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# REPONSE TO SELECTION FOR OVULATION RATE OR PRENATAL SURVIVAL IN LARGE WHITE PIGS

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**Abstract**. Effects of selection for ovulation rate or prenatal survival were examined using data from three pigs lines derived from the same base Large White population. Two lines were selected for seven generation on either high ovulation rate at puberty (OR line) or high prenatal survival corrected for ovulation rate in the first two parities (PS line). The third line was an unselected control (C) line. Genetic parameters for ovulation rate on the left, right and both ovaries at puberty (ORPL, ORPR and ORP, respectively) and at fertilization (ORFL, ORFR and ORF, respectively), prenatal survival (PS), total number of piglets born (TNB) and number of piglets born alive (NBA) per litter were estimated using REML methodology. Responses to selection were estimated by computing differences between OR or PS and C lines at each generation using both least-squares and mixed model methodology. Average genetic trends were computed by regressing line differences on generation number. Realized heritabilities were estimated using standard procedures. Heritabilities estimates were, respectively 0.17, 0.11, 0.34, 0.13, 0.09, 0.33, 0.14, 0.17 and 0.16 (s.e. 0.01 to 0.03) for ORPL, ORPR, ORFL, ORFR, ORF, PS, TNB and NBA respectively. Realized heritability were 0.39 and 0.10 for ORP and PS, respectively. The different measures of ovulation rate had strong genetic correlations ($r_g > 0.7$). ORP and ORF had moderately negative genetic correlations (-0.26 and -0.45, respectively) with PS. Litter size at birth was moderately correlated with ORP ($r_g = 0.41$ and 0.42, respectively, with TNB and NBA) and ORF (0.41 with TNB, 0.29 with NBA). Average genetic trends in OR and PS lines were, respectively, 0.38±0.08 and 0.13±0.09 for ORP; 0.34±0.08 and 0.08±0.09 for ORM. Responses to selection were slightly superior in the left than in the right ovary. No significant difference was found for PS, CPS and TNB in the two lines.

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## INTRODUCTION

In spite of its low heritability, sow prolificacy has been successfully selected in large populations by applying high selection intensities in so-called “hyperprolific” breeding schemes ((Legault and Gruand, 1976); Bidanel et al., 1994). For instance, a genetic gain of almost 3 piglets has been obtained over the last 15 years in French Large White breed (Tribout et al., 2003). However, efficiently selecting for litter size remains a difficult task in smaller populations. Several authors have proposed to use more heritable indirect criteria to improve the efficiency of selection for litter size, e.g. uterine capacity (Bennett and Leymaster, 1990a, b) or components of litter size (Johnson et al., 1984). In rabbits, selection for uterine capacity has resulted in a significant correlated response on litter size at birth (Blasco et al., 2001). In pigs, (Johnson et al., 1999) successfully increased litter size after ten generations of selection for an index combining ovulation rate and embryonic survival. Yet, the interest of indirect selection on components of litter size as compared to direct selection on litter size critically depends on the genetic parameters of these components (Perez-Enciso et al., 1996). A selection experiment has been carried out at INRA in order to estimate the genetic parameters of components of litter size in the French Large White breed. The objective of this study is to estimate genetic parameters of as well as direct and correlative responses on litter size and its components.

## MATERIALS AND METHODS

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### *Animals and experimental design*

The experiment took place at the INRA experimental herd of Galle (18520, Avord). The base generation was constituted by the progeny of 50 sows from another INRA experimental herd (35500, Saint-Gilles) inseminated with semen from 25 boars present in French artificial insemination centers. Males and females from this base generation were randomly allocated within-litter to three contemporary lines. Two lines were then selected for either ovulation rate at puberty (OR line) or prenatal survival over the first two parities, corrected for ovulation rate (PS line). The third line was kept as an unselected control line (C line). 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 three lines. Gilts were randomly chosen on a within-dam family basis in the C line and selected on a population basis in the two other lines. A mating plan was established in order to minimize inbreeding at each generation.

The sow herd was managed under a batch farrowing system. At each generation, females were distributed into seven farrowing batches. These batches then became postweaning and fattening batches of their progeny. Females were inseminated twice at a 24-h interval. Seven gilts from each line were introduced in each farrowing batch. All females that did not conceive at first mating joined the subsequent farrowing batch where they had the opportunity to be mated once more. Hence, there could be some variation in the number of females per line x batch combination, but each batch included females from the three lines. Litters were born in individual farrowing crates. When necessary, some piglets could be moved to another crate within the first few hours after farrowing.

Puberty was defined as the first estrus, indicated by a standing response to a teaser boar. Estrus detection on a daily basis was initiated at 150 days of age on and continued until almost all females reached puberty. Ovulation rate at puberty, estimated by counting the number of corpora lutea visible on the ovaries, was measured in females under general anesthesia by laparoscopy between 10 and 15 days after the first oestrus. The visual exam of the ovaries also allowed to check whether the first detected oestrus corresponded to the first ovulation. When a previous ovulation had occurred, gilts were removed from the experiment. Females kept for breeding were then mated at 11 months of age on average, after a synchronization treatment with a progestagen. Ovulation rate was measured as described above between 10 and 15 days after mating. Females were kept to produce two litters. The numbers of piglets born alive, stillborn et mummified were recorded at each farrowing.

The selection criterion in the OR line was ovulation rate at puberty. Gilts were selected on their own performance, boars on the performance of their dam. The selection criterion in the PS line was the average prenatal survival over the first two parities, corrected for ovulation rate (CPS) (Blasco et al., 1998).

## Statistical analyses

Traits. Nine traits were analysed, i.e. the numbers of corpora lutea in left and right ovaries and their sum at puberty (ORPL, ORPR and ORP, respectively) and at fertilisation (ORFL, ORFR and ORF, respectively), prenatal survival (PS), total number (TNB) and number of piglets born alive (NBA).

Least squares analyses of line differences and realized heritabilities. Line x generation means for each trait were estimated using a linear model including the fixed effects of generation number (0 to 7), line (OR, PS or C), a line x generation interaction. Sow and/or litter size inbreeding coefficients and age at puberty, at fertilization or at farrowing were also included as linear covariates (table 1). Further analyses of PS were performed by adding ORF as a linear covariate in the model. A similar procedure to that employed by Joakimsen and Baker (1977) and Bolet et al. (1989) was used to estimate realized heritabilities.

Mixed model analyses. Variance components were first estimated using REstricted Maximum Likelihood (REML) methodology (Patterson and Thompson, 1971) applied to a multivariate animal model. The models used to describe the different traits analyzed are shown in table 1.

**Table 1 - Models used to describe the different traits analysed**

| Trait | Covariables | | | | Fixed effects | | Random effects | | |
|---|---|---|---|---|---|---|---|---|---|
| | Age dam puberty | Age dam fert[1] | Age dam parity | Inbree dam[2] | Contemporary Group | Parity number | Common birth litter | Permanent environment | Animal |
| ORPL | x | | | | x | | x | | x |
| ORPR | x | | | | x | | x | | x |
| ORP | x | | | | x | | x | | x |
| ORFL | | x | | | x | x | x | x | x |
| ORFR | | x | | | x | x | x | x | x |
| ORF | | x | | | x | x | x | x | x |
| PS | | x | | | x | x | x | x | x |
| TNB | | | x | x | x | x | x | x | x |
| NBA | | | x | x | x | x | x | x | x |

1= Age of dam at fertilization; 2= inbreeding of dam; ORPL, ORPR, ORP = ovulation rate at puberty in the left, right and both, respectively; ORFL, ORFR, ORF = ovulation rate at fertilization in the left, right and both ovaries, respectively; PS = prenatal survival; TNB, NBA = total number of piglets born and born alive per litter, respectively.

The analyses were performed using VCE Neumaier and Groeneveld, 1998) and ASREML (Gilmour et al, 2002) computer packages. BLUP estimated breeding values were then computed as back-solutions of REML analyses. Genetic trends were estimated by either averaging estimated breeding values of animals for each line x generation combination or by regressing them on generation number within each line.

## RESULTS

REML estimates of genetic parameters are shown in table 2. Ovulation rate at puberty and at fertilization had rather high heritabilities. The number of corpora on each ovary was much less heritable, with significantly higher values on the left than on the right ovary. Low, but significant, heritabilities were obtained for prenatal survival and litter size traits at birth. Common litter effects, which include a large part of dominance effects (Johansson et al, 1994), were low for for all traits investigated. Permanent environmental effects were also low for ovulation rate measurements and prenatal survival, but much higher for litter size at birth.

**Table 2 - Estimates of heritability, common litter and permanent environmental effects and phenotypic standard deviation**

| Trait[1] | Heritability[2] | Common litter effect[2] | Permanent environment[2] | Phenotypic standard deviation |
|---|---|---|---|---|
| ORPL | 0.17 | 0.02 | - | 2.41 |
| ORPR | 0.11 | 0.03 | - | 2.43 |
| ORP | 0.34 | 0.03 | - | 2.81 |
| ORFL | 0.13 | 0.00 | 0.00 | 2.47 |
| ORFR | 0.09 | 0.03 | 0.03 | 2.47 |
| ORF | 0.33 | 0.03 | 0.01 | 3.01 |
| PS (%) | 0.14 | 0.04 | 0.02 | 18.43 |
| TNB | 0.17 | 0.01 | 0.09 | 2.88 |
| NBA | 0.16 | 0.03 | 0.08 | 2.89 |

[1] See table1 for the explanations of the traits; [2]parameter standard errors ranged from 0.01 to 0.03

Estimates of phenotypic and genetic correlations are shown in table 3. Phenotypic correlations between ovulation rate at puberty and at fertilization are weakly positive (0.09 to 0.33), whereas negative values were obtained between numbers of corpora lutea on the left and right ovaries (respectively, -0.40 and -0.30 at puberty and at fertilization). Conversely, the genetic correlations between the different ovulation rate measurements were all highly positive (0.7 to 1). Ovulation rate measurements were both phenotypically (-0.05 to -0.36) and genetically (-0.11 to -0.58) correlated with prenatal survival. Phenotypic correlations with litter size at birth were low (<0.22), whereas genetic correlations were moderately positive (0.29 to 0.42 with total ovulation rate). Phenotypic and genetic correlations between prenatal survival and litter size at birth were much higher (>0.65).

**Table 3 - Estimates of phenotypic and genetic correlation between components of litter size**
(phenotypic and genetic correlations below and above the diagonal, respectively).

| Trait | ORPL | ORPR | ORP | ORFL | ORFR | ORF | PS | TNB | NBA |
|---|---|---|---|---|---|---|---|---|---|
| ORPL | - | 0.72 | 0.94 | 0.78 | 0.88 | 0.78 | -0.34 | 0.30 | 0.32 |
| ORPR | -0,40 | - | 0.91 | 0.72 | 0.84 | 0.81 | -0.11 | 0.62 | 0.55 |
| ORP | 0.58 | 0.51 | - | 0.83 | 0.95 | 0.89 | -0.26 | 0.41 | 0.42 |
| ORFL | 0,16 | 0,13 | 0,26 | - | 0.99 | 0.99 | -0.66 | 0.24 | 0.18 |
| ORFR | 0,10 | 0,09 | 0,17 | -0,30 | - | 0.99 | -0.58 | 0.40 | 0.32 |
| ORF | 0,22 | 0,18 | 0,33 | 0,51 | 0,57 | - | -0.45 | 0.41 | 0.29 |
| PS | -0,05 | -0,08 | -0.18 | -0,23 | -0,22 | -0.36 | - | 0.66 | 0.68 |
| TNB | 0,06 | 0,01 | 0.09 | 0,10 | 0,10 | 0.21 | 0.82 | - | 0.99 |
| NBA | 0,06 | 0,01 | 0.06 | 0,10 | 0,08 | 0.20 | 0.78 | 0,89 | - |

Standard errors of genetic correlations ranged from 0.03 to 0.13

Least squares (LS) and mixed model (MM) estimates of responses to selection are shown in figures 1 to 3. Regression coefficients of response to selection on generation number are given in table 4. LS and MM estimates were generally rather consistent. Ovulation rate at puberty and at fertilization regularly increased with generation number in OR line. Regression coefficients of response to selection on generation number were close to 0.5 corpora lutea for both traits. Response to selection tended to be higher in the left than in the right ovary.

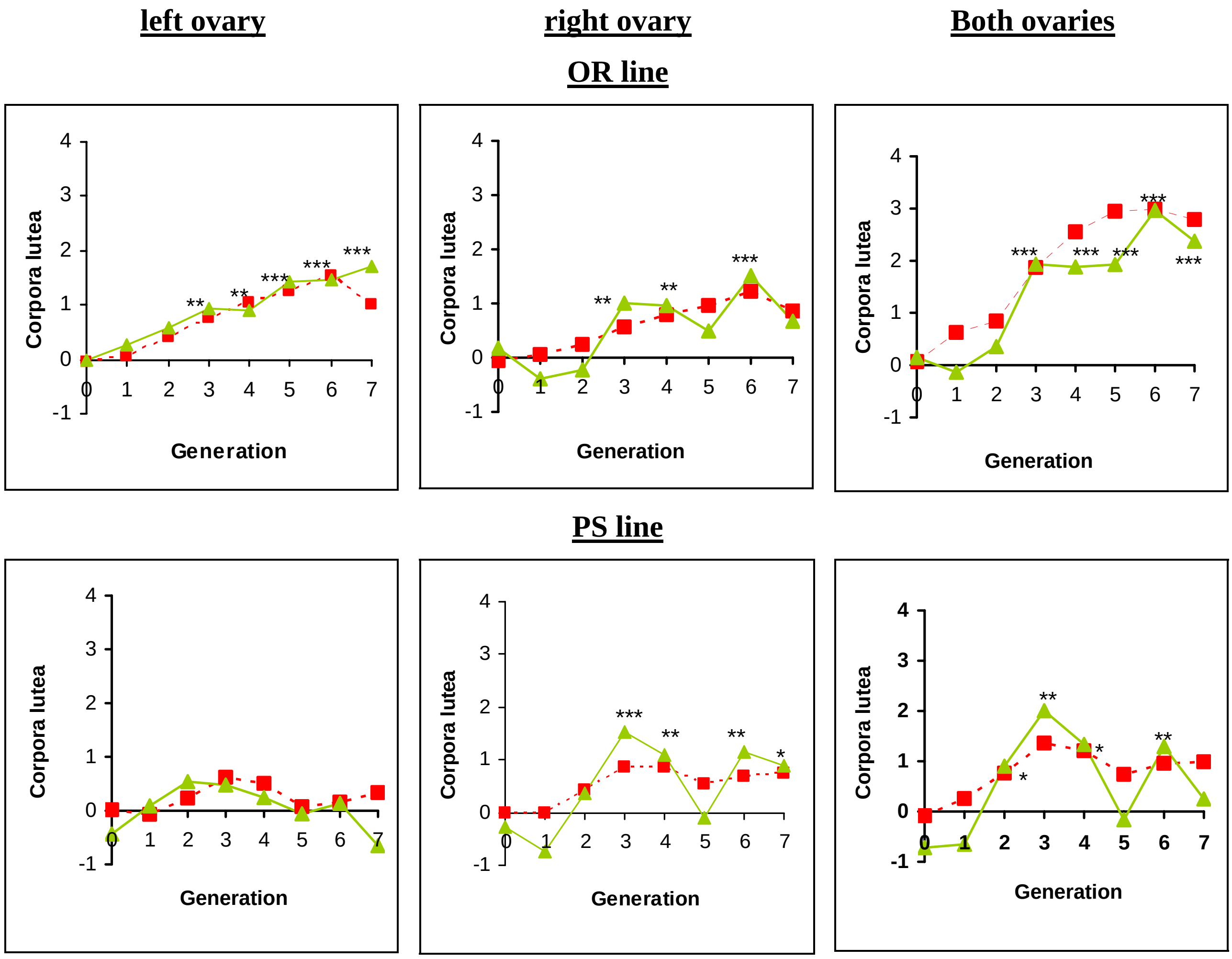
**Table 4 - Least squares and mixed model estimates of response to selection**

| Trait | OR line | | PS line | |
|---|---|---|---|---|
| | Least squares etimate[1] | Mixed Model estimate[2] | Least squares estimate | Mixed Model estimate |
| ORPL | **0.25** | **0.21** | -0.04 | 0.03 |
| ORPR | *0.18* | *0.17* | *0.19* | 0.11 |
| ORP | **0.43** | **0.38** | 0.15 | 0.13 |
| ORFL | **0.24** | **0.20** | 0.05 | 0.02 |
| ORFR | **0.25** | **0.17** | -0.01 | 0.02 |
| ORF | **0.45** | **0.34** | 0.01 | 0.08 |
| PS (%) | -1.29 | -0.61 | 0.93 | 0.57 |
| TNB | 0.07 | 0.09 | 0.23 | 0.18 |
| NBA | 0.01 | 0.06 | 0.16 | 0.15 |

[1] Regression of generation x line differences (selected - control lines) on generation number. [2] Differences (selected - control lines) between regression coefficients of estimated breeding values on generation number. Significant trends are shown in bold (P<0.001) or italic (P<0.01) characters.

OR also increased in PS line during the first 3 generations, particularly at puberty, but decreased in the last generations. The average response/generation was low and non significant at fertilization, but remained significantly positive at puberty. Prenatal survival tended to decreased in OR and slightly increased in PS line, but none of these trends reached significance. As a consequence, realized heritability was highly significant (P<0.001) for ORP ($\hat{h}_r^2$ =0.39±0.08), but did not reach significance (P>0.05) for PS ($\hat{h}_r^2$ =0.10±0.09.

**Figure 1 –** Differences between the average performance of lines selected for ovulation rate at puberty (OR) or prenatal survival (PS) and of the unselected control line at each generation. I – ovulation rate at puberty



* P<0.05; **: P<0.01; ***: P<0.001

## DISCUSSION

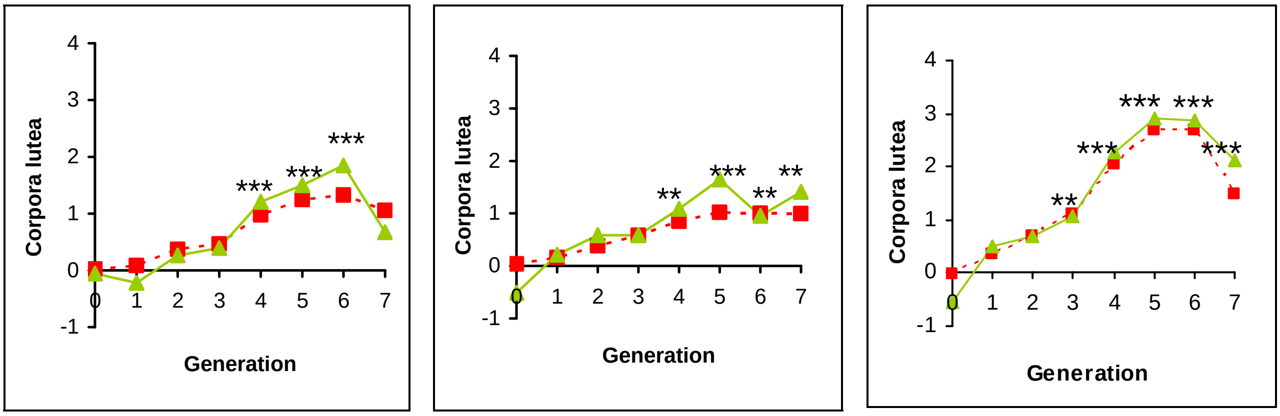
Heritability estimates are generally close to average literature values (Rothschild and Bidanel, 1998). The heritability of PS is similar to the estimates obtained by Johnson et al. (1999) at 50 days of gestation, but larger than the values reported by Gama *et al.* (1991) (also at 50 days of gestation), Bidanel *et al.* (1996) (at 30 days of gestation) and above all Haley and Lee (1992) who obtained no genetic variation in prenatal survival.

The moderate genetic correlations between PS and litter size at birth agree with the estimates obtained in the Nebraska experiment (Neal *et al.*, 1989) and with estimates obtained in rabbits and mice (Clutter *et al.*, 1990; Blasco *et al.*, 1993). The moderately positive genetic correlations between OR and TNB or NBA are very similar to the values obtained at 50 days of gestation in the Nebraska experiment (Neal *et al.*, 1989), but lower than the estimates obtained by Young *et al.* (1977), Bolet *et al.* (1989) and Bidanel *et al.* (1996) at 30 days of gestation. The genetic antagonism between ovulation rate at fertilisation and the subsequent prenatal survival is also much stronger than estimates obtained at 30 days (Young *et al.*, 1977 ; Bolet *et al.*, 1989 ; Bidanel *et al.*, 1996) or 50 days of gestation (Neal *et al.*, 1989). 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 hystero-ovariectomized females (Christenson *et al.*, 1987; Legault *et al.*, 1995). However, as evidenced in rabbits by Argente *et al.* (1997), competition between embryos after implantation does not solely explain variations in litter size, which also largely depend on the pre or peri - implantatory period.

**Figure 2 -** Differences between the average performance of lines selected for ovulation rate at puberty (OR) or prenatal survival (PS) and of the unselected control line at each generation. II – ovulation rate at fertilization

**left ovary** **right ovary** **Both ovaries**

**OR line**



**PS line**

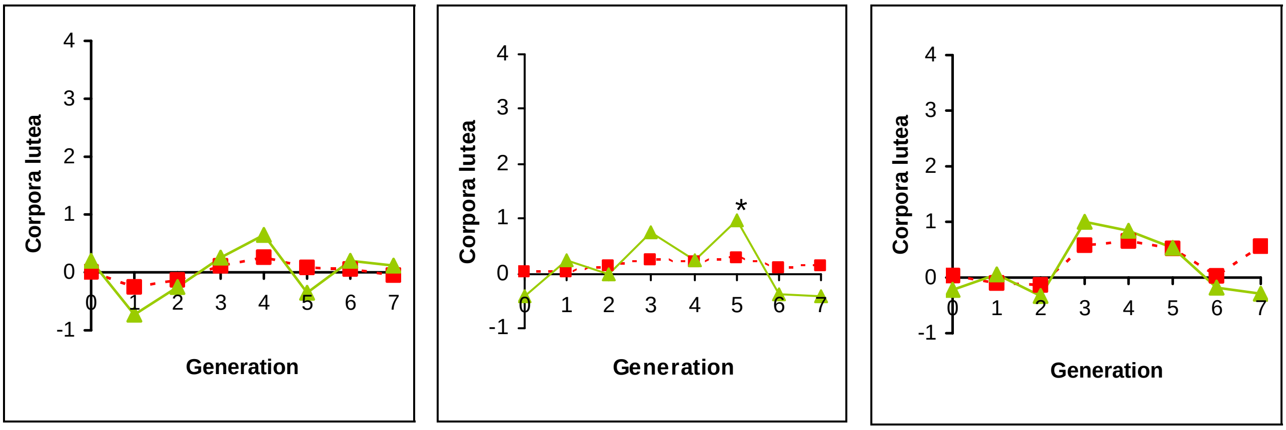
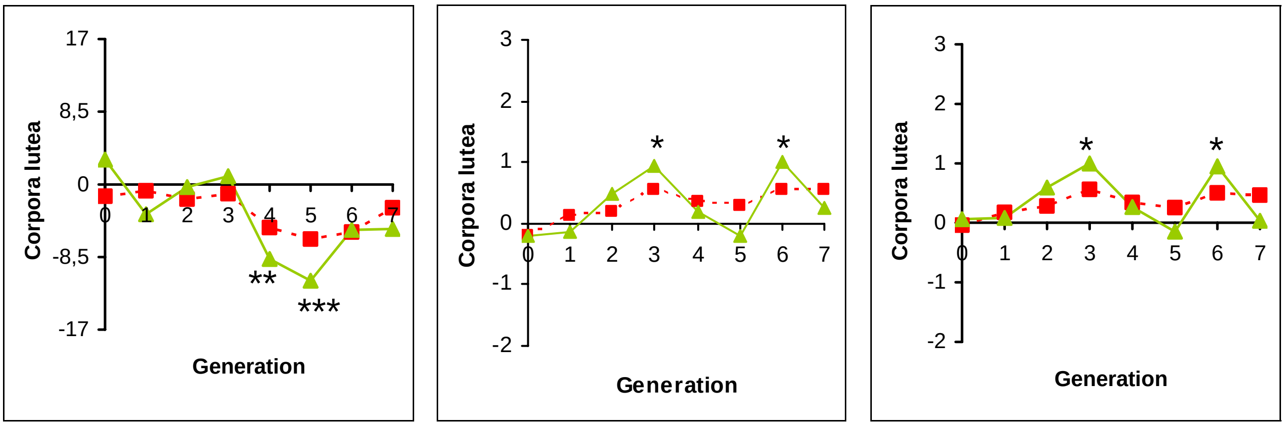


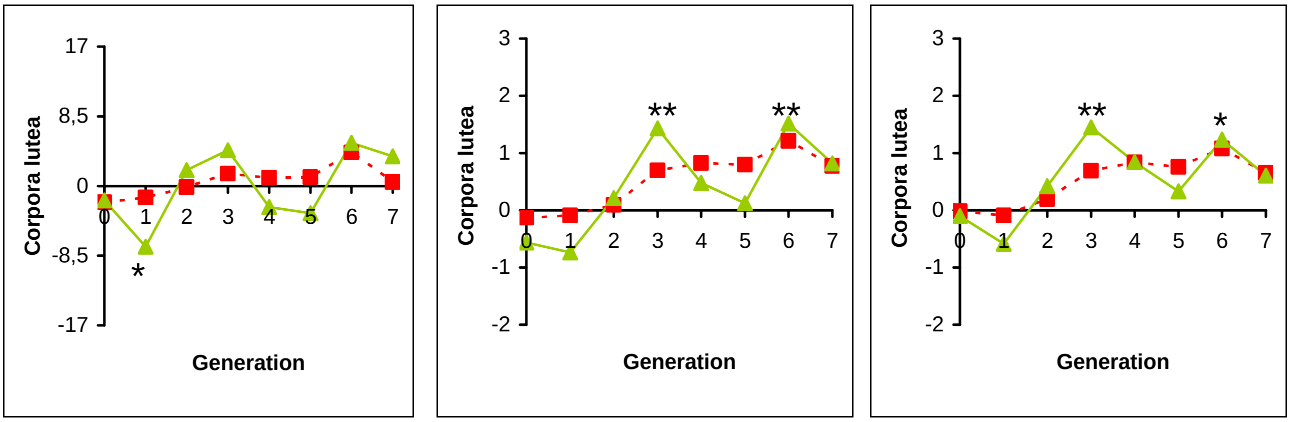
**Figure 3 -** Differences between the average performance of lines selected for ovulation rate at puberty (OR) or prenatal survival (PS) and of the unselected control line at each generation. III – prenatal survival and litter size at birth

**Prenatal survival** **Total number of piglets born** **Number of piglets born alive**

**OR line**



**PS line**



* P<0.05; **: P<0.01; ***: P<0.001

## CONCLUSION

These results confirm that ovulation rate is moderately heritable and can easily be improved through selection, but without any correlated response on litter size. They also show that genetic variation of prenatal survival is rather limited in French *Large White* population, with an heritability estimate which is similar to that of litter size at birth. As a consequence, the interest of ovulation rate and prenatal survival as indirect selection criteria to more efficiently improve litter size is limited in this population.

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