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Correlative responses for carcass and meat quality traits to selection for ovulation rate or prenatal survival in French Large White pigs[1]

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ABSTRACT: Correlated effects of selection for components of litter size on carcass and meat quality traits were estimated using data from 3 lines of pigs derived from the same Large White base population. Two lines were selected for 6 generations on high ovulation rate at puberty (OR) or high prenatal survival corrected for ovulation rate in the first 2 parities (PS). The third line was an unselected control (CON). The 3 lines were kept for a 7th generation, but without any selection. Carcass and meat quality traits were recorded on the 5th to 7th generation of the experiment. Carcass traits included dressing percentage, carcass length (LGTH), average backfat thickness (ABT), estimated lean meat content, and 8 carcass joint weight traits. Meat quality traits included pH recorded 24 h after slaughter (pH24) of LM, gluteus superficialis (GS), biceps femoris (BF), and adductor femoris (AD) muscles, as well as reflectance and water-holding capacity (WHC) of GS and BF muscles. Heritabilities of carcass and meat quality traits and their genetic correlations with OR and PS were estimated using REML methodology applied to a multiple trait animal model. Correlated responses to selection were then estimated by computing differences between OR or PS and CON lines at generations 5 to 7 using least squares and mixed model methodology. Heritability (h^2) estimates were 0.08 ± 0.04, 0.58 ± 0.10, 0.70 ± 0.10, and 0.74 ± 0.10 for dressing percentage, LGTH, ABT, and lean meat content, respectively, ranged from 0.28 to 0.72 for carcass joint traits, from 0.28 to 0.45 for pH24 and reflectance measurements, and from 0.03 to 0.11 for WHC measurements. Both OR and PS had weak genetic correlations with carcass ($r_G = -0.09$ to 0.17) and most meat quality traits. Selection for OR did not affect any carcass composition or meat quality trait. Correlated responses to selection for PS were also limited, with the exception of a decrease in pH24 of GS and BF muscles (−0.12 to −0.14 after 6 generations; $P < 0.05$), in WHC of GS muscle (−18.9 s after 6 generations; $P < 0.05$) and a tendency toward an increase in loin weight (0.44 kg after 6 generations; $P < 0.10$) .

Key words: carcass composition, meat quality, ovulation rate, pig, prenatal survival, selection experiment

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INTRODUCTION

Litter size is a major component of the breeding goal in pig dam lines (Estany et al., 2002; Holl and Robinson, 2003; Hamann et al., 2004). There is experimental evidence that prolificacy has been substantially improved by applying high selection intensities in pig maternal lines (Bidanel et al., 1994a; Tribout et al., 2003). However, direct selection for litter size remains difficult in closed maternal lines where extreme selection intensities cannot be applied. Selecting on ovulation rate and prenatal survival has been proposed as an alternative to direct selection to improve litter size at birth (Johnson et al., 1984). A selection experiment on ovulation rate or prenatal survival was set up at the Institut National de la Recherche Agronomique (**INRA**) to estimate their genetic parameters and check their potential as selection criteria for litter size (Blasco et al., 1998; Rosendo et al., 2007b). Before commercial application, direct and correlated responses to selection for the main traits of interest in pig production should be estimated. Correlated responses for reproductive and growth traits were presented in Rosendo et

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Table 1. Average reproductive performance of the 3 lines[1] (and their SE) on the 5th, 6th, and 7th generations (from Rosendo et al., 2007a,b)

Item	Control line	OR line	PS line
5th generation			
Ovulation rate	16.1 (0.3)	19.0 (0.3)	16.4 (0.3)
Prenatal survival	60.2 (2.4)	52.1 (2.4)	61.2 (2.4)
Litter size	9.7 (0.3)	9.9 (0.4)	9.8 (0.4)
Birth weight, kg	1.32 (0.04)	1.33 (0.04)	1.34 (0.04)
6th generation			
Ovulation rate	16.2 (0.3)	19.2 (0.3)	16.1 (0.3)
Prenatal survival	59.9 (2.4)	55.2 (2.4)	68.3 (2.4)
Litter size	9.7 (0.4)	10.6 (0.4)	11.0 (0.4)
Birth weight, kg	1.35 (0.04)	1.28 (0.04)	1.24 (0.04)
7th generation			
Ovulation rate	16.9 (0.4)	18.9 (0.5)	16.6 (0.4)
Prenatal survival	53.5 (3.1)	51.8 (3.3)	64.4 (3.1)
Litter size	10.2 (0.5)	9.9 (0.5)	10.7 (0.5)
Birth weight, kg	1.31 (0.05)	1.34 (0.05)	1.29 (0.05)

[1]Control line = unselected control; OR line = selected for high ovulation rate at puberty; PS line = selected for high prenatal survival.

al. (2007a,c). The objective of the present study is to analyze correlated responses to selection for ovulation rate or prenatal survival on various carcass and meat quality traits.

MATERIALS AND METHODS

Animal care followed the general guidelines outlined in the European welfare regulation (directive 91/630/EC).

Animals and Experimental Design

The experiment was carried out over 7 generations (6 generations of selection and a seventh generation of random mating) at the INRA experimental herd of Galle (Avord, France).

Two lines of pigs were selected for high ovulation rate at puberty (**OR**) or high prenatal survival (**PS**) over the first 2 parities corrected for ovulation rate at fertilization (**ORF**). Prenatal survival was computed as (total number born/ORF) + (0.018 × ORF) (Rosendo et al., 2007b). The correction term was introduced to avoid trends in PS associated with variation 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 (**CON** line). At each generation, approximately 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, whereas sows were selected on a population basis in the 2 selected lines and within-dam families in the CON line (Rosendo et al., 2007b). A mating plan was established that minimized inbreeding at each generation. Additional details on the experimental design are given by Rosendo et al. (2007b). Average reproductive performance of the 3 lines on the 5th, 6th, and 7th generations are given in Table 1.

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. Seven gilts from each line were introduced in each farrowing batch. Females produced 2 experimental litters. Replacement animals were chosen in first parity litters, whereas pigs from second parity litters were all slaughtered. All piglets were weaned at 4 wk of age and moved to a postweaning unit until 10 wk 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 the average BW within a pen reached 90 kg. Animals were fed ad libitum with a single pelleted diet based on cereals and soybean meal containing 3,100 kcal of DE/kg and 170 g of CP/kg during the whole test period and until the day before slaughter. Additional details on the performance test can be found in Rosendo et al. (2007a).

Carcass and meat quality traits were measured only on second litters from the 5th, 6th, and 7th generation of the experiment. On average, 2 pigs per litter (i.e., 1 gilt and 1 castrate) were chosen at random within each litter and were slaughtered in a commercial abattoir at an average BW of 100.6 ± 2.6 kg. All animals were fasted for 16 h before they were transported for 2 h to the abattoir where they were allowed to rest for an additional 18 h before they were killed by electrical stunning and immediate exsanguination.

Measurements

Carcass measurements were recorded on the day after slaughter. Dressing percentage (**DP**) was calculated as the ratio of cold carcass (with head and feet) to unfasted BW. Carcass length (**LGTH**), measured from the cervical vertebra to the anterior edge of the pubic symphysis, and average backfat thickness (**ABT**), mea-

sured at the levels of first rib, last rib, and last lumbar vertebrae, were recorded on the right half-carcass. The kidney and leaf fat were removed, and the right half-carcass was divided into 7 cuts. The front and back feet were separated from the limbs at the levels of the carpal bones and tibio-tarsal joint, respectively. The ham was isolated along a first line parallel to the general direction of the sacrum and a second line perpendicular to the long axis of the carcass between the last lumbar and the first sacral vertebrae. The loin was separated from the belly and the shoulder with a cut starting under the psoas muscle at the level of the last lumbar vertebra and ending under the blade bone. The belly and the shoulder were separated with a cut perpendicular to the long axis of the carcass between the 5th and the 6th rib. The backfat was dissected from the loin, but the other cuts remained untrimmed. The weight of 8 cuts [i.e., backfat (**BFWT**), belly (**BEWT**), feet (**FWT**), ham (**HAWT**), head (**HEWT**), leaf fat (**LFWT**), loin (**LOWT**), and shoulder (**SWT**)] were recorded, and carcass lean meat content (**LMC**) was estimated from the 3 joint weights using the following equation (Larzul et al., 1999b); LMC = 16.56 + (71.6 HAWT + 83.0 LOWT – 76.2 BFWT)/half-carcass weight.

Meat quality traits were also measured 24 h postmortem. Ultimate pH (**pH24**) was taken directly on different types of muscles [i.e., on LM, gluteus superficialis (**GS**), biceps femoris (**BF**), and adductor femoris (**AD**)] muscles using a combined glass electrode (Ingold, Metter Toledo, Switzerland) and a portable pH meter (CG818, Schott Geräte, Mainz, Germany). A Minolta Chromameter CR-300 (Minolta Camera Co. Ltd., Osaka, Japan) with a 8-mm aperture, a pulsed xenon arc lamp, CIE illuminant, and calibration to the white calibration plate, was used to measure lightness (**L***), redness/greenness (**a***), and yellowness/blueness (**b***) on BF and GS muscles. Water-holding capacity was measured on GS and BF muscles by the filter paper imbibition time method (Charpentier et al., 1971). This method consists of measuring the time required for the complete wetting of a piece of filter paper (around 1 cm^2) put on the freshly cut surface of the muscle. The time of the observation is limited to 3 min. Measurements on ham muscles (i.e., GS, BF, and AD muscles) were performed on the cut surface of the ham at the intersection of the ham and loin joints. Measurements on LM muscle were carried out at the level of the last rib. The number of records for each line × generation subclass ranged from 40 to 59.

Statistical Analyses

A total of 12 carcass traits were analyzed (i.e., DP, LGTH, ABT, LMC, and the BFWT, HAWT, LOWT, SWT, FWT, LFWT, BEWT, and HEWT). Twelve meat quality traits were considered (i.e., the 4 pH24 measurements, denoted by pH24_LM, pH24_GS, pH24_BF, and pH24_AD), 6 color measurements [i.e., a*GS and a*BF (redness/greenness), b*GS and b*BF (yellowness/blueness), and L*GS and L*BF (lightness)], and 2 water-holding capacity measures denoted by WHC_GS and WHC_BF. Elementary statistics for the traits studied are given in Table 2.

Least Squares Analyses of Line Differences. The data were first analyzed using least squares methodology with the GLM procedure (SAS Inst. Inc., Cary, NC). Least squares means for each line-generation subclass were computed using a linear model. Fixed effects for all traits included line (OR, PS, or CON), generation number (5, 6, or 7), their interaction, sex (female or castrate), and contemporary group. Contemporary group was defined by the fattening batch for carcass traits and slaughter date for meat quality traits. Parity of dam was included as a fixed effect in the model for carcass traits, and BW at slaughter and animal inbreeding coefficient were included in all models as linear covariates.

Mixed Model Analyses. Variance components were first estimated using REML methodology (Patterson and Thompson, 1971) applied to 3 trait mixed linear animal models including the selection criterion (OR and PS) and an additional trait. The models used depended on the trait (Table 3), but all derived from the following base model:

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

where $\mathbf{y}$ represents the vector of observations; $\mathbf{X}$, $\mathbf{Z}_a$, and $\mathbf{W}_c$ are known incidence matrices relating observations to fixed and random effects; $\boldsymbol{\beta}$ = vector of fixed effects (i.e., generation, line, sex, parity number of the dam, and contemporary group); $\mathbf{a}$ is the vector of direct genetics effects of the pig; $\mathbf{c}$ is a vector of random common litter effects of the animals; and $\mathbf{e}$ is the vector of random residual effects. The models used to estimate the variance components for OR and SP are detailed in Rosendo et al. (2007b). The following means and (co) variance structures were assumed across random effects in the model:

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

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

where σ_a^2 is the additive genetic variance; $\mathbf{A}$ is the additive relationship matrix; σ_c^2 and σ_e^2 are the random common litter and residual variances, respectively; and $\mathbf{I}$ are the identity matrices of appropriate dimension. The analyses were performed using VCE (Neumaier and Groeneveld, 1998) and ASREML (Gilmour et al., 2002) computer packages. Additive genetic effects were then estimated as back-solutions from REML analyses

Table 2. Descriptive statistics for carcass and meat quality traits

Carcass trait	Abbreviation	n[1]	Mean	SD
Dressing percentage, %	DP	584	76.6	2.5
Carcass length, mm	LGTH	593	956	28
Average backfat thickness, mm	ABT	593	28.1	4.6
Weight of joint, kg				
Backfat	BFWT	593	4.02	0.75
Ham	HAWT	593	8.83	0.57
Loin	LOWT	593	10.99	0.85
Shoulder	SWT	593	4.99	0.37
Feet	FWT	593	1.08	0.1
Leaf fat	LFWT	471	0.54	0.17
Belly	BEWT	593	4.64	0.53
Head	HEWT	588	6.76	0.58
Estimated lean meat content, %	LMC	588	51.6	3.3
Meat quality trait[2]				
pH24 of LM	pH24_LM	480	5.58	0.23
pH24 of gluteus superficialis muscle	pH24_GS	480	5.90	0.29
pH24 of biceps femoris muscle	pH24_BF	480	5.59	0.23
pH24 of adductor femoris muscle	pH24_AF	480	5.69	0.26
Reflectance of:				
Gluteus superficialis, a* value	a*GS	484	8.20	2.44
Biceps femoris, a* value	a*BF	484	7.63	2.37
Gluteus superficialis, b* value	b*GS	484	7.20	2.42
Biceps femoris, b* value	b*BF	484	6.39	2.30
Gluteus superficialis, L* value	L*GS	484	46.1	4.2
Biceps femoris, L* value	L*BF	484	47.0	4.0
Water-holding capacity, s				
Gluteus superficialis	WHC_GS	484	170.8	26.6
Biceps femoris	WHC_BF	484	112.2	63.0

[1]n = number of records.
[2]pH24 = pH recorded 24 h after slaughter.

at convergence and used to compute average values for each line × generation combination.

RESULTS

Significance of fixed effects, covariates, random effects, and total variation explained by fixed effects (R^2) are given in Table 3. A moderate proportion (24 to 29%) of the total variation was explained by the fixed effect model for LGTH, ABT, and LMC. In contrast, the fixed effect model explained 30 to 50% of the total variation for DP and the weight of joints traits, except for LFWT. Inbreeding significantly decreased performance level for BFWT, BEWT, FWT, and LOWT. Body weight affected ($P < 0.05$) all traits except DP and LMC. Date of slaughter was the main fixed effect influencing meat quality characteristics: it explained from 36 to 50% of the total variation of ultimate pH and color measurements. Its effect was of less importance for muscle lightness and water-holding capacity, explaining 13 to 21% of the phenotypic variation for these traits.

Genetic parameter estimates for OR and PS were remarkably stable across the different 3-trait analyses and were the same as those reported by Rosendo et al. (2007b). The REML estimates of heritability and common litter effects for carcass and meat quality traits are given in Table 4. Estimates had rather large SE due to the rather limited amount of data. With the exception of the small value obtained for DP (0.08) and the moderate estimates for SWT and HEWT (0.28 and 0.38, respectively), carcass traits had high heritability values (from 0.48 to 0.72). Common litter effects were close to zero for some traits, but were far from negligible for other traits (up to 0.09). Estimates of heritability were moderate for pH measurements, for a* and b* color parameters and the lightness of GS traits (from 0.26 to 0.45). Conversely, very low h^2 values were obtained for L*BF and the 2 water-holding capacity measurements. The magnitude of common litter effects was in the same range as that obtained for carcass traits (0.00 to 0.09).

Estimates of phenotypic and genetic correlations between the selection criteria and carcass traits and meat quality traits are shown in Table 5. Phenotypic correlations between both OR or SP and carcass composition traits were all very weak (−0.10 to 0.06). Genetic correlations between OR and carcass traits were also very low; only one value had an absolute value above 0.10 (−0.17 ± 0.14 with LGTH). The situation was not much different for PS; only 4 estimates were outside the interval −0.10 to 0.10. Though not significant, these values (i.e., −0.19 with LMC; −0.13 with LOWT; 0.16 with ABT) might indicate a small antagonism between PS and carcass leanness.

Similarly, phenotypic correlations with meat quality traits were all small (less than 0.10 in absolute values).

Table 3. Models of analyses, significance, and total variation explained by fixed-effect terms (R^2)

		Fixed effect				Covariate		Random effect[2]	
Trait[1]	R^2	Sex	Line	Parity of dam	Contemporary group[3]	Inbreeding	BW at slaughter	Animal	Litter
Dressing percentage	0.33	***	ns	ns	***	ns	ns	X	—
Carcass length	0.24	***	ns	*	**	ns	***	X	X
Average backfat thickness	0.27	***	ns	***	***	ns	***	X	X
Backfat weight	0.34	***	ns	***	**	***	***	X	X
Ham weight	0.50	***	ns	**	***	ns	***	X	X
Loin weight	0.35	***	+	*	***	*	***	X	X
Shoulder weight	0.30	*	+	*	***	ns	***	X	X
Feet weight	0.41	**	ns	ns	***	**	***	X	—
Leaf fat weight	0.19	***	ns	ns	**	**	***	X	—
Belly weight	0.33	ns	ns	ns	***	**	***	X	—
Head weight	0.37	ns	ns	ns	***	ns	***	X	—
Estimated lean meat content	0.29	***	ns	***	**	ns	ns	X	X
pH24 of LM muscle	0.38	**	+	ns	***	ns	ns	X	X
pH24 of GS muscle	0.35	**	*	ns	***	ns	*	X	X
pH24 of BF muscle	0.33	**	*	ns	***	ns	*	X	X
pH24 of AF muscle	0.38	***	+	ns	***	ns	ns	X	X
a* value, GS muscle	0.48	ns	ns	ns	***	ns	*	X	—
a* value, BF muscle	0.42	ns	ns	ns	***	ns	*	X	X
b* value, GS muscle	0.57	ns	+	ns	***	ns	*	X	X
b* value, BF muscle	0.55	ns	ns	ns	***	ns	ns	X	X
L* value, GS muscle	0.20	ns	+	ns	**	ns	ns	X	X
L* value, BF muscle	0.13	ns	ns	ns	**	ns	ns	X	X
WHC, GS muscle	0.18	ns	*	ns	**	ns	*	X	—
WHC, BF muscle	0.21	ns	ns	ns	**	ns	ns	X	—

[1]GS, BF, and AF = gluteus superficialis, biceps femoris, and adductor femoris muscles, respectively. pH24 = pH recorded 24 h after slaughter. a*, b*, and L* = reflectance measurements: redness/greenness, yellowness/blueness, and lightness, respectively. WHC = water-holding capacity.
[2]Random effect considered (X) or not considered (—) in the model.
[3]Contemporary group = batch effect for carcass traits and slaughter date effect for meat quality traits.
***$P < 0.001$; **$P < 0.01$; *$P < 0.05$; +$P < 0.10$; ns = not significant.

With a single exception, genetic correlations of OR and PS with pH measurements were nonsignificant ($P > 0.05$), but consistently positive (0.25 to 0.37). Consistently positive genetic correlations were also obtained between PS and a* and b* measurements, whereas positive and negative values were obtained with OR. Conversely, genetic correlations of muscle lightness and water-holding capacity with OR and PS were all negative.

First analyses of line differences on generations 5 to 7 did not show any significant ($P > 0.10$) line × generation interaction or generation effect. Average line effects and differences over the 3 generations were hence computed. Estimates for LC and mixed model of contrasts between these overall line effects are shown in Table 6. They were consistent in sign and magnitude. Line differences were not significant ($P > 0.10$) for the vast majority of the traits analyzed. The only exceptions for carcass traits were loin weight, which tended to increase in the PS line ($P < 0.10$), and SWT, which tended to increase in the OR line ($P < 0.10$). No difference ($P > 0.10$) was observed for meat quality traits in the OR line. Conversely, pH values tended to increase in the PS, with significant differences ($P < 0.05$) for 2 of the 4 pH measurements. There were also tendencies toward a greater b* value and a reduced water-holding capacity on GS muscle.

DISCUSSION

For most composition carcass traits, the heritability values found are in agreement with the average literature values reported by Sellier (1998) and with the estimates obtained by Larzul et al. (1999b) using data that were partly common (CON line) to the current data. Heritability of DP (0.08 ± 0.04) is close to previous estimates (0.11 ± 0.04) of Larzul et al. (1999b), but is noticeably less than the estimates reported by Ducos et al. (1993) and Tribout et al. (1996) and the average literature value of 0.30 reported by Ducos (1994). As suggested by Larzul et al. (1999b), the low heritability estimate might be due to the fact that slaughter BW was recorded before feed withdrawal in the present study, whereas it was recorded on fasted animals in most other studies. Conversely, the heritability value obtained for ABT is greater than most estimates reported in the literature (Lo et al., 1992; Bidanel et al., 1994b; Serenius et al., 2004) and close to the estimates reported by Larzul et al. (1997).

In this study, the ultimate pH traits had high heritability values. Estimates were 0.35 on average, superior to the average literature value of 0.21 reported in Sellier (1998). They were also greater than the estimates reported by Larzul et al. (1999a) and van Wijk et al. (2005), but were close to the value reported by Nguyen

Table 4. Estimates of heritability (±SE) and common litter effect for carcass and meat quality traits

Trait[1]	Heritability ± SE	Common litter effect[2]	Phenotypic variance
Dressing percentage, %	0.08 ± 0.04	—	6.8
Carcass length, mm	0.58 ± 0.10	0.09	747
Average backfat thickness, mm	0.70 ± 0.10	0.04	19.9
Backfat weight, kg	0.68 ± 0.08	0.04	0.45
Ham weight, kg	0.48 ± 0.11	0.08	0.24
Loin weight, kg	0.55 ± 0.09	0.07	0.56
Shoulder weight, kg	0.28 ± 0.06	0.03	0.12
Feet weight, kg	0.66 ± 0.09	—	0.01
Leaf fat weight, kg	0.72 ± 0.08	—	0.03
Belly weight, kg	0.69 ± 0.10	—	0.23
Head weight, kg	0.38 ± 0.08	—	0.74
Estimated lean meat content, %	0.74 ± 0.10	0.04	8.9
pH24 of LM muscle	0.35 ± 0.12	0.08	0.05
pH24 of GS muscle	0.34 ± 0.13	0.07	0.05
pH24 of BF muscle	0.29 ± 0.11	0.07	0.06
pH24 of AF muscle	0.45 ± 0.12	0.08	0.11
a* value, GS muscle	0.34 ± 0.12	—	3.78
a* value, BF muscle	0.45 ± 0.13	0.09	4.26
b* value, GS muscle	0.28 ± 0.11	0.02	3.05
b* value, BF muscle	0.26 ± 0.11	0.02	3.28
L* value, GS muscle	0.30 ± 0.11	0.04	16.4
L* value, BF muscle	0.13 ± 0.11	0.09	15.3
WHC, GS muscle, s	0.11 ± 0.06	—	645
WHC, BF muscle, s	0.03 ± 0.06	—	651

[1]GS, BF, and AF = gluteus superficialis, biceps femoris, and adductor femoris muscles, respectively. pH24 = pH recorded 24 h after slaughter. a*, b*, and L* = reflectance measurements: redness/greenness, yellowness/blueness, and lightness, respectively. WHC = water-holding capacity.

[2]The dash (—) indicates that the common litter effect was nonsignificant and was removed from final analyses.

Table 5. Estimates of phenotypic and genetic correlations (±SE) between the selection criteria and carcass composition and meat quality traits

	Ovulation rate		Prenatal survival	
Trait[1]	Phenotypic	Genetic	Phenotypic	Genetic
Dressing percentage	−0.03 ± 0.06	−0.09 ± 0.15	0.03 ± 0.05	0.14 ± 0.20
Carcass length	−0.08 ± 0.07	−0.17 ± 0.14	0.00 ± 0.07	0.01 ± 0.20
Average backfat thickness	0.00 ± 0.06	0.00 ± 0.13	0.06 ± 0.05	0.16 ± 0.17
Backfat weight	0.02 ± 0.07	0.05 ± 0.15	0.03 ± 0.07	0.07 ± 0.20
Ham weight	−0.01 ± 0.07	−0.02 ± 0.15	−0.04 ± 0.07	−0.13 ± 0.20
Loin weight	0.00 ± 0.07	0.00 ± 0.15	−0.03 ± 0.07	−0.08 ± 0.20
Shoulder weight	−0.10 ± 0.07	−0.08 ± 0.15	0.01 ± 0.06	0.03 ± 0.20
Feet weight	ne[2]	ne	ne	ne
Leaf fat weight	−0.01 ± 0.07	−0.02 ± 0.15	0.02 ± 0.07	0.06 ± 0.20
Belly weight	−0.01 ± 0.07	−0.03 ± 0.13	0.02 ± 0.07	0.06 ± 0.20
Head weight	0.02 ± 0.07	0.05 ± 0.15	0.03 ± 0.07	0.09 ± 0.20
Estimated lean meat content	−0.01 ± 0.06	−0.02 ± 0.12	−0.07 ± 0.06	−0.19 ± 0.17
pH24 of LM muscle	0.05 ± 0.07	0.13 ± 0.20	0.10 ± 0.06	0.37 ± 0.24
pH24 of GS muscle	0.04 ± 0.07	0.11 ± 0.20	0.07 ± 0.06	0.22 ± 0.24
pH24 of BF muscle	0.08 ± 0.07	0.25 ± 0.21	0.07 ± 0.06	0.31 ± 0.25
pH24 of AF muscle	0.07 ± 0.07	0.17 ± 0.17	−0.02 ± 0.06	−0.05 ± 0.23
a* value, GS muscle	0.02 ± 0.07	0.06 ± 0.20	0.08 ± 0.06	0.34 ± 0.25
a* value, BF muscle	0.04 ± 0.07	0.09 ± 0.18	0.09 ± 0.06	0.29 ± 0.24
b* value, GS muscle	−0.08 ± 0.07	−0.29 ± 0.21	0.03 ± 0.06	0.15 ± 0.25
b* value, BF muscle	−0.09 ± 0.07	−0.30 ± 0.21	0.03 ± 0.06	0.14 ± 0.25
L* value, GS muscle	−0.07 ± 0.07	−0.22 ± 0.20	−0.01 ± 0.06	−0.05 ± 0.25
L* value, BF muscle	−0.02 ± 0.07	−0.10 ± 0.21	0.00 ± 0.06	−0.01 ± 0.25
WHC, GS muscle	−0.03 ± 0.05	−0.15 ± 0.21	−0.03 ± 0.04	−0.33 ± 0.26
WHC, BF muscle	−0.03 ± 0.06	−0.08 ± 0.19	−0.03 ± 0.06	−0.13 ± 0.26

[1]GS, BF, and AF = gluteus superficialis, biceps femoris, and adductor femoris muscles, respectively. pH24 = pH recorded 24 h after slaughter. a*, b*, and L* = reflectance measurements: redness/greenness, yellowness/blueness, and lightness, respectively. WHC = water-holding capacity.

[2]ne = not estimated because of convergence problems.

Table 6. Least squares (LS) and mixed model (MM) estimates (±SE) of line differences for carcass and meat quality traits after 6 generations of selection

	Ovulation rate line[2]		Prenatal survival line[2]	
Trait[1]	LS estimate	MM estimate	LS estimate	MM estimate
Dressing percentage, %	−0.0 ± 0.3	−0.1 ± 0.3	0.4 ± 0.3	0.3 ± 0.3
Carcass length, mm	12.9 ± 8.1	9.9 ± 8.0	3.3 ± 7.9	−0.3 ± 8.0
Average backfat thickness, mm	−1.7 ± 1.5	−1.5 ± 1.5	−1.7 ± 1.5	−1.3 ± 1.4
Backfat weight, kg	−0.23 ± 0.21	−0.32 ± 0.20	0.00 ± 0.23	−0.16 ± 0.21
Ham weight, kg	0.06 ± 0.10	0.02 ± 0.08	0.12 ± 0.10	0.05 ± 0.09
Loin weight, kg	0.37 ± 0.26	0.37 ± 0.25	0.46 ± 0.27†	0.44 ± 0.26†
Shoulder weight, kg	0.16 ± 0.09†	0.05 ± 0.08	0.10 ± 0.09	0.04 ± 0.08
Feet weight, kg	−0.03 ± 0.06	ne[3]	−0.01 ± 0.06	ne
Leaf fat weight, kg	−0.02 ± 0.06	−0.09 ± 0.06	−0.05 ± 0.06	−0.07 ± 0.06
Belly weight, kg	0.02 ± 0.15	−0.03 ± 0.15	−0.01 ± 0.15	−0.06 ± 0.14
Head weight, kg	−0.21 ± 0.17	−0.24 ± 0.17	0.10 ± 0.18	0.05 ± 0.17
Estimated lean meat content, %	1.6 ± 1.1	1.6 ± 1.1	1.9 ± 1.2	1.8 ± 1.2
pH24 of LM muscle	−0.08 ± 0.06	−0.08 ± 0.06	−0.10 ± 0.06†	−0.09 ± 0.06
pH24 of GS muscle	−0.06 ± 0.06	−0.06 ± 0.06	−0.12 ± 0.06*	−0.11 ± 0.06†
pH24 of BF muscle	−0.06 ± 0.07	−0.02 ± 0.07	−0.14 ± 0.07*	−0.14 ± 0.07*
pH24 of AF muscle	−0.06 ± 0.10	−0.09 ± 0.10	−0.17 ± 0.10†	−0.11 ± 0.10
a* value, GS muscle	0.12 ± 0.54	0.02 ± 0.57	0.51 ± 0.53	0.42 ± 0.57
a* value, BF muscle	−0.00 ± 0.64	−0.06 ± 0.61	0.86 ± 0.64	0.72 ± 0.60
b* value, GS muscle	0.32 ± 0.45	0.27 ± 0.46	0.83 ± 0.45†	0.79 ± 0.46†
b* value, BF muscle	0.07 ± 0.45	0.07 ± 0.46	0.51 ± 0.42	0.44 ± 0.45
L* value, GS muscle	0.62 ± 1.06	0.41 ± 1.04	1.89 ± 1.08†	1.11 ± 1.14
L* value, BF muscle	0.49 ± 0.58	0.41 ± 0.59	0.57 ± 0.57	0.54 ± 0.59
WHC, GS muscle, s	−3.8 ± 8.4	−1.7 ± 8.8	−18.9 ± 8.4*	−12.2 ± 8.7
WHC, BF muscle, s	0.3 ± 3.7	0.2 ± 3.5	−0.2 ± 3.7	0.1 ± 3.5

[1]GS, BF, and AF = gluteus superficialis, biceps femoris, and adductor femoris muscles, respectively. pH24 = pH recorded 24 h after slaughter. a*, b*, and L* = reflectance measurements: redness/greenness, yellowness/blueness, and lightness, respectively. WHC = water-holding capacity.
[2]Difference between selected and control lines; †$P < 0.10$; *$P < 0.05$.
[3]ne = not estimated because of convergence problems.

et al. (2006). The heritability estimates for reflectance are within the range found in the literature (Lo et al., 1992; de Vries et al., 1994; Knapp et al., 1997; Sellier, 1998). Among meat quality traits, heritability values for WHC_GS and WHC_BF were in agreement with those reported by Tribout et al. (1996) and Sonesson et al. (1998), but less than the estimates presented by the most recent literature reviews (Larzul et al., 1999a; Hermesch et al., 2000a). With estimates ranging from 2 to 9% of the phenotypic variance, common litter effects fell in the range of values reported in the literature.

Overall, genetic correlations between OR or SP and carcass composition traits were not significantly different from zero. Yet, correlation estimates with fatness/leanness traits tended to show a small antagonism between carcass leanness and OR or SP. Literature estimates of the genetic correlation between ABT and OR are close to zero (Rothschild and Bidanel, 1998; Ruiz-Flores and Johnson, 2001). An absence of genetic association between production and reproduction traits has been reported in numerous studies (e.g., Noguera et al., 2002; Serenius et al., 2004; Arango et al., 2005). Yet other recent studies have found a small unfavorable genetic correlation between carcass composition and litter size (e.g., Hermesch et al., 2000b; Zhang et al., 2000; Chen et al., 2003; Holm et al., 2004; Tribout and Bidanel, 2008). This unfavorable relationship may result from the detrimental effects on placental development of increased uterine crowding during early gestation, which is a critical period for the muscle development of embryos (Foxcroft et al., 2006). Embryos are then more likely to suffer from intrauterine growth retardation and have reduced numbers of muscle fibers and result in pigs with reduced growth performance and lean content at slaughter (Foxcroft et al., 2006; Rehfeldt and Kuhn, 2006). It may also be because leaner sows would have more difficulties mobilizing their body reserves to support the needs of embryos/piglets during gestation and lactation, as well as because of an unfavorable effect of a nutritional unbalance in late lactation on the subsequent ovulation or implantation rates.

Estimates of genetic correlations between OR and the different ultimate pH traits varied from 0.11 to 0.25 and from −0.05 to 0.37 between SP and ultimate pH traits, but also had very large SE (from 0.17 to 0.21 and 0.23 to 0.25, respectively), making it difficult to draw a conclusion regarding the genetic relationships between OR and meat quality. No other estimate of genetic correlations between OR or PS and meat quality traits is, to our knowledge, available in the literature to compare with results reported herein. More generally, few estimates of genetic relationships between reproduction and meat quality traits are available in the literature. Hermesch et al. (2000b) reported a negative genetic

correlation (−0.26) between ultimate pH and number of piglets born alive, indicating that an increased litter size is associated with a smaller ultimate pH. Genetic correlations between reflectance, lightness, water-holding capacity, and OR or PS traits were inconsistent and mostly of small magnitude, indicating no clear genetic relationships between these traits. However, genetic correlation between OR or PS and water-holding capacity traits were weak and negative. In contrast, Hermesch et al. (2000b) presented slightly positive genetic correlations between water-holding capacity and number of piglets born alive in first and second parity, but this correlation was not confirmed for the number of piglets born alive in third parity litters.

Line differences in the last generations of the experiment indicate that correlated responses to selection on carcass traits are limited. It has to be noted that the tendency toward an increase in loin weight in the PS line is not consistent with the weakly unfavorable genetic correlations between PS and carcass leanness traits. No clear explanation for this discrepancy was found. Conversely, the tendency toward an increase in ultimate pH is consistent with genetic parameter estimates. Larzul et al. (1999b) estimated correlated responses to selection for a reduced muscle glycolytic potential, which is strongly correlated with ultimate pH, in a Large White population issued from the same base population and obtained little correlated response for litter traits.

In conclusion, this study provides first estimates of genetic correlations of components of litter size (i.e., OR and PS) with carcass and meat quality traits. They globally confirm that both groups of traits are weakly correlated, although there might be a small antagonism between OR or PS and carcass leanness and a weak positive (i.e., favorable) relationship with meat ultimate pH.

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