)	0.85 (0.01)		0.95 (0.01)
RFI	0.03 (0.01)	-0.02 (0.01)	0.77 (0.01)	-0.01 (0.01)	0.05 (0.01)	-0.06 (0.01)	-0.04 (0.01)	0.84 (0.01)	0.92 (0.01)	

¹Phenotypic correlations among purebred traits below and among crossbred traits above diagonal.²NC = analysis has not converged. Correlations in *italic* do not differ significantly from zero, in **bold** do differ in PB and CB, and underlined do differ in both REI and RFI ($P < 0.01$).

Table 8. Response to direct CB selection and correlated response for CB performance to indirect selection on PB performance

	ADG	ALDG	ADFI	LD	PD	MD	BF	FCR	REI	RFI
R_{CB}	21.76	12.68	53.00	16.76	4.82	1.41	1.11	0.03	27.25	30.22
CR_{CB}	12.48	7.24	31.22	11.90	2.52	1.28	0.95	0.02	18.26	16.65
$\frac{R_{CB}}{CR_{CB}}$	1.74	1.75	1.70	1.41	1.91	1.10	1.17	1.40	1.49	1.82

R_{CB} , response to direct CB selection; CR_{CB} , correlated response for CB performance to indirect selection on PB performance.

heritability estimates in CB are higher compared with PB for ADG, ALDG, PD, ADFI, and RFI (Table 4), and given the values of r_{pc} (Table 5), the direct selection on CB performance will lead to between 70% and 91% higher genetic gain for these traits. Because heritability estimates in PB and CB are equal or similar for LD, FCR, and REI, and given the values of r_{pc} (Table 5), the direct selection on CB performance will lead to between 40% and 49% higher genetic gain.

CONCLUSIONS

Genetic progress is being realized in CB at the production level from selection on PB performance at nucleus level for growth and carcass traits and also for FE traits. Including CB phenotypes recorded on production farms, when predicting breeding values, has the potential to increase genetic progress for the performance in CB. Given the r_g between growth performance and carcass traits, a larger overall genetic response in a multitrait breeding program could be expected with data collection in CB compared with the same program in PB. Group effects are major sources of variation in ADFI and FE traits. Given the r_g with growth performance traits and the genetic correlation between the performance of PB and CB, REI is an attractive FE parameter for a breeding program.

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