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Correlated responses of pre- and postweaning growth and backfat thickness to six generations of selection for ovulation rate or prenatal survival in French Large White pigs[1]

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Abstract: Correlative effects of 6 generations of selection for either ovulation rate (OR) or prenatal survival (PS) on growth rate and backfat thickness were estimated. Genetic parameters for piglet weight at birth (WW), at 3 weeks of age (W3W) and at weaning (WW), average daily gains from birth to weaning (ADGBW), from weaning to 10 weeks of age (ADGPW) and during performance test (ADGT), age (AGET) and backfat thickness at the end of test (ABT), were estimated using REML methodology applied to a multivariate animal model. Estimates of direct and maternal heritabilities were, respectively, 0.10, 0.12, 0.20, 0.24, 0.41 and 0.17, 0.33, 0.32, 0.41, 0.21 (SE = 0.03 to 0.04) for IWB, IW3W, IWW, ADGBW and ADGPW. Genetic correlations between direct and maternal effects were moderate at birth (-0.21 ± 0.18), but much larger after birth (-0.59 to -0.74). Maternal effects were not considered for on test performance traits. Direct heritabilities were 0.34, 0.46 and 0.21 (SE = 0.03 to 0.05) for ADGT, AGET and ABT, respectively. Genetic correlations of OR and PS with performance traits were low (below 0.30) except maternal genetic correlations of PS with preweaning growth traits (-0.34 to -0.65). Estimated genetic trends were low and non significant, except negative maternal trends for IBW and favourable direct trends for ADGT and AGET in both lines.

INTRODUCTION

Genetic improvement has proven to be an effective means of increasing the efficiency of pork production. Even lowly heritable traits, such as litter size at birth, have been successfully selected for either directly (Tribout et al., 2003) or through indirect selection on its component traits (Johnson et al., 1999). However, larger litters at birth have in most cases been accompanied by unfavorable trends in farrowing and birth to weaning piglet survival (Johnson et al., 1999; Tribout et al., 2003; Canario et al., 2006b). Decreased piglet weight has been suggested as a contributor to this increased mortality (Johnson et al., 1999). Indeed, piglet birth weight has been shown to have negative genetic correlations with number of piglets born and birth to weaning survival (Kerr and

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Cameron, 1995; Roehe, 1999; Rosendo et al., 2007a). However, birth weight and preweaning growth traits are genetically complex and depend on both piglet, and genetic and foster sow, genotypes (Knol et al., 2002; Bouquet et al., 2006). Recent studies (Kaufmann et al., 2000; Ruiz-Flores and Johnson, 2001) suggest that genetic correlations between litter size and direct and maternal effects on piglet growth differ to some extent. Moreover, maternal effects are not necessarily limited to the suckling period and may also affect pig postweaning performance (Robison, 1972; Bryner et al., 1992).

A selection experiment was carried out to estimate genetic parameters and responses to selection for components of litter size in the French Large White breed (Blasco et al., 1998; Rosendo et al., 2007b). The main objective of this study was to estimate the correlated responses to selection for either high ovulation rate or high prenatal survival on direct and maternal components of pig pre-weaning and post-weaning growth, as well as backfat thickness.

MATERIALS AND METHODS

Animals and Experimental Design

The experiment took place in the INRA experimental herd of Galle (Avord, France). Animal care followed the general guidelines outlined in the European animal welfare regulations (91/630/EC directive). Two lines of pigs were selected for either high ovulation rate at puberty (**OR**) or high prenatal survival (**PS**) over the first 2 parities corrected for ovulation rate at fertilization (ORF). PS was computed as total number born /ORF + 0.018 ORF (Rosendo et al., 2007a). The correction term was introduced to avoid trends in PS associated with variations in OR. The term 0.018 represented an average literature value for the phenotypic regression coefficient of PS on ORF. A third line was kept as an unselected control line (**C**). At each generation, about 50 gilts and 6 to 8 boars from first litters were kept for breeding. Boars were chosen on a within-sire family basis in the 3 lines. Gilts were randomly chosen on a within-dam family basis in the **C** line and selected on a population basis in the 2 other lines. A mating plan was established in order to minimize inbreeding at each generation. Additional details on the experimental design are given in Rosendo et al. (2007b).

The sow herd was managed under a batch farrowing system. Females were distributed into 7 farrowing batches, which then became postweaning and performance test batches of their progeny. Litters were born in individual farrowing crates. Some crossfostering (about 5% of the piglets) occurred on a within-line basis during the first 48 h after farrowing. Creep feed was provided to piglets beginning at about 5 d of age. Weaning occurred approximately 28 d post-farrowing. All piglets were weighed at birth (i.e., during the first 12 h after birth), at 3 and at 4 wk of age.

All available offspring from first and second parities were kept in a post-weaning unit from 28 to 70 d of age. They were then allotted to a performance test building in which they were housed in pens of 10 to 12 animals of the same line, where they stayed until the end of the test period when they reached 90 kg BW. Lines were randomly allocated to approximately 120 pens at each generation so as to avoid confounding between pen and selection line. Animals were fed *ad libitum* with a commercial diet formulated to contain 3,100 kcal DE/kg and 17% crude protein during the entire test period. All pigs were also weighed at the beginning and end of the test period. Ultrasonic backfat thickness was measured at the same time as final weight. The ultrasonic records were taken on each side of the spine, 4 cm from mid-dorsal line at the levels of the shoulder, the last rib, and hip joint, respectively.

Statistical Analyses

The traits analyzed were individual piglet BW at birth (**IWB**), at 3 wk (**IW3W**), and at weaning (**IWW**); average daily gain from birth to weaning (**ADGBW**), from weaning to the beginning of performance test (**ADGPW**), and for the performance test period **(ADGT)**, age (**AGET**), and average backfat thickness (**ABT**), computed as the mean of the 6 above mentioned measurements, at the end of performance test. The performance test started at approximately 25 kg BW and ended around 90 kg BW. Descriptive statistics for the 8 traits are given in Table 1.

Least Squares (LS) Analyses of Line Differences. The data were first analyzed by least squares using the GLM procedure of SAS (SAS Inst., Cary NC. 1999). Mean performances and standard errors for each line-generation subclass were estimated using a linear model including the fixed effects of selection line (**OR**, **PS,** or **C**), generation number (G = 0 to 6) and their interaction, parity of the dam, contemporary group (animals tested during the same period of time in the same building) within generation, sex (female, intact male, or castrate for all traits except ABT, which was measured only on intact males and females), crossfostering status (yes or no – except for IWB, AGET, and ABT). The dam and piglet inbreeding coefficients, the exact age of pigs at the different weight measurements (at 3 wk, at weaning), the number of piglets nurtured (preweaning traits and ADGPW), and BW at birth (ADGBW), at weaning (ADGPW), at the beginning (ADGT), and at the end of the test period (AGET and ABT) were also included as linear covariates. The exact model used for each trait is given in Table 2. Generations 6 and 7 were grouped in final analyses, as no selection occurred in generation 7 and preliminary analyses showed that line x generation least-squares means were very similar.

Table 1. Descriptive statistics for the growth and backfat thickness traits studied

Trait	Abbre-viation	N	Mean	SD	Min	Max
Individual BW at birth, kg	IWB	9,114	1.32	0.27	0.49	2.29
Individual BW at 3 wk, kg	IW3W	9,006	5.73	1.23	1.3	10.5
Individual BW at weaning, kg	IWW	9,114	7.59	1.58	1.95	13.85
Average daily gain from birth to weaning, g/d	ADGBW	9,114	215	50	21	430
Average daily gain from weaning to beginning of performance test, g/d	ADGPW	9,021	419	108	13	886
Average daily gain from 25 kg to 90 kg BW, g/d	ADGT	8,267	802	108	107	1213
Age at the end of performance test, d	AGET	8,408	165.4	12.7	105	238
Average backfat thickness, mm	ABT	3,540	26.9	7.3	12.7	47.7

Mixed Model (MM) Analyses. Variance components for the different traits and covariances between traits were first estimated using Restricted Maximum Likelihood (REML) methodology (Patterson and Thompson, 1971) applied to univariate and bivariate mixed linear animal models. With the exception of generation and line effects, the fixed part of the model was similar to that used for least squares analyses. The random part of the model initially included a common litter environmental effect, direct and maternal genetic effects, and the correlation between direct and maternal effects. Maternal effects were defined as effects of either the genetic (IWB) or the foster dam (IW3W, IWW, ADGBW, ADGPW). In matrix notation:

$$\mathbf{y} = \mathbf{X}\boldsymbol{\beta} + \mathbf{W}_a\,\mathbf{a} + \mathbf{W}_m\,\mathbf{m} + \mathbf{W}_c\,\mathbf{c} + \mathbf{e},$$

where $\mathbf{y}$ is the vector of observations, $\mathbf{X}$, $\mathbf{W}_a$, $\mathbf{W}_m$, and $\mathbf{W}_c$ are known incidence matrices relating observations to fixed and random effects; $\boldsymbol{\beta}$ = vector of fixed effects and covariates; $\mathbf{a}$ is the vector of direct genetic effects; $\mathbf{m}$ is a vector of maternal (genetic or foster dam) genetic effects; $\mathbf{c}$ is the vector of common litter environmental effects; and $\mathbf{e}$ is the vector of random residual effects. All random effects were assumed to follow a normal distribution with zero mean and the following distribution parameters:

$$\mathrm{E}(\mathbf{y}) = \mathbf{X}\boldsymbol{\beta}$$

$$\mathrm{var}\begin{bmatrix}\mathbf{a}\\ \mathbf{m}\\ \mathbf{c}\\ \mathbf{e}\end{bmatrix} = \begin{bmatrix}\mathbf{A}\sigma_a^2 & \mathbf{A}\sigma_{am} & \mathbf{0} & \mathbf{0}\\ \mathbf{A}\sigma_{am} & \mathbf{A}\sigma_m^2 & \mathbf{0} & \mathbf{0}\\ \mathbf{0} & \mathbf{0} & \mathbf{I}\sigma_c^2 & \mathbf{0}\\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{I}\sigma_e^2\end{bmatrix}$$

where **A** is the additive relationship matrix; σ_a^2 is the additive genetic variance for direct effects; σ_m^2 is the additive genetic variance for maternal effects; σ_{am} is the covariance between direct and maternal additive genetic effects; σ_c^2 and σ_e^2 are the variances for the random common litter environmental and residual effects, respectively. **I** is the identity matrix of appropriate dimension in each case. The genetic parameters were estimated using VCE (Neumaier and Groeneveld, 1998) and ASREML (Gilmour et al., 2002) computer packages. Maternal effects were non significant and were consequently removed from final analyses for AGET, ABT and ADGT. The final model used for each trait and the significance levels of the test statistics are shown in Table 2. The models for **OR** and **PS** were the same as those used by Rosendo et al. (2007b). Estimated breeding values were then computed as back-solutions of REML analyses at convergence. Genetic trends were estimated by averaging estimated breeding values of animals for each line x generation combination, and then regressing them on generation number within each line.

Table 2. Models used in analyses and significance[1] of effects

	Fixed effects[3]							Covariates[4]					Random effects[5]		
								Inbreeding							
Traits[2]	Cross fostering	Sex	L	G	L*G	CG	Sow parity	Dam	Animal	Age	Wt	Nurtured	Direct	Maternal	Common
IWB		***	*	***	***	***	***	***				***	***	***	***
IW3W	***	***	**	***	***	***	***		***	***		***	***	***	***
IWW	***	***	**	***	***	***	***		***	***		***	***	***	***
ADGBW	***	***	**	***	***	***	***		***		***	***	***	***	***
ADGPW	***	***	*	***	**	***			***		***	***	***	***	***
ADGT		***	***	***	***	***			***		***		***		***
AGET		***	***	***	***	***			***		***		***		*
ABT		***	+	***	+	***			***		***		***		***

[1] *** P<0.001; ** P<0.01; * P<0.05; + P<0.10; [2] See table 1 for the definition of trait abbreviations; [3]Crossfostering = Crossfostering status (yes, no); L = line (OR, PS, or C – LS model only); G = generation number (0 to 7 – LS model only); L*G = line x generation interaction (LS model only); CG = contemporary group within generation; Sow parity = 1, 2; [4]Dam, Animal = dam and animal inbreeding coefficient, respectively; Age = age of pigs at 3 wk (IW3W) or at weaning (IWW); Wt = body weight of pigs at birth (ADGBW), at weaning (ADGPW), at the beginning (ADGT) and at the end of performance test (AGET, ABT); Nurtured = number of piglets nurtured; [5]MM analyses only. Direct = direct genetic effects; Maternal = maternal genetic effects; Common = common litter environmental effects.

RESULTS

Significance levels of fixed effects, random effects, and covariates are given in Table 2. Sow contemporary group and sex affected all traits (P < 0.001). Males were heavier than females at birth (83 ± 6 g) and at weaning (281 ± 40 g), grew faster during the test period (61 ± 4 g/d), and had less backfat (-2.9 ± 0.3 mm) at 90 kg BW. Castrates had similar BW to females at weaning, had the fastest growth during the postweaning period (9 ± 3 g as compared to intact males and females), and had an intermediate growth rate on test (-18 ± 5 g as compared to intact males). Sow parity and fostering affected early growth, but had no effects on performance test traits. Second litter piglets were heavier at birth (92 ± 16 g) and at weaning (895 ± 89 g) than first parity piglets. The crossfostering status was not included in the final model for IWB, but was considered in a preliminary analysis to check whether crossfostered piglets were chosen at random. In fact, crossfostered piglets were slightly heavier at birth (27 ± 12 g), but had a lower preweaning growth rate than piglets raised by their own dam (-18 ± 3 g), and were hence lighter at weaning (-562 ± 73 g). All traits except IWB were significantly affected by litter inbreeding, which amounted to 15.7, 10.9 and 7.2%, respectively, in PS, OR, and C lines, at the end of the experiment (Rosendo et al., 2007a). Mean performance decreased by 159 ± 47 g, 146 ± 48 g, 5.2 ± 2.0 g/d, 15.2 ± 3.6 g/d, 20.2 ± 4.0 g/d, 2.2 ± 0.5 d, and 1.42 ± 0.35 mm, respectively, for IW3W, IWW, ADGBW, ADGPW, ADGT, AGET, and ABT per 10% increase in litter inbreeding. Maternal inbreeding only significantly affected IWB (-68 ± 12 g per 10% increase in inbreeding).

Estimates of heritability, of the genetic correlation between direct and maternal effects, and of common litter effects are given in Table 3. Both direct and maternal genetic effects determined growth during the suckling and postweaning periods, whereas only direct effects affected performance test traits. Maternal heritabilities were approximately twice as large as direct heritabilities up to weaning, still represented half of direct heritabilities during the postweaning period, and were non significant during the test period. Direct heritability estimates were low (0.10) at birth, then progressively increased to moderate to high values (0.34 to 0.46) after weaning. The only exception concerned ABT, which had a rather low heritability estimate (0.21). Genetic correlations between direct and maternal effects were all negative. The antagonism was low at birth, but was rather strong after birth (-0.59 to -0.74). Common litter effects explained a low to moderate (9 to 19%) proportion of the phenotypic variance, except for ABT, for which a large estimate (0.47) was obtained.

Table 3. Estimates of heritability, genetic correlation between direct and maternal effects, common litter effects, and standard deviations

Trait[1]	Heritability (± SE)		Direct – Maternal genetic correlation (± SE)	Common litter effect	Phenotypic SD
	Direct	Maternal			
IWB (kg)	0.10 ± 0.03	0.17 ± 0.04	-0.21 ± 0.18	0.14	0.3
IW3W (kg)	0.12 ± 0.03	0.33 ± 0.03	-0.61 ± 0.11	0.17	1.2
IWW (kg)	0.20 ± 0.03	0.32 ± 0.03	-0.68 ± 0.08	0.19	1.6
ADGBW (g/d)	0.24 ± 0.04	0.41 ± 0.03	-0.74 ± 0.06	0.19	48.1
ADGPW (g/d)	0.41 ± 0.04	0.21 ± 0.03	-0.59 ± 0.07	0.16	98.4
ADGT (g/d)	0.34 ± 0.05	-	-	0.14	97.6
AGET (d)	0.46 ± 0.03	-	-	0.09	12.6
ABT (mm)	0.21 ± 0.04	-	-	0.47	6.5

[1] See table 1 for the definition of trait abbreviations;.

Phenotypic and genetic correlations of the 8 traits with ovulation rate at puberty (OR) and prenatal survival (PS) are presented in Table 4. Phenotypic correlations were all weak (absolute value ≤ 0.10), except the direct correlation between OR and AGET (-0.20 ± 0.03) and the maternal correlation of OR with ADGPW (0.11 ± 0.05). Direct genetic correlations were low (absolute value ≤ 0.20) and non significant, except the correlations of AGET with OR (favorable correlation of -0.23 ± 0.09) and PS (unfavorable correlation of 0.30 ± 0.13). The maternal genetic correlations of OR with growth traits were moderately negative at birth (-0.28 ± 0.13 between OR and IWB) and became increasingly positive after birth (0.06 ± 0.10 to 0.23 ± 0.11). Maternal genetic correlations with PS were all negative, with a strong value at birth (-0.65 ± 0.11), a moderate value for preweaning growth rate (-0.34 ± 0.12), and a lower value during the postweaning period (-0.20 ± 0.15).

Least squares and mixed models estimates of genetic trends for the 8 traits are presented in Table 5, and, for the most significant results, in

Figures 1 to 3. Global estimates were obtained using least squares, whereas separate trends for direct and maternal effects were estimated using mixed model methodology. Global genetic trends in the OR line showed a significant (P<0.05) improvement in ADGBW and a tendency towards an improvement in growth rate during the test period (i.e., ADGT and AGET). This tendency became significant (P< 0.05) when estimated using MM methodology. A significant decrease in maternal genetic effects was also obtained for IBW (Figure 1). In the PS line, significantly negative global trends were estimated for IW3W and IWW, whereas trends after weaning indicated (ADGPW) or tended to indicate (AGET) an increase in post weaning growth. This increase was significant when estimated with AM-BLUP. Trends for maternal effects were low and non significant, except at birth, where a significantly negative trend was detected in the OR line.

Table 4. Estimates of phenotypic and genetic correlations of ovulation rate and prenatal survival with growth and backfat thickness traits

	Ovulation Rate			Prenatal Survival		
	Phenotypic	Genetic		Phenotypic	Genetic	
Trait[1]		Direct	Maternal		Direct	Maternal
IWB	0.08 ± 0.03	0.09 ±0.20	-0.28±0.13	-0.10 ±0.03	-0.19±0.24	-0.65±0.11
IW3W	0.04 ± 0.03	-0.17±0.16	0.09 ±0.10	-0.08 ±0.03	0.10 ± 0.20	-0.56±0.11
IWW	0.07 ± 0.03	0.11 ±0.12	0.06 ±0.10	-0.07±0.03	0.18 ± 0.14	-0.59±0.10
ADGBW	0.06 ± 0.03	0.12±0.12	0.16 ±0.09	-0.02±0.03	0.19 ± 0.16	-0.34±0.12
ADGPW	0.12 ± 0.03	0.03 ±0.11	0.23 ±0.11	-0.05 ±0.03	0.03 ± 0.15	-0.20±0.15
ADGT	0.10 ± 0.03	0.08 ±0.10	-	-0.02 ±0.03	-0.07±0.14	-
AGET	-0.20 0.03	-0.23±0.09	-	0.02 ± 0.03	0.30 ± 0.13	-
ABT	-0.02 ±0.03	-0.04±0.12	-	0.02 ± 0.03	-0.07±0.16	-

[1] See table 1 for the definition of trait abbreviations.

Table 5. Least squares (LS) and mixed model (MM) estimates[1] of genetic trends

	Ovulation rate line			Prenatal survival line		
Trait[2]	LS	MM estimates[4]		LS	MM estimates[4]	
	Estimates[3]	Direct	Maternal	Estimates[3]	Direct	Maternal
IWB	-0.01 ± 0.02	0.03 ± 0.02	-0.06 ± 0.02 *	-0.02 ± 0.02	-0.01 ± 0.02	-0.04 ± 0.02
IW3W	0.04 ± 0.03	-0.02 ± 0.03	0.06 ± 0.04	-0.11 ± 0.03 **	-0.02 ± 0.03	-0.05 ± 0.04
IWW	0.02 ± 0.03	0.00 ± 0.03	0.04 ± 0.04	-0.11 ± 0.03 **	-0.01 ± 0.03	-0.04 ± 0.04
ADGBW	1.4 ± 0.7 *	0.3 ± 0.7	1.1 ± 0.8	-1.2 ± 0.8	-0.2 ± 0.8	0.2 ± 0.9
ADGPW	-1.0 ± 1.4	-0.8 ± 1.5	-0.9 ± 1.5	4.7 ± 1.5 ***	4.3 ± 1.7 **	-1.8 ± 1.8
ADGT	2.9 ± 1.5 +	4.1 ± 1.6 *	-	1.4 ± 1.7	7.8 ± 1.6 ***	-
AGET	-0.4 ± 0.2 +	-0.6 ± 0.2 *	-	-0.3 ± 0.2 +	-0.8 ± 0.2 ***	
ABT	-0.1 ± 0.2	-0.1 ± 0.2	-	-0.1 ± 0.2	0.1 ± 0.02	-

[1] *** P<0.001, ** P<0.01, * P<0.05, + P<0.10; [2] See table 1 for the definition of trait abbreviations; [3] Regression of generation x line differences (selected - control lines) on generation number; [4] Differences (selected - control lines) between regression coefficients of estimated breeding values on generation number.

DISCUSSION

The first aim of this study was to estimate correlated responses in growth traits and backfat thickness to selection for the 2 major components of litter size (i.e., ovulation rate and prenatal survival). This objective required estimation of genetic parameters for traits characterizing pre- and postweaning pig growth up to harvest. Final models included 3 random effects (common birth litter effect, direct and maternal genetic effects) for traits expressed during or shortly after the suckling period and 2 random effects (common birth litter and direct genetic effects) for traits measured later in life. Preliminary analyses were performed with a 4 random effects model including the 3-above mentioned effects plus a permanent sow environmental effect. This latter effect explained a very limited proportion of the genetic variance for all traits and was consequently not considered in subsequent analyses. Both 4 and 3 random effects models also showed a low and non significant maternal effect for ADGT, AGET, and ABT, leading to removal of this effect in final analyses. The 3 random effects model is commonly used for early growth traits (Roehe, 1999; Kaufmann et al., 2000; Zhang et al., 2000; Solanes et al., 2004a). Reasonably accurate estimates of genetic parameters were obtained in spite of the rather limited size of the data set, because of a favorable structure (i.e., many generations, large dam families, and a large proportion of dams and grand-dams with records) (Gerstmayr, 1992; Meyer, 1992; Clement et al., 2001).

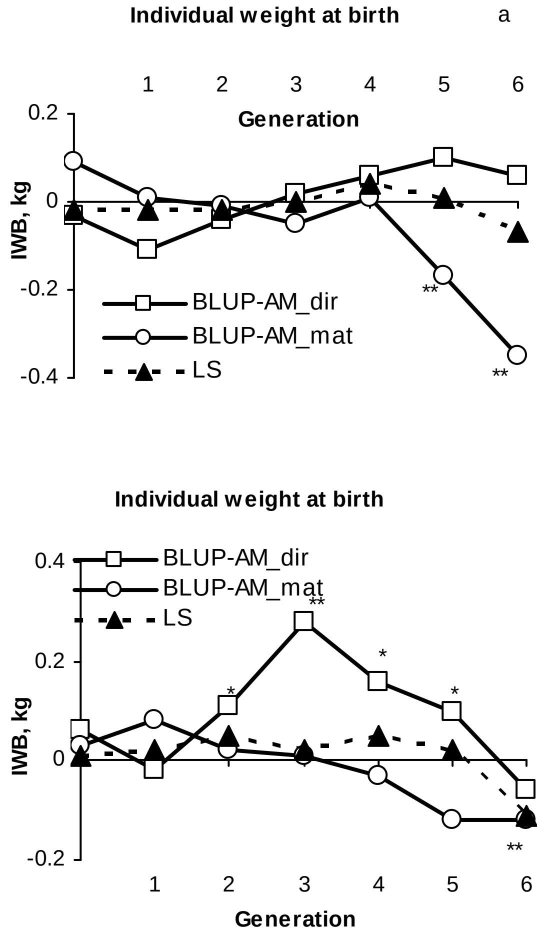
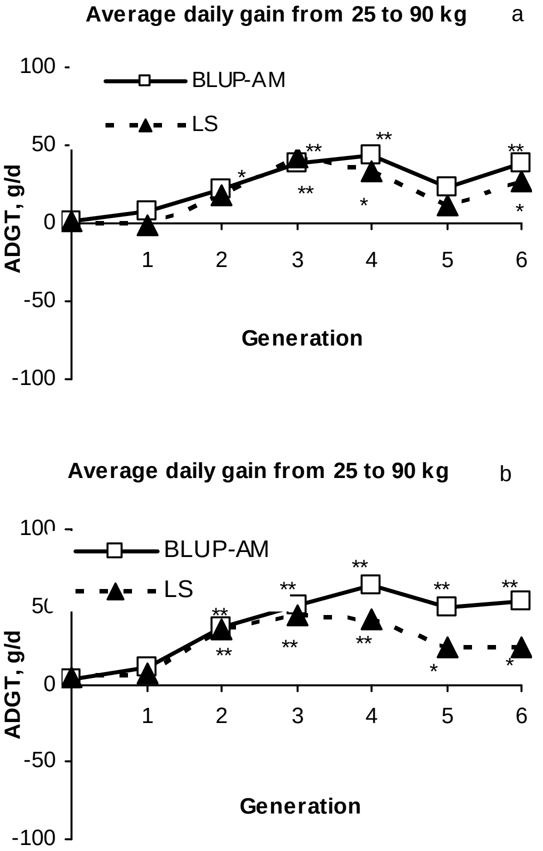


Figure 1. Difference (selected minus control line) in phenotypic least squares (LS) and average breeding value (BLUP-AM) for direct (dir) and maternal (mat) effects for individual weight at birth plotted by generation between the line selected for ovulation rate (a) or prenatal survival (b) and the unselected control line (*: P<0.05; **: P<0.01)

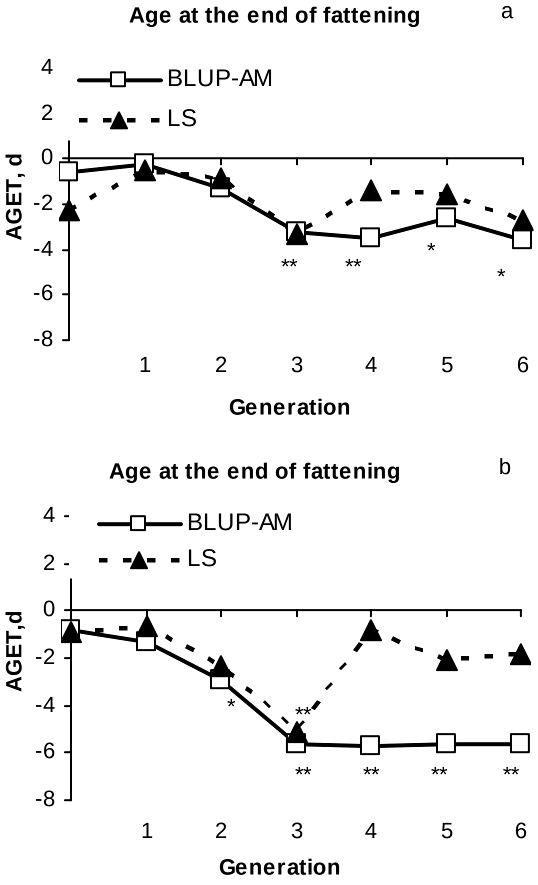
Figure 2. Difference (selected minus control line) in phenotypic least squares (LS) and average

breeding value (BLUP-AM) for average daily gain between 25 and 90 kg plotted by generation between the line selected for ovulation rate (a) or prenatal survival (b) and the unselected control line (*: P<0.05; **: P<0.01).



Our results showed the prominent influence of maternal genetic and litter environmental effects on the genetic variability of early growth traits in pigs. Direct genetic effects were of minor importance at birth, as also shown by Young et al. (1978), Roehe (1999), Knol et al. (2002), and Solanes et al. (2004a). The impact of direct genetic effects then increased, but remained much lower than that of maternal genetic effects until weaning, as also shown by Rodriguez et al. (1994), Kaufmann et al. (2000), and Solanes et al. (2004a). This maternal influence remained important during the postweaning period, in agreement with Zhang et al. (2000), but had a very limited effect during the on-test period.

Figure 3. Difference (selected minus control line) in phenotypic least squares (LS) and average breeding value (BLUP-AM) for age at the end of test plotted by generation between the line selected for ovulation rate (a) or prenatal survival (b) and the unselected control line (*: P<0.05; **: P<0.01).



This result is in line with most recent literature estimates (Crump et al., 1997; Zhang et al., 2000; Solanes et al., 2004b). Important maternal heritability estimates were reported for average daily gain and backfat thickness by Bryner et al. (1992), but their model did not include a random common birth litter effect. Johnson et al. (2002) confirmed the importance of maternal effects for BW at 100 d of age, but observed much lower maternal heritability estimates (0.02 to 0.11) than Bryner et al. (1992). High estimates of maternal heritability were also obtained in older studies, even for traits that are expressed later in life (e.g., Robison, 1972), but they are likely to be related to a much greater age at weaning. Direct heritability estimates from the current study were similar for growth, but lower for backfat thickness, than average literature values (Ducos, 1994; Clutter and Brascamp, 1998).

The moderately negative genetic correlation between direct and maternal effects at birth is consistent with the previous results of Roehe

(1999) and Knol et al. (2002), but differs slightly from the null or lowly positive correlations obtained by Kaufmann et al. (2000), Knol et al. (2002), and Solanes et al. (2004a), and the positive estimate reported by Grandinson et al. (2002). These differences may be due to the relative inaccuracy of estimates, but may also reflect breed or environmental differences. The antagonism between direct and maternal genetic effects was much larger at 3 and 4 wk of age than at birth. Though a similar trend towards a stronger antagonism during lactation was obtained in other studies (Kaufmann et al., 2000; Bouquet et al., 2006), it generally remained less pronounced than in the present study. As suggested by Solanes et al. (2004a), the distribution of supplementary feed to piglets compensating for poor milk production may lead to a negative correlation between direct and maternal effects. Moreover, the direct – maternal genetic correlation can be overestimated (in absolute value) in the presence of genotype x environment interaction or direct - maternal environmental correlations (Robinson, 1996).

Very few estimates of genetic correlations involving ovulation rate or prenatal survival are available in the literature. Estimates of genetic relationships between litter size and production traits are more numerous. Several literature reviews have shown that litter size is on average weakly correlated with growth and carcass traits (Brien, 1986; Haley et al., 1988). Yet, it has been hypothesized (Rauw et al., 1999; Holm et al., 2004) that selection for lean growth might result in negative genetic relationships with litter size in high producing animals. Biologically, resource allocation for growth could occur at the expense of the ability of young sows to give birth to large litters. Similarly, selection for leanness could reduce sow ability to mobilize lipid during late gestation and the suckling period (Holm et al., 2004). Indeed, several recent publications have reported antagonistic relationships between sow reproduction and growth (Ducos and Bidanel, 1996; Hermesch et al., 2000; Holm et al., 2004; Arango et al., 2005) or backfat thickness (Chen et al., 2003).Yet, near zero (Noguera et al., 2002a) or even favorable (Serenius et al., 2004) genetic correlations were obtained in other studies. These differences may in some cases be related to the limited precision of estimates, but also reflect genetic differences in average performance levels, and metabolic efficiency, as well as variation in management practices (including age at farrowing).

In any case, our results show globally low genetic correlations of ovulation rate with growth rate and backfat thickness. This is particularly true for direct effects, as a single significant genetic correlation was obtained for OR with AGET. In particular, the genetic correlation between OR and average daily gain was close to zero, unlike Young et al. (1977) and Bidanel et al. (1996), who reported significant positive genetic correlations between the two traits (0.41 and 0.20, respectively). Ruiz-Flores and Johnson (2001) reported a rather strong positive direct genetic correlation between birth weight and OR (0.44), but much lower values for subsequent weights and backfat thickness. They also obtained estimates of maternal genetic correlations with piglet weight at birth and at weaning (-0.26 and 0.11, respectively) that were very similar to those reported here. The low direct genetic correlation between most growth traits and prenatal survival is also consistent with the value obtained by Bidanel et al. (1996) and the estimates between growth traits and litter size at birth reported by Ruiz-Flores and Johnson (2001). There do not seem to be any previous estimates of the maternal genetic correlations between prenatal survival and growth traits in the literature, the only related result being the strong negative estimates between growth and litter size obtained in the Nebraska experiment (Ruiz-Flores and Johnson, 2001). The strongest negative correlation was that between PS and IBW, which may be due to uterine space acting as a limiting factor and resulting in a negative correlation between maternal effects on embryonic/fetal growth and prenatal survival.

Estimated genetic trends were globally consistent with genetic parameter estimates. Non significant trends were obtained for the traits weakly correlated with OR and PS (i.e., the majority of growth traits, as well as backfat thickness). The only exceptions concerned ADGT, where significant trends were estimated in spite of near zero genetic correlations, and maternal effects, mainly in the PS line, with non significant trends in spite of strong negative genetic correlations. These latter discrepancies are likely to stem from the strong negative correlations between direct and maternal effects for these traits, which would largely reduce the efficiency of selection on both components. The significant response obtained for ADGT and AGET is consistent with the genetic correlations of OR and PS with AGET, but somewhat larger than would be expected based on the correlations with ADGT.

The lack of response for most traits is in agreement with the results of selection experiments for increased litter size (Noguera et al., 2002b; Petry et al., 2004). Similarly, no significant response in litter size was obtained in several selection experiments for lean growth rate (Fredeen and Mikami, 1986; Cleveland et al., 1988; Kerr and Cameron, 1995). Ruiz-Flores and Johnson (2001) reported correlated responses for growth and backfat that somewhat differed between lines selected for litter size and its components. The negative trends for maternal effects on birth weight are consistent with the results of Johnson et al. (1999). Decreasing piglet weight by selecting on maternal effects might hence be associated with improved prenatal survival. However, it may also have important drawbacks, as lighter piglets are associated with a higher risk of mortality at birth (Canario et al., 2006a) and during the suckling period. Wilson et al. (1999) proposed to solve this problem by selecting for placental efficiency (i.e., the ratio of birth weight to placental weight), but no increase in litter size nor in piglet survival could be obtained after 4 generations of selection (Mesa et al., 2005).

IMPLICATIONS

In this experiment, correlated responses of direct effects for growth rate and backfat thickness to selection for either ovulation rate or prenatal survival were small for most traits. However, significant, though rather limited, favorable trends were obtained for growth rate during the test period. A negative trend was also observed for maternal effects on birth weight. This negative trend is likely to be undesirable, as lower birth weights are generally associated with a higher risk of mortality. Further research remains necessary to find the best method of increasing litter size without causing deterioration in birth weight or birth to weaning survival.

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