Genetic parameters for androstenone, skatole, indole, and human nose scores as measures of boar taint and their relationship with finishing traits


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ABSTRACT: The purpose of this study was to evaluate measures of boar (Sus scrofa) taint as potential selection criteria to reduce boar taint so that castration of piglets will become unnecessary. Therefore, genetic parameters of boar taint measures and their genetic correlations with finishing traits were estimated. In particular, the usefulness of a human panel assessing boar taint (human nose score) was compared with chemical assessment of boar taint compounds, androstenone, skatole, and indole. Heritability estimates for androstenone, skatole, and indole were 0.54, 0.41, and 0.33, respectively. The heritability for the human nose score using multiple panelists was 0.12, and ranged from 0.12 to 0.19 for individual panelists. Genetic correlations between scores of panelists were generally high up to unity. The genetic correlations between human nose scores and the boar taint compounds ranged from 0.64 to 0.999. The boar taint compounds and human nose scores had low or favorable genetic correlations with finishing traits. Selection index estimates indicated that the effectiveness of a breeding program based on human nose scores can be comparable to a breeding program based on the boar taint compounds themselves. Human nose scores can thus be used as a cheap and fast alternative for the costly determination of boar taint compounds, needed in breeding pigs without boar taint.

Key words: animal welfare, boar taint, genetics, pigs

INTRODUCTION

Male piglets are usually castrated to prevent the development of an unpleasant smell of their meat called boar taint. The castration is generally performed without analgesia or anesthesia, causing pain to the piglets and thus raising animal welfare concerns. This concern is on the increase; a ban on castration of piglets in most European countries is expected in the coming years (Pig Progress, 2010). Consequently, alternatives are needed and one possibility is to genetically select pigs for a low incidence of boar taint.

The main compounds responsible for boar taint are androstenone, skatole, and indole. Moderate to high heritabilities and differences between sire lines have been reported for these compounds (Merks et al., 2009). Consequently, breeding seems a promising way to produce pigs without boar taint. However, the compounds do not completely capture the variation in boar taint perception by consumers (Heid and Hamm, 2009). Moreover, in-line slaughter detection of these compounds at slaughter line speed and at an acceptable cost is not possible. An alternative is to use a score based on boar taint odor called human nose score.

The effectiveness of the human nose score for breeding pigs without boar taint depends in the first place on its heritability. In the second place, scoring between panelists should be consistent on the genetic level. In other words, the genetic correlations of human nose scores by different panelists need to be strong (i.e., the genetic ability of a pig to produce an odor perceived by a panelist as boar taint needs to be highly correlated to its ability to produce an odor perceived by another panelist as boar taint). Finally, the success of a breeding program will also depend on the relationship of the human nose scores with other economically important traits.
The objective of this study was to estimate the heritability of the boar taint compounds as well as the human nose score, and the genetic correlations among them, and to evaluate their consistency across panelists. In addition, genetic correlations of boar taint compounds and human nose score with finishing traits are estimated.

**MATERIALS AND METHODS**

Animal Care and Use Committee approval was not required for this study because data collected regularly in the TOPIGS breeding program (Vught, the Netherlands) were used. The TOPIGS breeding program operates according to the EFABAR code of conduct (Neeteson-van Nieuwenhoven et al., 2006).

The data included records on finishing pigs from 4 purebred sire lines with Duroc, Large White, and Pietrain backgrounds, three dam lines with Landrace and Yorkshire backgrounds, and crossbreds of these dam lines and purebred sire lines.

**Boar Taint Compounds**

Laboratory measurements of the concentration of the boar taint compounds androstenone, skatole, and indole in carcass fat samples were available. Fat samples were taken post-slaughter from the neck area of the left hand side of the carcass and were stored under vacuum at −20°C. The assays for estimation of androstenone, skatole, and indole were initially conducted at the Norwegian School of Veterinary Science (NSVS) in Oslo, Norway, and later at Co-operative Central laboratory (CCL-Nutricia) in Veghel, the Netherlands. At NSVS the concentrations of androstenone were determined by time-resolved fluoro-immunoassay as described by Tuomola et al. (1997), while at CCL gas chromatography-mass spectrometry (GC-MS) according to Verheyden et al. (2007) was used. More details about the methods used are available in Ampuero et al. (2011). At both laboratories, skatole and indole were extracted from the fat sample using a mixture of methanol and hexane at 40°C in an ultrasonic bath. Skatole and indole were separated by HPLC on a reversed phase column. Fluorescence was measured at 285 and 340 nm.

Androstenone and indole were lognormally distributed, and therefore the log of the concentrations of these compounds were analyzed. Although skatole was approximately lognormally distributed, a mixture of 3 lognormal distributions described the data better than a single distribution. The observed peak of the overall distribution of skatole fell within the first distribution, and the other 2 distributions explained the extended tail and the region where the peak and tail of the observed distribution interfaced. Therefore, both the log (skatole) was analyzed as well as the probability of a record not belonging to the first lognormal distribution (probability of high skatole).

The original data set contained 7,679 entire males with observations on androstenone, skatole, or indole concentration. Records that did not have observations on all 3 concentration traits or that had no HCW were discarded. Further edits applied were: HCW and age at slaughter associated with the observation had to lie within 3 SD of the mean value and each observation had to belong to a farm-line-week of slaughter group containing at least 5 records. After editing, 7,336 records remained.

**Human Nose Score**

A human nose score was used to evaluate the link between boar taint compounds and boar taint as perceived by humans. Scoring was carried out by 9 trained panelists in a controlled environment. Carcass fat samples were heated with a hot iron to release the smell normally experienced during cooking. The panelist then assigned a score from 0 (no detectable boar taint odor) to 4 (strong boar taint odor). The fat sample from each pig was independently scored by 3 panelists. During a typical session samples from around 100 pigs were scored individually and independently by 3 panelists. Occasionally, samples were scored by 6 panelists.

In total, 20,457 human nose score observations on 6,072 entire males were available. These data were edited such that HCW and age at slaughter of the pigs were within 3 SD of their respective means and all lines or crosses were represented by at least 10 pigs. Records were grouped according to scoring date within farm of birth and line (farm/line/day groups) and according to panelist within scoring date (panelist/day groups). Records in farm/line/day and panelist/day groups containing less than 5 observations were removed from the data. After this editing, all farm/line/day groups and panelist/day groups contained 2 or more different scores, and a total of 20,130 records on 5,971 pigs remained.

**Finishing Traits**

The finishing traits were ADG, carcass back fat depth (mm), and carcass loin depth (mm). Records on ADG, carcass fat depth, and carcass loin depth were considered from pigs which had phenotypic records on either boar taint compounds or human nose scores, their male or female full- and half-sibs, and all contemporaries of these pigs. These data consisted of 18,376 records across lines and crosses on males, females, and castrates. Data were edited such that HCW and age at slaughter lay within 3 SD of their respective means, and records from farm of birth \times sex \times line \times month of slaughter groups...
containing less than 5 observations were removed from the data set to leave 17,885 records for consideration in the analyses.

**Pedigree Data**

The pedigree used in the genetic analyses traced back 5 generations from pigs with observations on human nose scores, boar taint compounds, or carcass traits. This pedigree contained 32,573 animals, including 18,737 pigs with observations on traits. The latter were offspring of 770 sires and 2,425 dams, and grand-offspring of 844 sires and 1,815 dams.

**Genetic Analysis**

Genetic parameters were estimated using animal models. Before the animal model analyses, preliminary multiple regression analyses were used to assess the importance of litter of birth effects and to generate better starting values for bivariate analyses between the various traits.

**Boar Taint Compounds.** In preliminary linear multiple regression analyses, the purebred line or 3-way cross to which a pig belonged, farm of birth, laboratory carrying out the boar taint assays, and the week in which the pig was slaughtered and sampled all had highly significant effects upon the 3 boar taint compounds. All these effects were highly confounded with one another. Therefore, they were accounted for in the subsequent quantitative genetic analyses via a contemporary group comprising week of slaughter, farm of birth, and line.

Linear regression on HCW had a significant effect on boar taint compounds in the preliminary multiple regression analyses and its inclusion in the model chosen for variance component estimation analyses also reflected the production system, which is aiming for a constant HCW at around 90 kg. Higher-order regressions on HCW were not significant. Hot carcass weight was highly correlated with age, and therefore age was not included in the model as a separate factor.

The following individual animal model was fitted for the boar taint compounds:

\[ y_{ijkl} = DL_{i} + DL_{j} + b_1 \times HCW_k + \] 
\[ a_k + p_k + e_{ijkl} \]  

where \( y_{ijkl} \) is the natural log of the observed concentration [except for the analysis of probability (high skatole), where no transformation was performed]; \( DL_i \) was the date of scoring nested within panelist combination, \( DL_j \) was the jth nested effect of date of scoring within farm of birth and line (or cross), \( p_k \) being a random permanent environmental effect associated with the kth pig to account for multiple observations of different panelists on the same pig and other terms were as defined for Model [1]. In a small number of cases, pigs had repeated observations by the same panelist. To avoid the need to use a repeatability model in the multiple trait (between panelist) analyses, only the earliest observation per pig for each panelist was used. The model used in this case was:

\[ y_{ijkl} = DP_i + DL_{j} \times HCW_k + b_1 \times \] 
\[ HCW_k + a_k + e_{ijkl} \] 

Common litter of birth effects were excluded from the final models for human nose score (Eq. [2, 3]) on the basis of likelihood ratio tests carried out in univariate analyses. The common litter of birth variance exceeded 1% of the phenotypic variance for 2 panelists only (5.2 and 1.7%) and the P-value of the likelihood ratio test of comparing the reduced model without the litter of birth effect with the full model was in all cases larger than 0.10. For 5 of the 9 panelists, the common litter of birth variance approached zero.

To estimate (genetic) correlations between human nose scores observed by 2 panelists the following bivariate individual animal model was fitted:
\[ \begin{bmatrix} y_1 \\ y_2 \end{bmatrix} = \begin{bmatrix} X_1 & 0 \\ 0 & X_2 \end{bmatrix} \begin{bmatrix} b_1 \\ b_2 \end{bmatrix} + \begin{bmatrix} Z_1 & 0 \\ 0 & Z_2 \end{bmatrix} \begin{bmatrix} a_1 \\ a_2 \end{bmatrix} + e_1 + e_2 \] \tag{4}

In which \( y_1 \) and \( y_2 \) were vectors of observations on two panelists; \( b_1 \), \( a_1 \), and \( e_1 \) were vectors of fixed effect solutions, random animal and random residual effects, respectively, for the \( i \)th panelist, and \( X_i \) and \( Z_i \) were design matrices relating observations for panelist \( i \) to solutions. Fixed effects were as in Model [3].

Random variables were assumed to be normally distributed with mean zero and variance defined as:

\[ \text{var} = \begin{bmatrix} \sigma_a^2 A & \sigma_a^2 A & 0 & 0 \\ \sigma_a^2 A & \sigma_a^2 A & 0 & 0 \\ 0 & 0 & \sigma_e^2 I & \sigma_e^2 I \\ 0 & 0 & \sigma_e^2 I & \sigma_e^2 I \end{bmatrix} \] \tag{5}

In which \( \sigma_a^2 \) was the additive genetic variance for trait \( i \); \( \sigma_a^2 \) was the additive genetic covariance between traits 1 and 2; \( \sigma_e^2 \) was the residual variance for trait \( i \); \( \sigma_e \) was the residual covariance between Traits 1 and 2, and \( A \) is the numerator relationship matrix. \( \sigma_e \) was not estimated for some combinations of panelists with no pigs recorded by both panelists.

Carcass Traits. Average daily gain, carcass fat, and loin depths were analyzed using the model:

\[ y_{ijkl} = FSLM_l + b_1 \cdot HCW_j + a_j + l_k + e_{ijkl} \] \tag{6}

in which \( FSLM \) was the \( i \)th interaction of farm, sex, line, and month of slaughter (contemporary group), and the other parameters as in Eq. [1].

Bivariate Analyses. To determine the relationship among boar taint compounds, among finishing traits and between boar taint compounds and finishing traits the following bivariate animal model was used:

\[ \begin{bmatrix} y_1 \\ y_2 \end{bmatrix} = \begin{bmatrix} X_1 & 0 \\ 0 & X_2 \end{bmatrix} \begin{bmatrix} b_1 \\ b_2 \end{bmatrix} + \begin{bmatrix} Z_1 & 0 \\ 0 & Z_2 \end{bmatrix} \begin{bmatrix} a_1 \\ a_2 \end{bmatrix} + \begin{bmatrix} T_1 & 0 \\ 0 & T_2 \end{bmatrix} \begin{bmatrix} e_1 \\ e_2 \end{bmatrix} \] \tag{7}

With assumed variance structure:

\[ \begin{bmatrix} \sigma_a^2 A & \sigma_a^2 A \\ \sigma_a^2 A & \sigma_a^2 A \\ 0 & 0 \\ 0 & 0 \end{bmatrix} = \begin{bmatrix} \sigma_a^2 A & \sigma_a^2 A \\ \sigma_a^2 A & \sigma_a^2 A \\ 0 & 0 \\ 0 & 0 \end{bmatrix} + \begin{bmatrix} \sigma_e^2 I & \sigma_e^2 I \\ \sigma_e^2 I & \sigma_e^2 I \\ 0 & 0 \\ 0 & 0 \end{bmatrix} \]

In which \( e_i \) is a vector of common litter of birth effects for effect \( i \); \( T_i \) is a design matrix relating observations on trait \( i \) to litter of birth effects, and other terms are as in Eq. [5].

Bivariate analyses were also used to determine the relationship between human nose scores and boar taint compounds or carcass traits. In analyses of human nose scores for a single panelist, there is no common litter of birth effect included for the human nose score trait resulting in the model:

\[ \begin{bmatrix} y_1 \\ y_2 \end{bmatrix} = \begin{bmatrix} X_1 & 0 \\ 0 & X_2 \end{bmatrix} \begin{bmatrix} b_1 \\ b_2 \end{bmatrix} + \begin{bmatrix} Z_1 & 0 \\ 0 & Z_2 \end{bmatrix} \begin{bmatrix} a_1 \\ a_2 \end{bmatrix} + \begin{bmatrix} 0 & 0 \\ 0 & 0 \end{bmatrix} \begin{bmatrix} e_1 \\ e_2 \end{bmatrix} \] \tag{8}

In which Trait 1 was human nose score as measured by 1 of the panelists, and Trait 2 was either a boar taint compound or carcass trait, and the terms as described for Models [4] and [6]. In the bivariate analyses (Models 4, 7, and 8), fixed effects fitted were as described for the univariate models.

When human nose score was considered across panelists, a permanent environmental effect associated with repeated scoring of a sample taken from a boar and all other terms are as for previous bivariate models.

All model analyses were carried out using the average information residual maximum likelihood algorithm as implemented in the ASREML software (Gilmour et al., 2006).
RESULTS

Boar Taint Compounds

There was substantial variation in the concentration of boar taint compounds. For androstenone there was a 5-fold difference between the lines with the least and greatest average concentration, while for skatole a 6-fold and for indole an almost 3-fold difference was found (Table 1). Sire lines had generally less concentrations of boar taint compounds than dam lines, and crosses were intermediate. Within-line variation was also substantial with SD often exceeding the means.

A significant part of the variation in boar taint compounds was genetic. Heritabilities for the boar taint compounds were moderately high and ranged from 0.33 to 0.54 with SE close to 0.04 (Table 2). Litter effects were rather small (<5%) but significantly different from 0 except for probability (high Skatole). Both phenotypic and genetic correlations were positive and significantly different from 0. Those between androstenone and the other 2 compounds were between 0.33 and 0.46, with phenotypic correlations being slightly less than genetic correlations (Table 3). The phenotypic correlation between indole and skatole was 0.71, while the genetic correlation was 0.78. Consequently, the amount of genetic (co-)variation is adequate for breeding against increased concentrations for all 3 boar taint compounds simultaneously.

Human Nose Score

On average, about two-thirds of the samples were scored zero by the panelists, indicating no abnormal smell. The frequency of samples with zero score varied between panelists from 49 to 88% (Table 4). The frequency of Scores 3 and 4, considered as being unacceptably tainted, was 8.8% across panelists and ranged between 3.4 and 18.4%. The panel was thus able to identify samples with boar taint, but there was variation between panelists in the number of samples identified as such.

The incidence of boar taint was, on average, slightly greater than observed in the Dutch market, due to the greater frequency of pigs from dam lines, which have a greater frequency of boar taint than pigs from sire lines or from crosses between sire and dam lines (Table 1). Heritabilities of scores by individual panelists ranged from 0.12 to 0.19, and were all significantly different from 0 (Table 5). The $h^2$ of all scores was 0.12, clearly less than the heritability of the boar taint compounds. The repeatability was 0.29 (SE = 0.01), rather low as well. The common litter of birth variances only exceeded 1% of the phenotypic variance for 2 panelists (5.2% and 1.7%), for 5 of the 9 panelists the common litter of birth variance approached 0, and was never significantly different from 0. Results show that the human nose scores of boar taint are clearly heritable, but to a lesser extent than boar taint compounds.

Table 1. Number of pigs analyzed for boar taint compounds and mean and SD of boar taint compounds

<table>
<thead>
<tr>
<th>Line or cross</th>
<th>Androstenone, μg/g</th>
<th>Skatole, ng/g</th>
<th>Indole, ng/g</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>No.</td>
<td>Mean</td>
<td>SD</td>
</tr>
<tr>
<td>Duroc (D)</td>
<td>3,000</td>
<td>1.09</td>
<td>0.77</td>
</tr>
<tr>
<td>Large White (E)</td>
<td>710</td>
<td>1.02</td>
<td>1.59</td>
</tr>
<tr>
<td>Pietrain (P)</td>
<td>627</td>
<td>0.49</td>
<td>0.51</td>
</tr>
<tr>
<td>Spanish Duroc (U)</td>
<td>178</td>
<td>2.47</td>
<td>1.99</td>
</tr>
<tr>
<td>All sire lines</td>
<td>4515</td>
<td>1.05</td>
<td>1.05</td>
</tr>
<tr>
<td>Landrace line (F)</td>
<td>317</td>
<td>1.61</td>
<td>1.6</td>
</tr>
<tr>
<td>Landrace line (N)</td>
<td>443</td>
<td>1.25</td>
<td>1.06</td>
</tr>
<tr>
<td>York line (Z)</td>
<td>238</td>
<td>1.92</td>
<td>2.3</td>
</tr>
<tr>
<td>All dam lines</td>
<td>998</td>
<td>1.53</td>
<td>1.62</td>
</tr>
<tr>
<td>DDBZ1</td>
<td>75</td>
<td>1.26</td>
<td>1.08</td>
</tr>
<tr>
<td>DDBZ2</td>
<td>652</td>
<td>1.27</td>
<td>1.12</td>
</tr>
<tr>
<td>EENZ</td>
<td>582</td>
<td>0.89</td>
<td>0.95</td>
</tr>
<tr>
<td>PPBZ1</td>
<td>72</td>
<td>0.96</td>
<td>0.61</td>
</tr>
<tr>
<td>PPNZ</td>
<td>243</td>
<td>0.98</td>
<td>0.78</td>
</tr>
<tr>
<td>YYBZ1,2</td>
<td>70</td>
<td>0.72</td>
<td>0.37</td>
</tr>
<tr>
<td>YYNZZ</td>
<td>124</td>
<td>0.80</td>
<td>0.50</td>
</tr>
<tr>
<td>All crosses</td>
<td>1823</td>
<td>1.04</td>
<td>0.97</td>
</tr>
<tr>
<td>All lines and crosses</td>
<td>7336</td>
<td>1.11</td>
<td>1.14</td>
</tr>
</tbody>
</table>

1B refers to a synthetic dam line originating from Landrace and Large White. 2Y refers to a Yorkshire sire line.

Table 2. Phenotypic variance ($\sigma^2_p$), heritabilities ($h^2 \pm$ SE), and common litter of birth effect variance as a proportion of the phenotypic variance ($c^2$) from univariate analyses of boar taint compounds

<table>
<thead>
<tr>
<th>Trait</th>
<th>$\sigma^2_p$</th>
<th>$h^2$</th>
<th>$c^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Log androstenone</td>
<td>0.65</td>
<td>0.54 ± 0.040</td>
<td>0.05 ± 0.014</td>
</tr>
<tr>
<td>Log skatole</td>
<td>0.48</td>
<td>0.41 ± 0.039</td>
<td>0.05 ± 0.015</td>
</tr>
<tr>
<td>P (high skatole)</td>
<td>0.08</td>
<td>0.40 ± 0.038</td>
<td>0.02 ± 0.014</td>
</tr>
<tr>
<td>Log indole</td>
<td>0.35</td>
<td>0.33 ± 0.037</td>
<td>0.04 ± 0.015</td>
</tr>
</tbody>
</table>

Table 3. Additive genetic correlations (below diagonal) and phenotypic correlations (above diagonal) between boar taint compounds

<table>
<thead>
<tr>
<th>Trait</th>
<th>Log androstenone</th>
<th>Log skatole</th>
<th>P (high skatole)</th>
<th>Log indole</th>
</tr>
</thead>
<tbody>
<tr>
<td>Log androstenone</td>
<td>0.33 ± 0.015</td>
<td>0.31 ± 0.015</td>
<td>0.36 ± 0.014</td>
<td></td>
</tr>
<tr>
<td>Log skatole</td>
<td>0.37 ± 0.061</td>
<td>0.84 ± 0.004</td>
<td>0.71 ± 0.007</td>
<td></td>
</tr>
<tr>
<td>P (high skatole)</td>
<td>0.33 ± 0.064</td>
<td>0.96 ± 0.010</td>
<td>0.63 ± 0.009</td>
<td></td>
</tr>
<tr>
<td>Log indole</td>
<td>0.46 ± 0.061</td>
<td>0.78 ± 0.035</td>
<td>0.81 ± 0.035</td>
<td></td>
</tr>
</tbody>
</table>
Genetics of boar taint were generally strong (Table 6). All correlations except 2 were stronger than 0.70, ranging up to 1.00. The 2 lower correlations were 0.07 (SE = 0.43) and 0.33 (SE = 0.21) and involved the same panelist. Although these were not significantly different from 0, they were not significantly different from 0.70 either. Phenotypic correlations were weaker than genetic correlations, except for the 2 lowest genetic correlations, ranging from 0.06 to 0.51 (Table 6).

Genetic correlations of panelist scores with skatole (mean 0.88) and indole (mean 0.73) were greater than those with androstenone (mean 0.61; Table 7). Genetic correlations with probability (high skatol) were greater than with skatole itself. One panelist had consistently strong correlations with all compounds, one had consistently weaker correlations, but all other panelists had both relatively weak and strong correlations. The high and positive genetic correlations between boar taint compounds and human nose scores indicate that selection for low human nose scores will decrease the levels of boar taint compounds and vice versa.

**DISCUSSION**

The objective of this paper was to estimate the heritabilities of boar taint compounds, human nose scores and finishing traits, as well as genetic correlations among them. Overall, results show that heritabilities are high enough and genetic correlations strong enough, to set up a breeding program to reduce boar taint.
Among the boar taint compounds, heritability of androstenone (0.54) was high but in line with literature. Similar values have been reported (Sellier et al., 2000; Robic et al., 2008; Varona et al., 2005). Using a similar data structure, Merks et al. (2009) reported even a higher heritability of 0.64. In general, heritability estimates for androstenone range from 0.25 to 0.88 with an average of about 0.56 (Ciobanu et al., 2011). Heritability estimates for log skatole (0.41) and probability (high skatole; 0.40) were slightly greater than those reported in literature (Pedersen, 1998; Robic et al., 2008; Merks et al., 2009) ranging from 0.19 to 0.36. However, the estimates in the present study were within the range of those reported by Tajet et al. (2006), who estimated a heritability of 0.23 for Duroc and 0.55 for Landrace. There are fewer studies with respect to indole. The heritability estimate of 0.33 for indole was quite similar to the estimates by Tajet et al. (2006) and Merks et al. (2009).

Heritability Estimates

Among the boar taint compounds, heritability of androstenone (0.54) was high but in line with literature. Similar values have been reported (Sellier et al., 2000; Robic et al., 2008; Varona et al., 2005). Using a similar data structure, Merks et al. (2009) reported even a higher heritability of 0.64. In general, heritability estimates for androstenone range from 0.25 to 0.88 with an average of about 0.56 (Ciobanu et al., 2011). Heritability estimates for log skatole (0.41) and probability (high skatole; 0.40) were slightly greater than those reported in literature (Pedersen, 1998; Robic et al., 2008; Merks et al., 2009) ranging from 0.19 to 0.36. However, the estimates in the present study were within the range of those reported by Tajet et al. (2006), who estimated a heritability of 0.23 for Duroc and 0.55 for Landrace. There are fewer studies with respect to indole. The heritability estimate of 0.33 for indole was quite similar to the estimates by Tajet et al. (2006) and Merks et al. (2009).

The moderate to high heritabilities for the boar taint compounds indicate that breeding pigs with low boar taint is possible. There are 2 issues that may prevent wider use of boar taint compounds for successful breeding of entire males without boar taint. The first issue is that these analyses are both costly and time consuming. This will be very costly for large scale datasets required for accurate breeding value estimation. The other issue is the uncertainty about the relationship between the boar taint compounds and the unpleasant boar taint odor as perceived by humans. There is no agreement on the thresholds below which boar taint compound concentrations should stay in order not to be perceived as boar taint, or regarding the best procedure to determine androstenone concentrations (Ampuero Kragten et al., 2011). Threshold concentrations of 1.0 μg/g for androstenone have frequently been suggested (Desmoulin and Bonneau, 1982; Babol et al., 1996; Xue et al., 1996; Walstra et al., 1999) as well as a much lower threshold of 0.5 μg/g (Desmoulin and Bonneau, 1982; Di Natale et al., 2003; Aldal et al., 2005). Consequently, it is not clear how long breeding for lower compounds should continue before the breeding goal of no perceptible boar taint is reached.

Human nose scores largely avoided both of these problems. In the first place, it is faster and less costly. Although in this study scoring took place in a laboratory setting, under standardized conditions, it can be readily extended to in line slaughter detection, enabling a large scale recording of boar taint. In the second place, human nose scores are a direct estimate of boar taint as perceived by humans, and the breeding goal is clear: no scores of 3 and 4 (bad or very bad smell). There is considerable variation between humans in the perception of boar taint. In most

### Table 7. Genetic ($r_g$) and phenotypic correlations ($r_p$) between human nose scores of trained panelists A to I and boar taint compounds, and of human nose score with boar taint compounds in a repeatability model (All)

<table>
<thead>
<tr>
<th>Panelist</th>
<th>Log androstenone</th>
<th>Log skatole</th>
<th>$P$ (high skatole)</th>
<th>Log indole</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>$r_g$ 0.64, $r_p$ 0.25</td>
<td>$r_g$ 0.67, $r_p$ 0.21</td>
<td>$r_g$ 0.77, $r_p$ 0.20</td>
<td>$r_g$ 0.92, $r_p$ 0.21</td>
</tr>
<tr>
<td>B</td>
<td>$r_g$ 0.53, $r_p$ 0.19</td>
<td>$r_g$ 1.00, $r_p$ 0.28</td>
<td>$r_g$ 0.99, $r_p$ 0.27</td>
<td>$r_g$ 0.88, $r_p$ 0.26</td>
</tr>
<tr>
<td>C</td>
<td>$r_g$ 0.71, $r_p$ 0.35</td>
<td>$r_g$ 0.86, $r_p$ 0.34</td>
<td>$r_g$ 0.92, $r_p$ 0.33</td>
<td>$r_g$ 0.78, $r_p$ 0.27</td>
</tr>
<tr>
<td>D</td>
<td>$r_g$ 0.55, $r_p$ 0.22</td>
<td>$r_g$ 0.92, $r_p$ 0.42</td>
<td>$r_g$ 0.97, $r_p$ 0.42</td>
<td>$r_g$ 0.88, $r_p$ 0.37</td>
</tr>
<tr>
<td>E</td>
<td>$r_g$ 0.54, $r_p$ 0.26</td>
<td>$r_g$ 0.94, $r_p$ 0.44</td>
<td>$r_g$ 0.98, $r_p$ 0.44</td>
<td>$r_g$ 0.87, $r_p$ 0.39</td>
</tr>
<tr>
<td>F</td>
<td>$r_g$ 0.43, $r_p$ 0.27</td>
<td>$r_g$ 0.74, $r_p$ 0.47</td>
<td>$r_g$ 0.77, $r_p$ 0.47</td>
<td>$r_g$ 0.67, $r_p$ 0.39</td>
</tr>
<tr>
<td>G</td>
<td>$r_g$ 0.71, $r_p$ 0.28</td>
<td>$r_g$ 0.90, $r_p$ 0.39</td>
<td>$r_g$ 0.93, $r_p$ 0.38</td>
<td>$r_g$ 0.78, $r_p$ 0.33</td>
</tr>
<tr>
<td>H</td>
<td>$r_g$ 0.79, $r_p$ 0.37</td>
<td>$r_g$ 1.00, $r_p$ 0.47</td>
<td>$r_g$ 0.99, $r_p$ 0.40</td>
<td>$r_g$ 1.00, $r_p$ 0.44</td>
</tr>
<tr>
<td>I</td>
<td>$r_g$ 0.59, $r_p$ 0.33</td>
<td>$r_g$ 0.85, $r_p$ 0.35</td>
<td>$r_g$ 0.79, $r_p$ 0.33</td>
<td>$r_g$ 0.70, $r_p$ 0.34</td>
</tr>
<tr>
<td>All</td>
<td>$r_g$ 0.65, $r_p$ 0.27</td>
<td>$r_g$ 0.90, $r_p$ 0.36</td>
<td>$r_g$ 0.93, $r_p$ 0.35</td>
<td>$r_g$ 0.84, $r_p$ 0.32</td>
</tr>
</tbody>
</table>

1Standard errors of genetic correlation estimates for individual panelists ranged from 0.074 to 0.537, for repeatability model from 0.035 to 0.058.

### Table 8. Heritability ($h^2$) of slaughter traits and additive genetic correlations with boar taint compounds and boar taint scores of panelists

<table>
<thead>
<tr>
<th>Item</th>
<th>$h^2$</th>
<th>$c^2$</th>
<th>Log (androstenone)</th>
<th>Log (skatole)</th>
<th>$P$ (high skatole)</th>
<th>Log (indole)</th>
<th>Human nose scores</th>
</tr>
</thead>
<tbody>
<tr>
<td>ADG</td>
<td>0.33 ± 0.027</td>
<td>0.13 ± 0.010</td>
<td>-0.06 ± 0.069</td>
<td>-0.10 ± 0.076</td>
<td>-0.15 ± 0.075</td>
<td>-0.02 ± 0.081</td>
<td>-0.07 ± 0.089</td>
</tr>
<tr>
<td>Fat depth</td>
<td>0.38 ± 0.024</td>
<td>0.03 ± 0.006</td>
<td>0.17 ± 0.062</td>
<td>0.12 ± 0.069</td>
<td>0.13 ± 0.068</td>
<td>0.15 ± 0.073</td>
<td>0.29 ± 0.077</td>
</tr>
<tr>
<td>Loin depth</td>
<td>0.21 ± 0.019</td>
<td>0.02 ± 0.006</td>
<td>-0.13 ± 0.071</td>
<td>-0.10 ± 0.078</td>
<td>-0.13 ± 0.078</td>
<td>-0.07 ± 0.084</td>
<td>-0.11 ± 0.090</td>
</tr>
</tbody>
</table>

1Heritability and phenotypic variance ($c^2$) for carcass traits come from univariate analyses, rg from bivariate analyses. The human nose scores were analyzed across panelists using a repeatability model.
cases, the boar taint cannot be detected in cold pork (Field, 1971) and about 7.6% of the women and 44.3% of the men are unable to detect boar taint even in warm cooked pork (Rhodes, 1969). The threshold for the perception of the boar taint tends to increase with age in men but decrease in women (Dorries et al., 1989). Panelists in this research were selected on the ability to detect boar taint. However, it is clear from the results that within the group that can detect boar taint, there is considerable variation in the perception. Consequently, care is needed in the composition of the panel, so that it does cover the consumers that perceive boar taint as problematic. In this respect, the panel actually represented the true situation among pork consumers.

Heritabilities of the human nose scores are less than those of the boar taint compounds, but still indicate the usefulness of human nose scores for breeding for lower boar taint.

**Correlations among Boar Taint Compounds**

As expected, the genetic correlation between log skatole and probability (high skatole) was 0.96. The genetic correlations of log skatole as well as probability (high skatole) with log indole were also very high, 0.78 and 0.81, respectively. However, the genetic correlation between log androstenone and log skatole was not as high but rather moderate (0.37). These estimates are very similar to those reported in the literature (Tajet et al., 2006; Merks et al., 2009). These results suggest that genetic selection can be based on log androstenone and log skatole as the main boar taint compounds. That should result in significant correlated responses in probability (high skatole) and indole.

**Correlations between Human Nose Scores and Boar Taint Compounds**

Genetic correlations among human nose scores by different panelists were generally high, with some of them being close to unity. A genetic correlation of unity between the human nose score of two panelists indicates that the genetic ability of the pig to produce an odor perceived by the first panelist as boar taint is the same as the ability of the pig to produce an odor perceived as boar taint by the second panelist. In other words, the genetic ranking of pigs based on human nose score of the first panelist will be identical to the genetic ranking of pigs based on the human nose score of the second panelist. Therefore selection of pigs with a low boar taint predisposition will be very similar when based on different panelists. On the other hand, if the genetic correlation between human nose scores of different panelists is much less than unity, different pigs would be selected when the aim is to reduce boar taint. The phenotypic correlations ranged from 0.06 to 0.51. Among them, the lower correlations were indicative of the variation in perception in boar taint among panelists, allowing for representation of true variation in the consumer perception of boar taint. Variation between panelists could also be due to environmental circumstances and random noise. Consequently, repeated sampling of the same pig by multiple panelists is recommended to increase the accuracy of the EBV and increase response to selection.

There were some differences between the panelists with respect to the genetic correlations with the boar taint compounds [note that, as for the human nose scores, the genetic correlations are between traits of the pigs (i.e., the genetic ability of a pig to produce an odor perceived by a panelist as boar taint, and the genetic ability of a pig to produce a boar taint compound)]. In general, genetic correlations with skatole and probability (high skatole) were greater than the correlations with androstenone. Correlations with androstenone varied independently from the other 2 compounds. Thus androstenone causes some variation in human nose scores apart from skatole and indole. Part of the differences among the panelists was due to natural differences among humans in their sensitivities to unpleasant odors. As with the correlations between panelists, genetic correlations between human nose scores and boar taint compounds were greater than the phenotypic correlations. The strong genetic correlations between human nose score and boar taint compounds indicate that breeding for decreased concentrations of boar taint compounds will also decrease the human nose score, and the other way around.

The high genetic correlations between boar taint compounds and human nose scores also open up the possibility of using a combination of both in breeding, either with traditional BLUP methods or with genomic selection. With genomic selection the relationships between a dense panel of DNA-markers with the phenotypes is estimated in a reference population, after which breeding values of pigs can be predicted from a DNA sample (e.g., by a blood sample). The data assembled in this paper can serve as a basis for setting up such a scheme, where boar taint compounds are determined in the reference population only. When all animals with phenotypes in this study are genotyped and we assume that 1,000 QTL are affecting the traits, the accuracy of EBV can be estimated using Eq. [1] in Daetwyler et al. (2008). In this case, the accuracy of genomic EBV would be 0.89 for androstenone, 0.88 for skatole, and 0.68 for human nose. However, we assume that the equation is valid for multi-breed composed reference populations, as in this study. If genomic selection is restricted to the Duroc line and the 3,000 pigs in the current study are used as a reference population, the accuracy of genomic EBV would be 0.79 for androstenone, 0.78 for skatole, and 0.51 for human nose score. These accuracies are sub-
stantially greater than those of conventional EBV (see below), and enable more accurate breeding values just after birth, reducing the need to specifically record (and therefore slaughter) relatives of the selection candidates.

It has been shown that the 3 boar taint compounds measured in this study are the main compounds that influence human perception of boar taint tissue (Vold, 1970; Bonneau, 1982; Zamaratskaia and Squires, 2009). A breeding program can concentrate on decreasing concentrations of these compounds. However, it may not address some of the variation among humans caused by genetic and cultural differences in the ability to perceive boar taint. Opinions also differ on the actual threshold below which the compounds should be brought to avoid detection. However, a breeding program can decrease the overall concentrations of the boar taint compounds, so that more and more pigs will fall below any threshold. The consequence of a different threshold will be that a breeding program takes longer or shorter to reach the acceptable threshold.

Correlations with Finishing and Reproduction Traits

The genetic correlations between boar taint measures and finishing traits indicate that selection against boar taint is expected to result in somewhat greater ADG, reduced backfat, and more loin depth. The genetic correlation of androstenone with ADG in the present study is smaller than the one reported by Merks et al. (2009), those with backfat and loin depth are larger, whereas the SE of these estimates are all smaller than in Merks et al. (2009). All these effects are in favorable directions. Selection for greater ADG, decreased backfat, and more loin depth, may thus result in lower boar taint. However, this will take much longer than direct selection on boar taint, because genetic correlations are generally small. Consequently, direct selection on boar taint compounds or human nose scores will be needed to eliminate boar taint. Moreover, genetic correlations with reproduction traits such male as fertility or libido may not be favorable, since androstenone is produced in the same biochemical pathway as testosterone and androgens that determine sexual maturity (Moe et al., 2009). Androstenone in fat has a highly significant positive correlation (0.48) with free estrone (Zamaratskaia et al., 2005) as well. Further research is needed to quantify the genetic relationships of boar taint and boar taint compounds with reproduction traits.

Selection against Skatole

Skatole, reduced to the probability that an observation does not belong to the first lognormal distribution (probability (high skatole)] and log-transformed skatole (log skatole) have similar heritability estimates [0.40 and 0.41, respectively]. Thus, although the information content was reduced from a continuous trait to an almost binary trait, there was very little change in heritability estimates. Moreover, the genetic correlation between probability (high skatole) and human nose scores was lower than the genetic correlation between log skatole and human nose score for only 1 of the 9 panelists. This is a strong indication that the genetic variation in skatole is almost completely determined by the likelihood of being in a state (high or low) rather than the variation within a state. There are various biological interpretations of such states possible, such as maximum skatole clearance capacity in the liver not yet reached (first lognormal distribution) or exceeded (other distributions). Possible mechanisms include different forms of enzymes involved in the catabolism of skatole in the liver, absence or presence of suppressive impact of androstenone concentrations, and a low maximum clearance capacity per se.

Implications for Genetic Selection against Boar Taint

The effect of selection on changing the level of boar taint compounds using either information on boar taint compounds or information on human nose scores can be compared using selection index calculations. For this, a breeding program where boars are mated to 20 sows resulting in litters with 5 male piglets each was assumed. In the case of boar taint compounds, it was modeled that the carcass fat samples were collected on 1 piglet of each litter, as it is a common practice for carcass and meat quality evaluations. In case of human nose scores, each sample was analyzed by three panelists. Hence, the scores of 3 panelists with the highest average genetic correlation with boar taint compounds were considered. It was assumed that human nose scores are available on 4 out of 5 male piglets within the litter, the fifth being available as a selection candidate. Thus, in case of a boar taint compound based breeding program, there is information on 1 full sib and 19 half sibs, and in case of a human nose score based breeding program, on 4 full sibs and 76 half sibs. Using index calculations (Van der Werf, 2006) with a breeding goal of equal reduction for all 3 boar taint compounds, an accuracy of 0.55 is estimated using information on boar taint compounds and of 0.53 using information on human nose scores. Predicted responses for skatole and indole are slightly greater, and for androstenone slightly less when using human nose scores instead of boar taint compounds. Thus, using human nose scores of more relatives instead of boar taint compounds will result in an almost equally effective breeding program. Using a simulation study and similar estimates of genetic parameters, Merks et al. (2009) concluded that boar taint can be eliminated in about four generations of genetic selection, and pork can be pro-
duced from males without castration. This conclusion still holds true in view of the results of our study.

Breeding can be useful as a tool to increase animal welfare (Kanis et al., 2004). Breeding against boar taint to avoid castration of piglets is just one example. The same tools that have been used successfully to increase production can be used to improve animal welfare. However, translation of welfare aspects into a clear breeding goal is not always straightforward. Tools such as the human nose score evaluated in this paper will help to efficiently breed pigs for welfare friendly husbandry.

**LITERATURE CITED**


Pig Progress, Doetinchem, the Netherlands.


