Responses to restricted index selection and genetic parameters for fat androstenone level and sexual maturity status of young boars

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Abstract

A restricted index selection experiment was conducted over four generations in order to investigate whether it is possible to reduce fat androstenone (AND) level with no adverse effect on sexual maturity status in young boars. Fat AND level was measured on a biopsy sample of backfat taken at 118 kg live weight. Sexual maturity status was assessed by bulbo-urethral gland (BUG) thickness measured by echotomography at 99 kg live weight. The experimental design included a control and a select line having a Large White–Landrace genetic background, and both lines were intended to comprise five sires at each generation. A total of 949 boars were recorded for both index traits throughout the experiment. The pattern of direct responses to this ‘antagonistic’ selection differed from expectation, and consisted of no response in fat AND level and a significant positive genetic trend in BUG development. The reasons for this discrepancy are discussed in terms of selection differential being achieved for each index trait (‘index in retrospect’) and deviations of the estimated (by REML) genetic parameters from the expected ones. Heritability estimates were close to 0.50 for fat AND level and 0.60 for BUG development whereas the genetic correlation among them amounted to about 0.65. Moreover, a significant genetic correlation of 0.30–0.40 was found between the sexual maturation of boars and that of related gilts. © 2000 Elsevier Science B.V. All rights reserved.

Keywords: Pig; Intact male; Fat androstenone level; Sexual maturity; Selection experiment

1. Introduction

The adverse effects of castration of male pigs upon growth performance, carcass merit and nitrogen output have been thoroughly investigated. Lean and fat tissue growth rates are approximately increased by a third and decreased by a fifth, respectively, in intact compared to castrated males (Noblet et al., 1994). Castration of male piglets may also cause concern in terms of animal welfare. However, raising intact males for pork production is discouraged in most countries, especially in those having heavier slaughter weights of market pigs.

The reason is that unpleasant off odors (boar taint) occur during cooking of meat from a proportion of intact males, which makes it unacceptable to many
consumers of fresh pork (Malmfors and Lundström, 1983; Diestre et al., 1990; Bonneau et al., 1992). Along with skatole (3-methylindole), the pheromone androstenone (5α-androst-16-en-3-one) is known to be a major chemical compound responsible for the development of boar taint, as reviewed by Bonneau (1998). This lipophilic C19Δ16 steroid, having an intense urine-like odor, is synthesized by the Leydig cells of the testis of sexually mature boars, then released into the blood, and finally stored in the adipose tissue (Brooks and Pearson, 1986).

It was shown by Willeke et al. (1987) and Sellier and Bonneau (1988) that downward selection on fat androstenone (AND) level in boars can be effective. A restricted index selection experiment has been carried out in order to investigate whether it is possible to reduce fat AND levels with no unfavorable effect on the sexual maturity status in young boars. The development of accessory sex glands being under the direct control of androgen and estrogens (Joshi and Raeside, 1973; Booth, 1980), sexual maturity status was appraised by the bulbourethral gland (BUG) size measured on the live animal at a fixed body weight. This article reports on responses to selection and genetic parameters for AND and BUG, which were the two component traits of the selection index, and for a number of other male and female traits.

2. Materials and methods

2.1. Experimental design

A selection experiment was conducted over four generations (G₀–G₄) at the INRA-SESP experimental farm in connection with the INRA-SEIA artificial insemination center (Rouillé, Vienne, France). From a foundation stock (G₀), consisting of 141 Large White × Landrace (F₁) intact males sired by 18 different boars, two lines of boars were established, namely one line kept as control (C) and one select line (S). Each line was intended to comprise five sires in each generation (Table 1), with one boar generation per year. In the line C, replacement boars were randomly chosen (one son per sire). In the line S, replacement boars were selected among those having the greatest values of the two-trait selection index described below.

<table>
<thead>
<tr>
<th>Generation</th>
<th>Sex</th>
<th>Base population</th>
<th>Line C</th>
<th>Line S</th>
</tr>
</thead>
<tbody>
<tr>
<td>G₀</td>
<td>M</td>
<td>141(18,68)</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>G₁</td>
<td>M</td>
<td>69(5,20) 124(5,51)</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>G₂</td>
<td>M</td>
<td>70(5,24) 143(5,57)</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>G₃</td>
<td>M</td>
<td>60(4,16) 130(5,36)</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>G₄</td>
<td>M</td>
<td>69(5,33) 143(5,48)</td>
<td>–</td>
<td>–</td>
</tr>
</tbody>
</table>

* Between brackets, numbers of sires and dams, respectively.

A particular feature of this experiment lies in the mating policy used. In each generation, the selected sires from both lines were put at the INRA AI center in Rouillé during a six-week period (March–April), and semen from these boars was utilized at random for insemination of F₁ sows kept in about 15 herds depending on a single breeding scheme. Each sire of the lines S and C was intended to produce 8–12 and 4–6 litters, respectively. In each generation, 210–230 male and 120–130 female offspring, born from F₁ sows in commercial herds, were put on test contemporarily in the INRA-SESP fattening facilities. So, only the sire-son pathway of gene transmission was exploited for selection, with an expected intensity of selection (i) close to 2.2 at each generation in the line S (proportion selected was 5 out of around 135 candidate boars). Due to mating boars to an unselected dam population, the expected cumulative intensity of selection after n generations was $i_n = 2i(1 - 1/2^n)$ for the sire-son pathway. The realized cumulative intensity of selection after four generations amounted to 3.6 for the sire-son pathway, and was therefore slightly less than the expected value of 4.1.

2.2. Selection index

The criterion of selection used in the line S was an index combining the following two traits:

1. the average thickness of right and left BUG (TBUG1, in mm) measured by echotomography using a rectal probe on the live animal at
99.1±2.7 kg body weight (BW). Average age at measurement was 162 days. The phenotypic correlation of that live thickness measurement with the BUG weight recorded after slaughter a few days later was 0.86 in a sample of 175 boars (Sellier et al., 1993).

2. The AND level (AND2) of a small biopsy sample of backfat taken in the neck region at 117.6±2.4 kg BW (average age was 185 days). The radioimmunoassay procedure described by Bonneau and Russeil (1985) was used for determination of AND2 (as μg/g ether extract). A logarithmic transformation was applied owing to the marked skewness of the frequency distribution of raw AND2 data, and the variable included in the selection index was LAND2 = log(AND2×10^2).

The selection index used in this experiment (I = 100+4×TBUG1−63×LAND2) was constructed with the objective of reducing LAND2 while maintaining a normal sexual maturity status of young boars, i.e. no expected genetic change in weight of bulbo-urethral glands. A set of phenotypic and genetic parameters was derived from earlier studies (Bonneau and Sellier, 1986; Sellier and Bonneau, 1988), and it was assumed that heritability was 0.4 for TBUG1 and 0.6 for LAND2, and phenotypic and genetic correlations between the two traits were 0.5.

As shown in Table 1, a total of 949 boars, from 57 sires and 353 dams, were recorded for both index traits through the generations G₀−G₁.

### 2.3. Traits

Beside TBUG1 and LAND2, a number of traits were recorded at generations G₁−G₄ in males and/or females from both lines. Male and female offspring entered the INRA-SESP farm at about 25 kg BW. They were raised in single-sex pens of ten animals, with boars and gilts housed in different open-fronted buildings. Animals were given ad libitum access to a pelleted grower diet in self-feeders, and average daily gain (ADG) was recorded as the daily BW gain and 4 values, respectively, from 31.5 to 98.9 kg. Live backfat thickness (BFAT) was recorded at 98.9±2.5 kg BW as the average value of six ultrasonic measurements taken on either side of the spine, 4 cm from the mid-line at the shoulder, last rib and hip joint levels, respectively.

In male offspring from the generations G₁−G₄, a biopsy of backfat was taken at 99.1±2.7 kg BW for determination of fat AND level (AND1). The boars not kept for breeding were slaughtered in a commercial abattoir at 122.7±3.8 kg BW (average age was 194 days). Male genital tract was removed on the slaughter line for further dissection according to Bonneau and Russeil (1985). Total weight (WBUG2) and the average length (LBUG2) of bulbo-urethral glands and the total weight of testes (WTES2) were recorded.

In female offspring (54–60 gilts per line and generation, Table 1), the daily detection of first oestrus began at 140 days of age and continued until they reached either puberty or 115 kg BW. Puberty was defined as the occurrence of a standing response to a teaser boar. Puberal gilts (n=115) were slaughtered within the 10 days following the first heat in order to check the presence of ovarian corpora lutea, and their genital tract was removed on the slaughter line and then dissected as described by Legault (1969). Corpora lutea were counted for assessing ovulation rate. The gilts having not expressed puberty (n=340) were slaughtered at 116.8±3.2 kg (average age was 201 days), and were submitted to the same genital tract measurements as the puberal gilts. Postmortem examination of ovaries showed that neither silent nor false first heats occurred in the course of the experiment.

In an attempt to ascertain whether a non-puberal gilt was near to her first oestrus, a linear function (L) of four genital tract records (total weight and average length of uterine horns, total weight of ovaries and weight of vagina+uterine cervix), which made it possible to completely discriminate puberal and non-puberal gilts, was developed by using the procedure CANDISC of SAS (1989). On the basis of individual L values, the non-puberal gilts were divided into three classes, and an ordered categorical variable (GPUBS, ‘gilt puberty status’) was defined as follows: 1,2,3=gilts assumed to be far from, rather close to or very close to the first oestrus (25% lower, 50% medium or 25% higher L values, respectively), and 4=puberal gilts.

### 2.4. Statistical analysis

The coefficients of the ‘index-in-retrospect’ (Berger and Harvey, 1975) actually used in each generation in choosing sires of the line S were
calculated from the weighted selection differentials achieved for each of the index traits, the weighting factor being the number of sons recorded per sire.

Direct and correlated responses to selection for male traits, ADG and BFAT were estimated by using the procedure GLM of SAS (1989). The model included the fixed effects of line, generation (year) and line × generation interaction, as well as the fixed effects of sex and sex × line interaction for ADG and BFAT, and a covariate as appropriate (weight on test for ADG and weight at measurement for BFAT and male traits). Data on the proportion of puberal gilts at 116.8 kg BW and the categorical GPUBS variable were analyzed according to Grizzle et al. (1969). Analysis was based on logits using the maximum likelihood method available in the procedure CATMOD of SAS (1989).

Variance-covariance components were estimated by using a restricted maximum likelihood (REML) procedure applied to a multivariate individual animal model. The model varied depending on the trait as mentioned above, but the basic mixed model included the fixed effect of generation (year) and the random effects of litter of birth and additive genetic value of the animal. Suitable Box–Cox power transformations were performed for fat AND data (BCAND1 and BCAND2) using the following formula (MacLean et al., 1976): $y = \left(\frac{r}{p}\right)\left(\frac{x}{r+1}\right)^p - 1$ where $y$ and $x$ are transformed and raw values, respectively, $r = 10$ and $p = -19.3$.

A series of three- or four-trait analyses were performed using the version 4.2 of the vce software package (Neumaier and Groeneveld, 1998). All vce runs comprised the traits TBUG1 and BCAND2 in order to account for the effects of the selection being achieved on these traits (see Hofer, 1998) There were 1935 animals in the pedigree file going back to the parents of the foundation population. Approximate standard errors of estimated genetic parameters were obtained from an approximation of the Hessian matrix when convergence was reached.

3. Results

3.1. Direct and correlated responses to selection

The trends displayed by the select line compared to the control line are presented in Fig. 1 for LAND2 and TBUG1. There was no significant change across generations in the difference between select and control lines in fat AND level at 117.6 kg BW. In contrast, a significant increase in the difference between select and control lines in average BUG thickness at 99.1 kg BW occurred, mainly from the third generation of selection. The pattern of direct responses to selection clearly differed from that intended when defining the breeding goal, i.e. reducing LAND2 while holding TBUG1 constant. One of the reasons contributing to this unexpected result lies in that the 'index-in-retrospect' actually applied in each generation (except the first one) gave a higher weighting to TBUG1 than intended, as shown in Table 2. Over the four generations of selection, the average realized relative weight of TBUG1 compared to LAND2 (when expressing the traits in SD units) was 1.12 instead of the intended value of 0.76.

Correlated responses in LAND1 and WBUG2 (Table 3) were in general agreement with those found for LAND2 and TBUG1, respectively. No
response to selection was observed for fat AND level at 99.1 kg BW (LAND1). A significant positive trend occurred in line S for BUG weight at 122.7 kg BW (WBUG2), and was similar to that displayed by BUG size at 99.1 kg BW (TBUG1). Weight of testes at 122.7 kg BW (WTES2) was consistently greater in the select than in the control line through the generations G1 to G4, but the line difference was significant only at generation G1.

The overall proportion of gilts having shown first oestrus prior to 116.8 kg BW was 0.25 in this experiment. The proportion of puberal gilts was higher whatever the generation in line S compared to line C (0.35 vs. 0.16, on average), and the line difference in this trait was significant at generations G1 and G2 (Table 4). Regarding the ovulation rate at the pubertal oestrus, line S (14.2±0.3, n = 79) did not significantly differ from line C (14.7±0.4, n = 36) whatever the generation.

There were no significant correlated responses to selection in ADG and BFAT (results not shown).

3.2. Estimated genetic parameters

The REML-estimated parameters pertaining to nine traits recorded in this experiment are presented in Table 5 for heritabilities (h²) and common litter environment effects (c²), and in Table 6 for phenotypic (r_p) and genetic (r_g) correlations. The traits BCAND2 and TBUG1 showed similar heritabilities, a positive phenotypic correlation, and a close genetic correlation of 0.66±0.06. The h² estimate for BCAND1 did not differ from that for BCAND2, and the two traits were closely correlated both at the phenotypic and genetic levels. Similarly,

Table 2

<table>
<thead>
<tr>
<th>Generation</th>
<th>w1 (TBUG1)</th>
<th>w2 (LAND2)</th>
<th>RRW1</th>
</tr>
</thead>
<tbody>
<tr>
<td>G1</td>
<td>1.59</td>
<td>-2.63</td>
<td>0.60</td>
</tr>
<tr>
<td>G2</td>
<td>2.03</td>
<td>-1.68</td>
<td>1.21</td>
</tr>
<tr>
<td>G3</td>
<td>1.90</td>
<td>-1.20</td>
<td>1.58</td>
</tr>
<tr>
<td>G4</td>
<td>1.71</td>
<td>-1.61</td>
<td>1.06</td>
</tr>
</tbody>
</table>

* RRW1 is the realized relative weighting for TBUG1 (absolute value of the ratio of w1 to w2). The relative weighting for TBUG1 was 0.76.

Table 4

<table>
<thead>
<tr>
<th>Generation</th>
<th>Control line</th>
<th>Select line</th>
<th>Significance of the line difference</th>
</tr>
</thead>
<tbody>
<tr>
<td>G1</td>
<td>15.8</td>
<td>24.1</td>
<td>-</td>
</tr>
<tr>
<td>G2</td>
<td>8.9</td>
<td>33.3</td>
<td>**</td>
</tr>
<tr>
<td>G3</td>
<td>15.8</td>
<td>40.7</td>
<td>**</td>
</tr>
<tr>
<td>G4</td>
<td>23.2</td>
<td>40.4</td>
<td>-</td>
</tr>
</tbody>
</table>

** = P<0.01.

Table 3

<table>
<thead>
<tr>
<th>Line differences' (select-control) across generations in fat androstenone level at 99.1 kg BW (LAND1) and male genital tract measurements at 122.7 kg BW (LBUG2, WBUG2, WTES2)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Generation</td>
</tr>
<tr>
<td>------------</td>
</tr>
<tr>
<td>G1</td>
</tr>
<tr>
<td>G2</td>
</tr>
<tr>
<td>G3</td>
</tr>
<tr>
<td>G4</td>
</tr>
</tbody>
</table>

* Differences expressed in SD units of the trait.
* = P<0.05, ** = P<0.01, *** = P<0.001.
Table 6
Estimates of phenotypic and genetic correlations\(^a\) among fat androstenone levels (BCAND1, BCAND2), male genital tract measurements (TBUG1, LBUG2, WBUG2, WTES2), gilt puberty status (GPUBS), average daily gain (ADG) and backfat thickness (BFAT)

<table>
<thead>
<tr>
<th>Trait</th>
<th>BCAND1</th>
<th>BCAND2</th>
<th>TBUG1</th>
<th>LBUG2</th>
<th>WBUG2</th>
<th>WTES2</th>
<th>GPUBS</th>
<th>ADG</th>
<th>BFAT</th>
</tr>
</thead>
<tbody>
<tr>
<td>BCAND1</td>
<td>0.97</td>
<td>–</td>
<td>0.65</td>
<td>0.34</td>
<td>0.58</td>
<td>0.47</td>
<td>0.22</td>
<td>0.04</td>
<td>0.11</td>
</tr>
<tr>
<td></td>
<td>(0.02)</td>
<td>(0.06)</td>
<td>(0.08)</td>
<td>(0.06)</td>
<td>(0.08)</td>
<td>(0.09)</td>
<td>(0.14)</td>
<td>(0.12)</td>
<td></td>
</tr>
<tr>
<td>BCAND2</td>
<td>0.71</td>
<td>–</td>
<td>0.66</td>
<td>0.54</td>
<td>0.68</td>
<td>0.41</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td></td>
<td>(0.06)</td>
<td>(0.10)</td>
<td>(0.07)</td>
<td>(0.08)</td>
<td>(0.13)</td>
<td>(0.12)</td>
<td>(0.09)</td>
<td>(0.08)</td>
<td></td>
</tr>
<tr>
<td>TBUG1</td>
<td>0.37</td>
<td>0.38</td>
<td>–</td>
<td>0.83</td>
<td>0.93</td>
<td>0.54</td>
<td>0.41</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td></td>
<td>(0.03)</td>
<td>(0.07)</td>
<td>(0.07)</td>
<td>(0.07)</td>
<td>(0.12)</td>
<td>(0.09)</td>
<td>(0.08)</td>
<td>(0.08)</td>
<td></td>
</tr>
<tr>
<td>LBUG2</td>
<td>0.30</td>
<td>0.42</td>
<td>0.60</td>
<td>–</td>
<td>0.90</td>
<td>0.26</td>
<td>0.12</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td></td>
<td>(0.07)</td>
<td>(0.03)</td>
<td>(0.07)</td>
<td>(0.12)</td>
<td>(0.11)</td>
<td>(0.11)</td>
<td>(0.15)</td>
<td>(0.15)</td>
<td></td>
</tr>
<tr>
<td>WBUG2</td>
<td>0.35</td>
<td>0.51</td>
<td>0.80</td>
<td>0.84</td>
<td>–</td>
<td>0.46</td>
<td>0.34</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td></td>
<td>(0.07)</td>
<td>(0.15)</td>
<td>(0.15)</td>
<td>(0.13)</td>
<td>(0.13)</td>
<td>(0.13)</td>
<td>(0.13)</td>
<td>(0.13)</td>
<td></td>
</tr>
<tr>
<td>WTES2</td>
<td>0.18</td>
<td>0.22</td>
<td>0.26</td>
<td>0.32</td>
<td>0.37</td>
<td>–</td>
<td>0.45</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td></td>
<td>(0.10)</td>
<td>(0.09)</td>
<td>(0.11)</td>
<td>(0.10)</td>
<td>(0.09)</td>
<td>(0.09)</td>
<td>(0.09)</td>
<td>(0.09)</td>
<td></td>
</tr>
<tr>
<td>GPUBS</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>0.58</td>
<td>0.02</td>
</tr>
<tr>
<td></td>
<td></td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>(0.10)</td>
<td>(0.09)</td>
</tr>
<tr>
<td>ADG</td>
<td>0.13</td>
<td>–0.06</td>
<td>–0.16</td>
<td>–0.15</td>
<td>–0.22</td>
<td>–0.13</td>
<td>–0.16</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td></td>
<td>(0.12)</td>
<td>(0.12)</td>
<td>(0.12)</td>
<td>(0.12)</td>
<td>(0.12)</td>
<td>(0.12)</td>
<td>(0.12)</td>
<td>(0.12)</td>
<td></td>
</tr>
<tr>
<td>BFAT</td>
<td>0.12</td>
<td>0.18</td>
<td>–0.19</td>
<td>–0.10</td>
<td>–0.13</td>
<td>–0.12</td>
<td>0.04</td>
<td>0.29</td>
<td>–</td>
</tr>
</tbody>
</table>

\(^a\) Phenotypic correlations below the diagonal, genetic correlations (SE between brackets) above the diagonal.

The \(h^2\) estimates for WBUG2 and TBUG1 were of the same order and the two traits were highly correlated. Heritability of testes weight (WTES2) was similar to that of WBUG2, whereas the genetic association of WTES2 with BUG size measurements was of medium magnitude. The genetic correlation of fat AND level (BCAND1 or BCAND2) with BUG size (TBUG1 or WBUG2) was of the same order whatever the respective stages of measurement of the two traits. The \(h^2\) estimate for gilt puberty status (GPUBS) was about 0.50, and this trait showed positive genetic correlations with TBUG1, WBUG2 and WTES2. There was a significant negative genetic relationship between GPUBS and ADG. The phenotypic and genetic correlations of fat AND levels with ADG and BFAT were of small magnitude. The two latter traits showed moderate negative genetic correlations with male genital tract measurements.

4. Discussion

The primary incitement to perform the present experiment came from the fairly encouraging results obtained by Sellier and Bonneau (1988) in a single-generation selection experiment. This earlier experiment comprised a control line, a line selected for low fat AND level and small testis size (‘agonistic’ selection), and a line selected for low fat AND level and large testis size (‘antagonistic’ selection). The responses found in the latter line, i.e. a significant decline of fat AND level and no genetic change in weights of testes and bulbo-urethral glands, suggested that it would be feasible by breeding to reduce fat AND level without adversely affecting sexual maturity status in boars. The study reported here was designed for confirming this finding over a greater number of generations of selection while replacing testis size by the development of accessory sex glands (BUG) for appraising the stage of sexual maturation attained by young boars at a fixed body weight.

4.1. Responses to selection

4.1.1. Direct responses

Using a restricted selection index has resulted in realized genetic trends for each component trait which disagreed with expectation. Such unexpected patterns of responses to ‘antagonistic’ selection are not unusual in the studies relying on selection indices with constraint. Some restricted index selection experiments have been successful in mice, and
showed both significant changes in the trait selected for and no or little change in the restricted trait (e.g. Atchley et al., 1997). However, there are several studies in which unintended responses in the component traits of the restricted selection index occurred (for references, see Eisen, 1992). The present experiment exemplifies a typical case, i.e. the trait selected downward (AND) did not noticeably change while the restricted trait (BUG size) showed a significant positive response to selection.

Restricted index selection appears to be very sensitive to the degree of accordance of expected with true genetic parameters involved in the selection index. Here, the genetic parameters as estimated by a REML analysis of data from the whole experiment somewhat differed from those inferred for constructing the selection index. In particular, the REML-estimated heritability of TBUG1 was noticeably higher than the expected one \((h^2 = 0.63 \text{ vs. } 0.40)\), which has ‘favoured’ the response in this trait in comparison with LAND2. In addition, the two index traits were revealed as exhibiting a slightly closer genetic correlation than expected \((0.66 \text{ vs. } 0.50)\). This discrepancy between expected and true values of genetic correlation is likely to have reduced the negative response in LAND2 due to a larger than expected counteracting effect of the upward selection pressure achieved on TBUG1. Given the REML-estimated genetic parameters of the two index traits, the selection index to be used should have put less emphasis on TBUG1 for having an effective restriction of zero genetic gain in bulbo-urethral gland development.

As already mentioned, another factor which has probably contributed to the unexpected responses in the index traits refers to the realized selection differentials for each trait. Considering the ‘average’ index actually applied over the four generations of selection, the weighting given to TBUG1 relative to LAND2 was almost 50% higher than expected. The indices in retrospect greatly varied among generations. This occurred partly by chance due to the small number of sires selected in each generation. However, it should be noted that our experimental population whose genetic background was half Large White–half Landrace exhibited a smaller mean value and a lower phenotypic variability of fat AND level than could be expected from our previous studies with Large White purebred boars. This has resulted in a relatively small selection pressure on this trait, except in the first generation.

4.1.2. Correlated responses

The trends found in the select line for fat androstenone level and bulbo-urethral gland development were similar for both stages of measurement, in agreement with the very high genetic correlations between homologous traits. The correlated response observed in females of the select line, i.e. an increased percentage of gilts showing first oestrus prior to 116.8 kg BW, is in line with the earlier sexual maturity of the males of this line (as demonstrated by the greater development of BUG). This suggests that, provided that the weightings of TBUG1 and LAND2 are correctly balanced in the selection index (see above), it is probably possible to reduce fat androstenone levels with no adverse effect on sexual maturity of both males and females by using BUG development as an estimate of sexual maturity status. On the contrary, selection against androstenone with no consideration of sexual development (Willeke et al., 1987) or using testes development as an estimate of sexual maturity status (Sellier and Bonneau, 1988) resulted in a delay in the sexual maturity of related females.

4.2. Genetic parameters

4.2.1. Fat androstenone level

Regarding fat AND level, the genetic parameters estimated in the present study are in general agreement with those published earlier (Jonsson and Andresen, 1979; Bonneau and Sellier, 1986; Willeke et al., 1987; Sellier and Bonneau, 1988; Willeke and Pirchner, 1989). The \(h^2\) estimates for BCAND1 and BCAND2 are very close to the average literature value of 0.56 quoted by Sellier (1998). Fat AND levels and growth rate were poorly associated both at the phenotypic and genetic level. It should however be mentioned that Willeke and Pirchner (1989) found positive realized genetic correlations of about 0.35 between fat AND levels and body weights at various fixed ages. The genetic independence found here between fat AND level and backfat thickness is consistent with the lack of any genetic trend for backfat thickness in the select line.
4.2.2. Sexual maturity of boars

Among the genital tract measurements utilized for assessing sexual maturation in young boars, testis size has been by far the most studied on genetic grounds (e.g. Legault et al., 1979; Toelle et al., 1984; Sellier and Bonneau, 1988; Johnson et al., 1994). Our heritability estimate for testes weight falls within the range of values previously published for various traits pertaining to testicular development at fixed body weights or, most often, at fixed ages. It is, however, well above the average literature values of 0.33–0.44 quoted by Rothschild and Bidanel (1998) for heritability of testis width, length or weight. The same authors concluded from their literature review that a positive genetic correlation of about 0.50 exists between ADG and testis size when the latter trait is measured at constant age, whereas available results are more discordant when testis size is measured at constant weight. In the present study, all male genital tract measurements (performed at fixed BW) exhibited a moderate negative genetic association with ADG. Sexual maturation of the young boar therefore appears to be differently associated with growth rate depending on whether it is assessed at constant age or at constant weight. Regarding the genetic relationship of testis size with backfat thickness, our study showed a moderate negative correlation between the two traits. This result is in line with that of Toelle et al. (1984), but not with the very low or slightly positive genetic correlations reported by Young et al. (1986), Lubritz et al. (1991) and Johnson et al. (1994).

4.2.3. Association of fat androstenone level with sexual maturity of boars

The close genetic relationship found here between fat AND level and BUG or testis size confirms the previous findings of Bonneau and Sellier (1986) and Sellier and Bonneau (1988). One may put forward that the genetic correlation of fat AND level with the sexual maturity status of the boar is equal or superior to 0.50. Highly significant phenotypic correlations, ranging from 0.30 to 0.70, have been repeatedly reported among the same traits (e.g. Forland et al., 1980; Bonneau and Russeil, 1985; Xue et al., 1996; Andersson et al., 1997). These correlations result from the fact that the sexual maturity of boars is associated with a dramatic increase in the production of all testicular steroids including androstenone, androgens and oestrogens, the latter two being responsible for the development of bulbo-urethral glands (Joshi and Raeside, 1973; Booth, 1980).

4.2.4. Puberty in females

The current $h^2$ estimate of 0.53 for the gilt puberty status variable is in the range of the $h^2$ values previously found for the age at puberty of gilts, while being noticeably higher than the average literature value of 0.33 quoted by Rothschild and Bidanel (1998). It should however be noted that heritability was higher for weight than for age at puberty (0.51 vs. 0.29) in the study of Bidanel et al. (1996). A close negative genetic correlation was found in the present study between ADG and GPUBS. This result agrees with the finding by Bidanel et al. (1996) of a moderate positive genetic association of growth rate with weight at puberty in gilts. The genetic independence found here between backfat thickness and gilt puberty status is in line with average literature results (Rothschild and Bidanel, 1998).

4.2.5. Genetic association of male with female puberty traits

Fat AND levels in boars were poorly genetically linked with gilt puberty status in the present study. As already mentioned, the studies of Willeke et al. (1987) and Sellier and Bonneau (1988) concurred to show a markedly positive genetic association among the fat AND level in young boars and sexual precocity in gilts. The genetic relationship between sexes for attainment of puberty was found to be near zero in some studies (Schinckel et al., 1983; Sellier and Bonneau, 1988; Johnson et al., 1994), but it was positive in other studies (Bates et al., 1986; Young et al., 1986). The present experiment shows a significant genetic correlation of 0.30–0.40 between sexual maturation of males, as assessed by the development of testes and accessory sex glands at constant BW, and sexual maturation of females, as assessed by the categorical ‘gilt puberty status’ variable.

5. Conclusion

This study confirms that fat androstenone level in young boars is a highly heritable trait, which exhibits a strongly positive genetic correlation with the
development of bulbo-urethral glands. The latter trait showed a higher heritability value than that assumed for constructing the restricted selection index used throughout the experiment. This feature partly explains that the pattern of direct responses to selection differed from expectation. Another reason lies in that the average weighting given to bulbo-urethral gland development in the selection actually performed was higher than expected. Moreover, the present study gave evidence for a significant genetic relationship between sexes with respect to sexual maturation, as shown by the REML estimate of genetic correlation and the similar genetic trends for sexual maturity status of boars and gilts.

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