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# Genetic variability of age and weight at puberty, ovulation rate and embryo survival in gilts and relations with production traits

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**Summary** – Age (AFE), weight (WFE) and ovulation rate (OR) at first estrus, number of embryos (NE) and embryo survival (ES = NE/OR) at 30 days of gestation of French Large White (LW), French Landrace (LF) and crossbred LW × LF gilts and their genetic relationships with average daily gain between 30 and 85 kg (ADG) and average backfat thickness at 85 kg (ABT) were analyzed. Breed differences, as well as genetic parameters in the LW breed, were estimated using a restricted maximum likelihood procedure applied to a multiple trait animal model. A total of 3 664 male and female pigs were measured for ADG and ABT between 1966 and 1979; 1 919 gilts were checked daily for puberty between 140 and 300 days of age. Most females were then bred and slaughtered at 30 days of gestation for measuring the number of corpora lutea and the number of embryos. Breed marginal means were, respectively,  $214.9 \pm 1.4$ ,  $197.8 \pm 3.3$  and  $190.1 \pm 2.1$  days for AFE,  $116.1 \pm 0.9$ ,  $102.5 \pm 2.2$  and  $97.7 \pm 1.4$  kg for WFE,  $14.4 \pm 0.1$ ,  $13.0 \pm 0.3$  and  $13.9 \pm 0.2$  for OR and  $9.6 \pm 0.1$ ,  $9.6 \pm 0.4$  and  $10.5 \pm 0.3$  for NE in LW, LF and LW × LF gilts. Heritability estimates were 0.29, 0.51, 0.27, 0.14 and 0.08 (se 0.03), respectively, for AFE, WFE, OR, NE and ES. Genetic correlations between AFE and WFE, between NE and OR or ES were rather large ( $0.84 \pm 0.05$ ,  $0.73 \pm 0.12$  and  $0.79 \pm 0.15$  respectively). OR and ES had a low genetic correlation ( $-0.11 \pm 0.15$ ). AFE was negatively correlated with ADG ( $-0.18 \pm 0.05$ ), ABT ( $-0.21 \pm 0.05$ ), OR ( $-0.36 \pm 0.09$ ) and NE ( $-0.35 \pm 0.08$ ). WFE also tended to be negatively correlated with OR ( $-0.26 \pm 0.11$ ) and NE ( $-0.18 \pm 0.10$ ), but exhibited low or positive genetic correlations with ABT ( $0.08 \pm 0.05$ ) and ADG ( $0.34 \pm 0.05$ ). OR, NE and ES had low or favourable genetic correlations with both ADG and ABT.

pig / genetic parameter / puberty / production trait / reproduction trait

**Résumé – Variabilité génétique de l'âge et du poids à la puberté, du taux d'ovulation et de la mortalité embryonnaire chez la cochette. Relations avec les caractères de production et de reproduction.** L'âge (APO), le poids (PPO) et le taux d'ovulation (TO) au premier œstrus, le nombre d'embryons (NE) et la survie embryonnaire ( $ES = NE/TO$ ) à 30 jours de gestation de cochettes Large White (LW), Landrace Français (LF) et croisées  $LW \times LF$ , ainsi que leurs relations avec le gain moyen quotidien entre 30 et 85 kg (GMQ) et l'épaisseur moyenne de lard dorsal à 85 kg ont été analysés. Les différences entre races, ainsi que les paramètres génétiques de la race LW, ont été estimés à l'aide d'une procédure du maximum de vraisemblance restreinte appliquée à un modèle animal multicaractère. Un total de 3 664 porcs mâles et femelles ont été mesurés pour GMQ et ELD entre 1966 et 1979. Un contrôle quotidien de la puberté a été réalisé entre 140 et 300 jours d'âge sur un total de 1 919 cochettes. La plupart des femelles ont ensuite été mises à la reproduction et abattues à 30 jours de gestation afin de mesurer TO et NE. Les moyennes marginales s'élèvent à, respectivement,  $214,9 \pm 1,4$ ;  $197,8 \pm 3,3$  et  $190,1 \pm 2,1$  jours d'âge pour APO,  $116,1 \pm 0,9$ ;  $102,5 \pm 2,2$  et  $97,7 \pm 1,4$  kg pour PPO,  $14,4 \pm 0,1$ ;  $13,0 \pm 0,3$  et  $13,9 \pm 0,2$  pour TO et  $9,6 \pm 0,1$ ;  $9,6 \pm 0,4$  et  $10,5 \pm 0,3$  pour NE chez les cochettes LW, LF et  $LW \times LF$ . Les estimations de l'héritabilité s'élèvent à 0,29; 0,51; 0,27; 0,14 et 0,08 (es 0,03), respectivement, pour APO, PPO, TO, NE et SE. Les corrélations génétiques entre APO et PPO, ainsi qu'entre NE et TO ou SE, sont élevées (respectivement  $0,84 \pm 0,05$ ;  $0,73 \pm 0,12$  et  $0,79 \pm 0,15$ ). TO et ES sont faiblement corrélés ( $-0,11 \pm 0,15$ ). APO est négativement corrélé à GMQ ( $-0,18 \pm 0,05$ ), ELD ( $-0,21 \pm 0,05$ ), TO ( $-0,36 \pm 0,11$ ) et NE ( $-0,35 \pm 0,08$ ). PPO tend également à présenter des corrélations négatives avec TO ( $-0,26 \pm 0,11$ ) et NE ( $-0,18 \pm 0,10$ ), mais présente des corrélations génétiques faibles ou positives avec ELD ( $0,08 \pm 0,05$ ) et GMQ ( $0,34 \pm 0,05$ ). TO, NE et SE présentent des corrélations génétiques faibles ou favorables avec GMQ et ELD.

**porc / paramètre génétique / puberté / caractère de production / caractère de reproduction**

## INTRODUCTION

Until recently, pig breeding programmes have concentrated on the improvement of growth rate, food conversion efficiency and carcass quality (Ollivier et al, 1990). Little selection effort has been devoted to reproduction traits, ie, sexual maturity, fertility and prolificacy.

Litter size at birth is the main contributor to variation in sow reproductive efficiency (Tess et al, 1983), but is poorly heritable and consequently rather difficult to improve through selection (Bolet et al, 1989). Johnson et al (1984) suggested that the rate of genetic improvement in litter size could be increased by selecting on its components, ie, ovulation rate and prenatal survival. Selection for ovulation rate in pigs has been effective, but without any significantly correlated response on litter size (Cunningham et al, 1979). Subsequent selection for litter size produced a significant increase in litter size (Lamberson et al, 1991). This tends to indicate that embryo and/or fetal survival take a prominent part in the variation of litter size at birth.

Early sexual maturity of gilts is also likely to have a beneficial influence on the economic efficiency of pig production. A delayed age at puberty increases the length of the unproductive period prior to first farrowing and complicates the management

of batch farrowing systems (Tess et al, 1983; Rydhmer, 1993). Moreover, early puberty may improve genetic progress by shortening the generation interval (Hixon et al, 1987). The value of selecting for early puberty and/or components of litter size depends on their genetic variability and genetic relationships with other economically important traits. The aim of the present study is to estimate breed differences and genetic parameters of age and weight at first estrus, ovulation rate and embryo survival and their relationships with production traits in gilts.

## MATERIALS AND METHODS

### *Animals and data collection*

The experiment took place at the INRA experimental farm of Rouillé (Vienne, France). Puberty traits were recorded on a total of 1393 Large White (LW), 110 French Landrace (LF) and 501 LW  $\times$  LF (LW sire and LF dam) gilts between 1966 and 1979. LW gilts were produced in the scope of a selection experiment for lean tissue growth rate (Ollivier, 1977, 1980). The design of the experiment, which began in 1965, is detailed by Ollivier (1977). In March of each year, all male offspring (except runt piglets) of the boars selected the previous year and of sows picked at random in a LW population of about 5000 sows located in small herds were grouped in the INRA experimental station of Rouillé (Vienne, France) and selected on their performance test results as described below. The animals originated from a large number of farms located around the INRA experimental herd, as only one or two litters were produced in each herd. Selected boars were then placed in the INRA artificial insemination (AI) center of Rouillé and their semen used on sows from the above-mentioned LW population to produce the next generation. In September of each year, daughters from these AI boars were also grouped in Rouillé to study puberty and prolificacy traits. It should be noted that LW males and females were born at different periods of time. Hence, they were either half- or full-sibs, but could not be littermates. Randomly sampled contemporary LF and LW  $\times$  LF females were introduced into the herd in 1971, 1972, 1977 and 1978 to study breed differences. These females also came from a large number of small herds. Crossbred females were generally daughters from the same LW boars as LW gilts. Their dams were sometimes, but not systematically, related to the dams of LF gilts. As for males, all females (except runt piglets) from each litter produced were grouped at the INRA experimental station for performance testing.

Piglets were purchased at 20–25 kg live weight and allotted to pens of about ten animals in a semiopen building. They were performance tested from 30 to 80 kg, extended to 85 kg from 1977 onwards. Animals were given ad libitum access to a pelleted diet in self feeders and to water during the whole test period. Then, gilts were given a daily ration of feed averaging 2.5 kg until slaughter. A preliminary diet formulated to contain 3.2 Mcal and 17% crude protein/kg was fed until 60 kg liveweight. The energy and protein contents of the diet were then reduced to 3.0 Mcal and 15% crude protein/kg until slaughter.

Animals were weighed at the beginning and at the end of the test period. Backfat thickness was measured at the same time as final weight. The ultrasonic measurements were taken on each side of the spine, 4 cm from the mid-dorsal line

at the levels of the shoulder, the last rib and the hip joint, respectively. LW boar candidates were selected on the basis of a performance test index:

$$I = 0.01ADG - 0.5ABT$$

where ADG is average daily gain (in g) over the test period and ABT is the average of the six backfat measurements (in mm), adjusted for final weight.

Puberty was defined as the first estrus, indicated by a standing response to a teaser boar. Estrus detection on a daily basis was initiated when the heaviest gilt in a pen reached 80 kg (ie, at approximately 140 days of age) and continued until 300 days of age. Gilts were weighed when they reached first-detected estrus and immediately inseminated (except in 1967, 1968 and 1971). They were then slaughtered 27–30 days after reaching first estrus. Ovaries were dissected to count corpora lutea and embryo number recorded in pregnant females. Females that did not conceive were not bred again. The ovulation rate of gilts which did not conceive at the first estrus records were measured at the second estrus and were excluded from the analysis. Similarly, reproductive measurements from gilts ovulating without any detectable estrus symptoms and from gilts showing estrus symptoms without ovulation were discarded from the appropriate data vectors. Conversely, puberty and ovulation rate records from gilts born in 1967, 1968 and 1971, which were not inseminated but were slaughtered 7–13 days after puberty, were retained in the analyzes.

Seven traits were defined and analyzed from the above-mentioned measurements, ie, ADG, ABT, age (AFE) and weight (WFE) at first detectable estrus, ovulation rate (OR) estimated as the total number of corpora lutea, the number of living embryos (NE) at 30 days of gestation and embryo survival rate (ES) defined as the ratio of number of embryos to ovulation rate.

The structure of the data studied is shown in table I. LW ancestors were known over the experiment on the male side. Conversely, the parents of most dams and the paternal grandams were generally unknown. Part of these data were previously analyzed by Legault (1973) and Legault and Gruand (1981), but genetic parameter estimation was limited to heritabilities.

### ***Statistical analyzes***

Preliminary analyzes showed that: i) most gilts reached puberty before 300 days of age (95, 98 and 98% of animals checked for puberty, respectively, in LW, LF and LW × LF populations); and ii) gilts ovulating without any detectable estrus symptoms and gilts showing estrus symptoms without ovulating represented less than 1% of the total number of gilts. Hence, there was almost no left or right censorship on reproductive traits. Moreover, all traits except ES were almost normally distributed, (puberty traits were only slightly skewed) so that standard mixed linear model procedures were considered adequate to analyze the data.

Genetic and environmental parameters were estimated in the LW breed using a derivative-free restricted maximum likelihood (REML) procedure applied to a multiple trait individual animal model. The data set was too large to allow a single seven-trait REML analysis. Hence, ten successive four-trait analyzes were performed. These four-trait analyzes systematically included ADG and ABT in

**Table I.** Structure of the data studied.

	<i>Large White (LW)</i>	<i>French Landrace (LF)</i>	<i>LW × LF</i>
Number of records			
Growth traits			
Males	1 660	—	—
Females	1 393	110	501
Puberty traits	1 393	103	423
Ovulation rate	1 111	103	423
Number of embryos	634	76	172
Number of year × batches	40	7	10
Number of sires	270	18	31
Number of dams	1 178	36	143
Number of litters	1 393	36	143

order to account for the effects of selection, plus two reproduction traits in order to get estimates of the covariances between reproduction traits and between reproduction and production traits. The model for ADG and ABT included sex and year with batch interaction as fixed effects, with litter of birth and animal fitted as random effects. The same model, but without the sex effect, was used for AFE, WFE, OR, NE and ES. The analyzes were performed using version 2.2 of the VCE computer package (Groeneveld, 1993). Approximate standard errors of variance components and genetic parameters were obtained from an approximation of the Hessian matrix when convergence was reached.

Estimates of breed marginal means were computed using BLUP (best linear unbiased prediction; Henderson, 1973) methodology applied to an individual animal model. The model was a seven-trait animal model including breed, year with batch interaction and sex (for ADG and ABT only) as fixed effects, with litter of birth and animal fitted as random effects. The PEST computer package (Groeneveld and Kovac, 1990) was used for this purpose. Genetic and environmental (co)variances used were the REML estimates obtained in the LW breed. Variance estimates from univariate REML analyzes on the whole set of data were similar to those obtained in the LW breed, thus indicating that genetic parameters did not widely differ between genetic types.

## RESULTS

Genetic type marginal means are shown in table II. LW animals grew faster ( $+68 \pm 12$  g/d) and were fatter ( $+2.6 \pm 0.3$  mm of backfat thickness) than their LF contemporaries. Crossbred LW × LF animals were intermediate (deviations from purebred means were, respectively,  $+6 \pm 9$  g/day and  $+0.3 \pm 0.3$  mm, for ADG and ABT). LW gilts were older ( $+17.1 \pm 3.5$  days) and heavier at puberty ( $+13.6 \pm 1.8$  kg) than LF gilts. They also had more corpora lutea ( $+1.3 \pm 0.3$ ), but a lower embryo survival ( $-7.1 \pm 2.7$ ) than LF gilts, so that the number of embryos was similar in both breeds. Crossbred females had an earlier sexual maturity than

both purebreds. Deviations from purebred average performance were  $-16.2 \pm 2.8$  days and  $-11.6 \pm 1.8$  kg, respectively, for AFE and WFE. Crossbred gilts were almost intermediate for OR, but had a better embryo survival ( $5.2 \pm 2.2$  %) and more living embryos than purebred animals ( $+0.9 \pm 0.3$  embryos).

**Table II.** Estimates of genetic type marginal means ( $\pm$  se) for the traits studied.

<i>Trait</i>	<i>Large White (LW)</i>	<i>French Landrace (LF)</i>	<i>LW <math>\times</math> LF</i>
Average daily gain (ADG) (g/day)	814 $\pm$ 4	746 $\pm$ 12	786 $\pm$ 7
Average backfat thickness (ABT) (mm)	21.2 $\pm$ 0.1	18.6 $\pm$ 0.3	20.2 $\pm$ 0.2
Age at first estrus (AFE) (days)	214.9 $\pm$ 1.4	197.8 $\pm$ 3.3	190.1 $\pm$ 2.1
Weight at first estrus (WFE) (kg)	116.1 $\pm$ 0.9	102.5 $\pm$ 2.2	97.7 $\pm$ 1.4
Ovulation rate (OR)	14.4 $\pm$ 0.1	13.0 $\pm$ 0.3	13.9 $\pm$ 0.2
Number of embryos (NE)	9.6 $\pm$ 0.1	9.6 $\pm$ 0.4	10.5 $\pm$ 0.3
Embryo survival (ES) (%)	66.7 $\pm$ 0.9	73.8 $\pm$ 2.5	75.5 $\pm$ 1.2

Several estimates of variance components were available for each trait. However, variation among estimates was very small (less than 1% between extreme values), so that the average values of heritability and common litter effect presented in table III are almost the same as estimates obtained in each individual analysis. Heritability estimates of 0.5 for ABF and WFE were higher than those for NE and ES (0.1), with intermediate heritability estimates for ADG, AFE and OR. Common environmental effects were equal to 0.1, with high and low estimates for ADG and ES, respectively.

**Table III.** Estimates of phenotypic standard deviation, heritability and common litter effect in the Large White breed.

<i>Trait</i>	<i>Phenotypic standard deviation</i>	<i>Heritability (<math>\pm</math> se)</i>	<i>Common litter effect (<math>\pm</math> se)</i>
Average daily gain (ADG) (g/day)	115	0.24 $\pm$ 0.01	0.24 $\pm$ 0.01
Average backfat thickness (ABT) (mm)	2.85	0.48 $\pm$ 0.01	0.11 $\pm$ 0.01
Age at first estrus (AFE) (days)	30.3	0.29 $\pm$ 0.02	0.08 $\pm$ 0.02
Weight at first estrus (WFE) (kg)	20.2	0.51 $\pm$ 0.02	0.08 $\pm$ 0.02
Ovulation rate (OR)	2.61	0.27 $\pm$ 0.02	0.06 $\pm$ 0.02
Number of embryos (NE)	3.37	0.14 $\pm$ 0.03	0.02 $\pm$ 0.03
Embryo survival (ES) (%)	21.8	0.08 $\pm$ 0.03	0.00*

\* The standard error could not be calculated as the estimate was zero.

Estimates of phenotypic and genetic correlations are shown in table IV. ADG and ABT exhibited a slightly positive, ie, unfavourable, relationship. Large positive phenotypic and genetic correlations were obtained between AFE and WFE. Similarly, NE had strongly positive genetic correlations with both OR and ES, which were poorly correlated.

Table IV. Estimates of phenotypic (below diagonal) and genetic (above diagonal) correlations ( $\pm$  se) between the traits studied in the Large White breed.

	Average daily gain (ADG)	Average backfat thickness (ABT)	Age at first estrus (AFE)	Weight at first estrus (WFE)	Ovulation rate (OR)	Number of embryos (NE)	Embryo survival (ES)
Average daily gain (ADG)	—	0.13 $\pm$ 0.04	-0.18 $\pm$ 0.06	0.34 $\pm$ 0.06	0.20 $\pm$ 0.08	0.18 $\pm$ 0.10	0.06 $\pm$ 0.12
Average backfat thickness (ABT)	0.28 $\pm$ 0.02	—	-0.21 $\pm$ 0.06	0.08 $\pm$ 0.06	-0.09 $\pm$ 0.09	-0.46 $\pm$ 0.09	-0.56 $\pm$ 0.11
Age at first estrus (AFE)	-0.16 $\pm$ 0.02	-0.11 $\pm$ 0.02	—	0.84 $\pm$ 0.05	-0.36 $\pm$ 0.09	-0.35 $\pm$ 0.08	0.04 $\pm$ 0.12
Weight at first estrus (WFE)	0.26 $\pm$ 0.02	0.07 $\pm$ 0.02	0.66 $\pm$ 0.03	—	-0.26 $\pm$ 0.11	-0.18 $\pm$ 0.10	0.18 $\pm$ 0.12
Ovulation rate (OR)	0.11 $\pm$ 0.03	-0.02 $\pm$ 0.03	-0.04 $\pm$ 0.03	0.15 $\pm$ 0.03	—	0.73 $\pm$ 0.14	-0.11 $\pm$ 0.15
Number of embryos (NE)	0.04 $\pm$ 0.03	-0.06 $\pm$ 0.03	0.00 $\pm$ 0.04	0.13 $\pm$ 0.04	0.37 $\pm$ 0.04	—	0.79 $\pm$ 0.15
Embryo survival (ES)	-0.04 $\pm$ 0.03	-0.08 $\pm$ 0.03	0.01 $\pm$ 0.04	-0.03 $\pm$ 0.04	-0.12 $\pm$ 0.04	0.84 $\pm$ 0.05	—



ADG was negatively, ie, favourably, correlated with AFE, but had a positive genetic correlation with WFE. Genetic correlations between ADG and prolificacy traits were low or positive, ie, favourable. ABT also tended to be favourably correlated with prolificacy traits, but showed some genetic antagonism with AFE. Puberty traits had negative genetic correlations with OR of NE and were poorly correlated with ES.

## DISCUSSION

Estimates of the between- or within-breed genetic variability of sexual maturity traits are not very numerous in the literature. Moreover, available estimates generally have a low accuracy. This is likely due to the fact that puberty attainment is very tedious to detect. However, the delayed puberty of LW gilts as compared to LF gilts and the earlier sexual maturity of crossbred gilts as compared to pure breeds in the present study is in agreement with most other results in the literature (Christenson, 1981; Hutchens et al, 1982; Legault and Caritez, 1983; Allrich et al, 1985; Irgang et al, 1992). Heterosis effects could not be estimated without bias in this study because the LW  $\times$  LF reciprocal cross was lacking, so that heterosis and maternal effects were confounded. However, maternal effects on age at puberty are of limited importance (Christenson, 1981; Allrich et al, 1985), so that the deviation of LW  $\times$  LF from the purebred average should be close to heterosis effects. Indeed, the value obtained does not differ much from the literature average ( $-11.3$  days; Bidanel, 1988). The larger OR of LW as compared to LF and the intermediate position of crossbred LW  $\times$  LF, as well as the lack of difference between purebreds for NE and the larger litter size of LW  $\times$  LF gilts, also agree with results from the literature (see, for instance, the reviews of Bidanel, 1989, and Blasco et al, 1993a).

Heritability estimates for ADG, ABT, age at puberty, OR and NE are close to previous estimates of Legault and Gruand (1981) and to average literature values (Bidanel, 1989; Lamberson, 1990; Stewart and Schinckel, 1990; Blasco et al, 1993a; Ducos, 1994). Conversely, the value obtained for weight at puberty is larger than most literature estimates (Young et al, 1978; Hutchens et al, 1981). The heritability of ES is lower than the values reported by Johnson et al (1984), Neal et al (1989) or Gama et al (1991) in synthetic populations but, unlike Haley and Lee (1992), tends to show that some genetic variation for ES exists in a LW population. Common litter effects ( $c^2$ ) tend to be larger than usual literature values, particularly for ADG and ABT. This is probably due to a partial confounding between birth litter and herd of origin (litters generally came from different herds), both of which have an effect on growth performance.

The strong genetic correlation between NE and ES agrees with the estimates obtained in the Nebraska experiment (Neal et al, 1989) and with estimates obtained in mice and rabbits (Clutter et al, 1990; Blasco et al, 1993b). Conversely, a much stronger association between OR and NE and a lower relationship between OR and ES than in most other studies at 30 days of gestation (Young et al, 1977), 50 days of gestation (Neal et al, 1989) or at birth (Young et al, 1978) is observed. This may be due to differences in the populations studied, but may also indicate that uterine competition tends to increase throughout gestation. This increased competition has been evidenced by superovulation and embryo transfer experiments (Dziuk,

1968; Pope et al, 1972; Webel and Dziuk, 1974) or more recently by experiments on unilaterally hysterio-ovariectomized females (Christenson et al, 1987; Legault et al, 1995). Bennett and Leymaster (1989) proposed a model for litter size with two independent components, OR and uterine capacity, defined as the maximum number of fetuses that the uterine environment can support. In this model, OR is uncorrelated with ES and negatively correlated with fetal survival. The results from the present study are in fairly good agreement with this model, even if the small negative correlation between OR and ES might indicate that uterine capacity could also have some effect during early gestation. Similar results, ie, a low correlation between OR and ES and a much stronger one between OR and fetal survival, were obtained in intact (Blasco et al, 1993a) and unilaterally ovariectomized does (Blasco et al, unpublished results), where a laparoscopic technique makes it possible to count rabbit fetuses during gestation with no detectable impact on subsequent fetal survival (Santacreu et al, 1990).

The large phenotypic and genetic correlations between age and weight at puberty are in close agreement with most available literature estimates (Reutzel and Sumption, 1968; Young et al, 1978; Hutchens et al, 1981). However, in spite of their close genetic relationship, age and weight at puberty show rather different correlations with growth rate. Indeed, negative relationships with age at puberty and positive ones with weight at puberty were obtained in all available studies (Reutzel and Sumption, 1968; Young et al, 1978, Hutchens et al, 1981, Rydhmer et al, 1992). This difference can be explained by noting that the correlation between growth rate and weight at puberty is the result of two antagonistic relationships, ie, a slight negative relationship between growth rate and age at puberty and a rather strong positive one between growth rate and weight at a given age. The relationships between puberty traits and backfat thickness are less clear. Negative, ie, unfavourable, genetic correlations with age at puberty were obtained by Gama and Johnson (1992), Rydhmer et al (1992) and in the present study. Conversely, null or positive correlations were reported by Young et al (1978), Hutchens et al (1981) and Hixon et al (1987). These discrepancies are partly due to the low accuracy of most estimates but may also, as argued by Rydhmer et al (1992), be due to genotype  $\times$  feeding regime interactions between studies.

The negative, ie, favourable, genetic correlations between age at puberty and ovulation rate or number of embryos are consistent with the estimates obtained by Young et al (1978). Conversely, Rydhmer et al (1992) obtained positive genetic correlations between age at puberty and litter size at birth. These discrepancies may partly be due to differences in the traits analyzed (litter size at 30 days of gestation versus at birth). It may also be related to the fact that litter size was measured at a constant chronological age in the study of Rydhmer et al (1992), but at a constant physiological age in Young et al (1978) and in the present study (second and first estrus, respectively). However, a negative correlation is more likely to occur between age at puberty and litter size at a constant chronological age in young gilts, as prolificacy increases with estrus number. Thus late maturing gilts, which have a lower estrus number, would tend to have small litters (Rydhmer et al, 1992). The results of Després et al (1992), who found a decrease in age at puberty in the so-called 'hyperprolific' LW line selected for litter size in France, also tend to show that age at puberty is negatively correlated with sow prolificacy.

In any case, results from the present study tend to indicate that selection for growth rate has an opposite effect to selection against backfat thickness on age and weight at puberty in the LW population studied. As a consequence, the correlated response of sexual maturity traits to selection on an index based on growth rate and backfat thickness will depend on the relative emphasis given to each trait in the selection index. A slight increase of both age and weight at puberty can be predicted from the index used and the genetic parameter estimates from the present study. Selection objectives in France have until now put a stronger emphasis on carcass lean content than on growth rate. Hence, a delayed sexual maturity may be expected based on the genetic parameters of the present study, provided that the genetic parameters obtained from these fairly old data are still valid for current pig populations. This delayed puberty may be accompanied by a reduced intensity of estrus symptoms, as recently shown by Rydhmer et al (1994). However, selection objectives in pigs are currently changing towards a lower emphasis on lean content and a stronger one on growth rate and prolificacy. A more favourable genetic trend for age at puberty can be expected from an increased economic weight of growth rate. Conversely, the impact of the growing economic weight of prolificacy remains unclear, because its relationship with age at puberty is not well established.

## CONCLUSION

This study confirms that puberty traits are not genetically independent of production traits in gilts. As a consequence, age at puberty can be changed by selection for growth rate or carcass lean content. Favourable genetic trends can be expected from selection for growth rate, but unfavourable changes should result from selection for lean content. The evolution of puberty traits in pig breeding programs will therefore depend on the relative emphases placed on these traits, but also on other economically important traits such as food conversion ratio, meat quality or prolificacy. This study also provides genetic parameter estimates of components of litter size at 30 days of gestation, ie, ovulation rate and embryo survival. It tends to confirm the existence of some genetic variation in embryo survival, which is almost independent of genetic variation in ovulation rate.

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