Genetic parameters for androstenone and skatole as indicators of boar taint and their relationship to production and litter size traits in Danish Landrace

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ABSTRACT: Boar taint is an offensive odor that affects the smell and taste of cooked pork, resulting mainly from the accumulation of skatole and androstenone in the back fat of intact males. The aim of the study was to estimate genetic parameters for skatole and androstenone and their genetic relationship to production and litter size traits. Concentrations of skatole and androstenone in the back fat were available for approximately 6,000 and 1,000 Landrace boars, respectively. The concentrations were log-transformed to align phenotypic measures to a normal distribution. Heritability estimates for Log(skatole) and Log(androstenone) were 0.33 and 0.59, respectively. The genetic correlation between the 2 measures of boar taint was 0.37, suggesting that genetic selection against boar taint based on only 1 of the chemical compounds could be insufficient. The boar taint compounds had low and mostly favorable genetic correlations with the production traits. Most noticeable, a favorable genetic correlation of −0.20 between meat percentage and Log(skatole) was estimated and hence continued selection for lean pigs can also slowly reduce the level of boar taint if the desired carcass weight is kept constant. The relationship between litter size traits (measured on sows related to boars) and boar taint compounds was low and not significantly different from 0. In conclusion, skatole and androstenone can be reduced through selection without affecting important economical production and litter size traits. Therefore, animal breeding offers an effective and sustainable solution to surgical castration of male piglets.

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

INTRODUCTION

Boar taint is characterized by an offensive taste or odor of the meat that emits during cooking, which makes it unpleasant for consumers. It is caused primarily by the compounds androstenone and skatole, which accumulate mainly in the back fat of intact males (Zamaratskaia and Squires, 2008). A significant proportion of all carcasses from intact males are classified as tainted pork unless surgical or immunological castration of male piglets at 2 to 4 d of age is performed. Castration reduces the concentrations of skatole and androstenone in fat under the threshold levels starting mostly at 0.20 to 0.25 μg/g for skatole and 0.5 to 1 μg/g for androstenone. Public pressure to abandon castration has led stakeholders (i.e., producers, meat industry, retailers, scientists, veterinarians, and animal welfare nongovernmental organizations) within the European Union to sign a voluntary declaration to end castration practices by January 1, 2018 (EU, 2012). It is well established that a fraction of the Danish and other pig populations carry genes that enable entire male pigs to develop boar taint (e.g., Pedersen, 1998). Reduction of boar taint through genetic selection is promising because concentrations of boar taint compounds are moderately to highly heritable (e.g., Robic et al., 2008; Grindflek et al., 2011).
The profitability of intensive swine production systems depends mainly on the number of healthy and vital piglets born, their growth rate from birth to slaughter, and their efficiency of use of resources (e.g., feed). Several pig breeding companies or organizations in the European Union, including Denmark, are currently exploring possibilities to include boar taint in the industry breeding goal. Hence, estimation of genetic correlations of boar taint to economically important traits such as production and litter size traits is critical because these will be used to construct a balanced selection index that places simultaneous selection emphasis on these traits and boar taint compounds.

The objective of the study was to estimate genetic parameters for boar taint compounds and their relationship to key production and litter size traits included in the breeding goal for Danish Landrace.

MATERIALS AND METHODS

Animal Care and Use Committee approval was not obtained for this study because fat samples were obtained from a commercial slaughter facility.

Boar Taint Traits

The concentration of the boar taint compounds, androstenone and skatole-equivalents, were measured in carcass fat samples. The fat samples were taken after slaughter from the neck area of the carcass and were stored at −20°C. A skatole-equivalent represented a combined measurement of skatole and indole and it was measured by a calorimetric method (Mortensen and Sørensen, 1984). In addition, androstenone was measured by the Norwegian School of Veterinary Sciences (NVH) on a subset of the boars. Concentrations of androstenone were analyzed by modified time-resolved fluoroimmunoassay (Tuomola et al., 1997), using an antibody (Andresen, 1974) produced at NVH. The original dataset contained skatole-equivalent concentrations on 6,166 intact males and androstenone concentrations on 1,002 intact males. Androstenone, which is more expensive to measure, was selectively phenotyped on pairs of full sibs. More specifically, 501 pigs with very high skatole (>0.3 μg/g) at slaughter were identified and matched with a low skatole litter mate. Boar taint records that could not be matched with observations on age at slaughter and carcass weight were discarded. Furthermore, each skatole-equivalent observation had to belong to a contemporary group containing at least 5 records to be included in the analyses. After these data edits, the final dataset consisted of 5,936 and 920 records of skatole-equivalent and androstenone, respectively. Finally, the natural logarithm was applied to transform the boar taint traits to normality. In the remainder of the article, the transformed boar taint traits will be termed Log(skatole) and Log(androstenone).

Production Traits

The production traits were ADG from birth to 30 kg (ADG30) and from 30 to 100 kg BW (ADG100), feed conversion ratio (FCR), meat percentage (MP), total number born (TBN), live piglets at d 5 (LP5), and survival rate until d 5 (SV5).

Table 1. Summary statistics for the traits included in the dataset

<table>
<thead>
<tr>
<th>Trait</th>
<th>No. records</th>
<th>Mean</th>
<th>SD</th>
<th>Minimum</th>
<th>Maximum</th>
</tr>
</thead>
<tbody>
<tr>
<td>ADG30</td>
<td>17,817</td>
<td>377.9</td>
<td>39.02</td>
<td>294.7</td>
<td>586.2</td>
</tr>
<tr>
<td>ADG100</td>
<td>18,966</td>
<td>946.0</td>
<td>110.0</td>
<td>571.1</td>
<td>1,307</td>
</tr>
<tr>
<td>FCR</td>
<td>1,102</td>
<td>2.390</td>
<td>0.207</td>
<td>1.580</td>
<td>3.310</td>
</tr>
<tr>
<td>MP</td>
<td>18,966</td>
<td>61.90</td>
<td>1.060</td>
<td>56.20</td>
<td>65.70</td>
</tr>
<tr>
<td>TBN</td>
<td>35,715</td>
<td>13.56</td>
<td>3.832</td>
<td>1.000</td>
<td>28.00</td>
</tr>
<tr>
<td>LP5</td>
<td>34,991</td>
<td>10.47</td>
<td>3.453</td>
<td>0.000</td>
<td>22.00</td>
</tr>
<tr>
<td>SV5</td>
<td>34,991</td>
<td>0.780</td>
<td>0.188</td>
<td>0.000</td>
<td>1.000</td>
</tr>
<tr>
<td>Skatole</td>
<td>5,937</td>
<td>0.197</td>
<td>0.145</td>
<td>0.020</td>
<td>2.860</td>
</tr>
<tr>
<td>Log(skatole)</td>
<td>5,937</td>
<td>−1.786</td>
<td>0.545</td>
<td>−3.912</td>
<td>1.051</td>
</tr>
<tr>
<td>Androstenone</td>
<td>920</td>
<td>1.080</td>
<td>0.985</td>
<td>0.010</td>
<td>10.60</td>
</tr>
<tr>
<td>Log(androstenone)</td>
<td>920</td>
<td>−0.191</td>
<td>0.712</td>
<td>−2.207</td>
<td>2.363</td>
</tr>
</tbody>
</table>

1Average daily gain from birth to 30 kg BW (ADG30), ADG from 30 to 100 kg BW (ADG100), feed conversion ratio (FCR), meat percentage (MP), total number born (TBN), live piglets at d 5 (LP5), and survival rate until d 5 (SV5).
Genetic parameters for boar taint

Litter Size Traits

Recordings on total number of piglets born (TNB) piglets and live piglets at d 5 (LP5) were considered from sows that had male full and half sibs with phenotypic records on Log(skatole) and all contemporary group members of these sows. We considered only data from the first parity, pure breed pigs, and contemporary group sizes of at least 5 records. The survival rate until d 5 (SV5) was expressed as LP5/TNB. This yielded 35,715, 34,991, and 34,991 records for TNB, LP5, and SV5, respectively. It must be mentioned that litter size traits are recorded more frequently than production traits because litter size traits are recorded in both nucleus and multiplier herds in Denmark, explaining the larger data size despite the fact that the traits are only measured on sows. Descriptive statistics for the litter size traits included in the analyses are presented in Table 1.

Litter size traits – pedigree. A pedigree for animals that had records on either boar taint or litter size traits was constructed. The pedigree was traced back 5 generations and it contained 55,047 animals including 43,070 animals with phenotypic records. These descended from 1,325 sires and 12,588 dams. The size of the base population was 563 animals.

Bivariate Linear Mixed Models

All genetic parameters were estimated using animal models where informative fixed effects were derived from multiple regression analyses before fitting the multitrait animal models. First, a 2-trait linear mixed model was specified and fitted to the boar taint data, establishing relationships between boar taint compounds. Second, a series of 2-trait models were specified for boar taint and production traits, which were also used to generate starting values for the variance components for the final 6-trait model.

A bivariate model to estimate correlations between Log(skatole) and Log(androstenone) was as follows:

\[
\begin{bmatrix}
y_1 \\
y_2
\end{bmatrix} = \begin{bmatrix} X_1 & 0 \\ 0 & X_2 \end{bmatrix} \begin{bmatrix} b_1 \\ b_2 \end{bmatrix} + \begin{bmatrix} Z_{a_1} & 0 \\ 0 & Z_{a_2} \end{bmatrix} \begin{bmatrix} a_1 \\ a_2 \end{bmatrix} + \begin{bmatrix} Z_{c_1} & 0 \\ 0 & Z_{c_2} \end{bmatrix} \begin{bmatrix} c_1 \\ c_2 \end{bmatrix} + \begin{bmatrix} e_1 \\ e_2 \end{bmatrix},
\]

in which \(y_1\) and \(y_2\) were vectors of observations on Log(skatole) and Log(androstenone), which were denoted by indices 1 and 2, respectively, and \(b, a, c,\) and \(e\) were vectors of solutions for the 2 boar taint traits, which were fixed, random additive genetic, litter, and residual effects, respectively. The vectors of fixed effects for \(y_1\) and \(y_2\) were \(b_1 = [\mu, \text{HYS}, \text{ASL}, \text{WSL}]^\prime\) and \(b_2 = [\mu, \text{HERD}, \text{ASL}, \text{WSL}]^\prime\), in which \(\mu\) is the overall mean, HYS (herd–year–season) and HERD were categorical variables, and ASL (age at slaughter) and WSL (weight at slaughter) denoted the continuous regression variables, age (in days) and carcass weight (in kg) at slaughter. These were confounded partially as the Spearman rank correlation was estimated to 0.40. We chose to use both variables to adjust for systematic differences in sexual maturation between boars. This approach assumed that sexual maturity is related to both BW and age. Higher order terms for ASL and WSL were not significant \((P > 0.10)\) in preliminary multiple regressions analyses and therefore not considered further. Design matrices \(X_1\) and \(X_2\) related fixed effects to \(y_1\) and \(y_2\).

Index matrices \(Z_a\) and \(Z_c\) allocated records to random effects were known indices matrices allocating records to random effects. The random effects were assumed to be independent and normally distributed with mean 0. The covariance or variance structure among random effects was defined as

\[
\begin{bmatrix}
a \\ c
\end{bmatrix} \sim \begin{bmatrix} A \otimes G & 0 & 0 \\ 0 & I \otimes C & 0 \\ 0 & 0 & I \otimes R
\end{bmatrix},
\]

in which \(A\) is the matrix of additive genetic relationships among animals in the pedigree (Quaas, 1976) and \(I\) is an identity matrix. Here \(G, C,\) and \(R\) were full unstructured covariance or variance matrices.

Multitrait Model To Estimate Parameters for Production and Boar Taint Traits

A 6-trait model was specified on the basis of the bivariate mixed model analyses, that is,

\[
y = Xb + Z_d a + Z_c c + Z_p p + e,
\]

in which \(y\) was the vector of observations \([\text{ADG30, ADG100, FCR, MP, Log(skatole), and Log(androstenone)]}\) and \(b\) was the vector of fixed effects which were different for the different traits. All equations for production traits included HYS effects and equations for traits ADG30, ADG100, and FCR included a BW continuous regression variable, which was adjusted to 30 kg BW, accounting for systematic differences in the planned BW recordings at 30 kg. In addition, fixed effects were defined above for the boar taint compounds, being continuous regression variables ASL and WSL.
The random effects were $a$, the vector of additive genetic effects; $c$, the vector of litter of birth effects; and $p$, the vector of pen effects (included only for traits ADG100 and MP), and $e$ was the vector of random residuals. Design matrices $X, Z_p, Z_t,$ and $Z_p$ were incidence matrices associating $b, a, c,$ and $p$ with $y$. The random effects $a, c,$ $p,$ and $e$ were assumed to be mutually independent and normally distributed:

$$a \sim N(0, A \otimes G), \quad c \sim N(0, I \otimes C),$$  

$$p \sim N(0, I \otimes P), \quad e \sim N(0, I \otimes R),$$  

in which $G, C, P,$ and $R$ were covariance or variance matrices for additive genetic effects, litter of birth effects, pen effects, and residuals, respectively, $A$ was the matrix of additive genetic relationships among animals in the pedigree, and $I$ was the identity matrix. Here $G$ and $R$ were full unstructured covariance or variance matrices whereas all covariance parameters between traits in $C$ and $P$ were set to 0. This was possible because the estimated correlations between traits in these random effects were not significantly different from 0 based on the bivariate animal model analyses. These variance restrictions ensured proper convergence of the Average Information Restricted Maximum Likelihood (AI-REML) routine.

MULTITRAIT MODELS TO ESTIMATE PARAMETERS FOR LITTER SIZE AND BOAR TAINT TRAITS

Estimation of genetic and environmental parameters for litter size and boar taint traits were performed in 3-trait [SV5, Log(skatole), and Log(androstene)] or 4-trait [TNB, LP5, Log(skatole), and Log(androstene)] linear mixed model analyses. Model descriptions were limited to the 4 trait model, because the 2 models were similar (i.e., same explanatory effects). The 4-trait model to describe the relationships among animals in the pedigree. All random effects were assumed to be normally distributed. Thus,

$$b_1 = \begin{bmatrix} \mu \\ \text{HYQ} \\ \text{AGE} \\ \text{AGE}^2 \end{bmatrix}, \quad b_2 = \begin{bmatrix} \mu \\ \text{HYQ} \\ \text{AGE} \\ \text{AGE}^2 \end{bmatrix},$$

$$b_3 = \begin{bmatrix} \mu \\ \text{HYQ} \\ \text{ASL} \\ \text{WSL} \end{bmatrix}, \quad b_4 = \begin{bmatrix} \mu \\ \text{HYQ} \\ \text{ASL} \\ \text{WSL} \end{bmatrix},$$

in which $\mu$ is the overall mean, HYQ (herd–year–quarter) effects, HERD effects, and HYS were categorical variables, AGE and AGE$^2$ were linear and quadratic effects of the continuous regression variable, age at first mating (days), and ASL and WSL denoted the continuous regression variables age (days) and carcass weight at slaughter (kg).

The vector $p_s$ contained the permanent service sire effects, $d$ was the vector of genetic effects of the sow, $a$ was the vector of direct animal genetic effects, $e$ was the vector of litter effects, $e$ was the vector of random residuals, and $Z_{ps}, Z_{dt},$ and $Z_a$ were incidence matrices associating $p_s, d,$ and $a$ with $y$. The random effects were assumed to be independent of each other, except for $d$ and $a$, which were assumed to be correlated via the additive genetic relationship matrix $A$, describing the relationships among animals in the pedigree. All random effects were assumed to be normally distributed. Thus,

$$p_s \sim N(0, I \otimes S_0), \quad e \sim N(0, I \otimes C_0),$$

$$d \sim N(0, A \otimes G_0), \quad e \sim N(0, I \otimes R_0),$$

in which $S_0, C_0, G_0,$ and $R_0$ represented covariance matrices for permanent effects service sire, litter effects, genetic effects of sow, and direct animal genetic effects, and residuals, respectively, and $I$ was the identity matrix of appropriate size. The residual covariances between litter size traits and boar taint compounds were assumed to be 0 because litter size traits were collected on sows and boar taint compounds were collected on slaughter boars. Based on the covariance structures defined above, the phenotypic variances were
Genetic parameters for boar taint

Genetic parameters for boar taint are defined as
\[
\sigma^2_p = \sigma^2_d + \sigma^2_e \quad \text{for litter size traits}
\]
and
\[
\sigma^2_p = \sigma^2_c + \sigma^2_d + \sigma^2_e \quad \text{for boar taint compounds.}
\]

An additional analysis was conducted for the SV5 trait on the arc-sine scale, \(SV5_t = \arcsin((SV5)^{1/2})\) because it is often used for binomial proportions. In the transformation, a 0 survival rate was counted as \(1/4n\) and a 100% survival rate as \((n - 1/4)/n\), in which \(n\) was litter size at birth. The inferences based on the transformed scale were almost identical to those based on the original scale and therefore, we chose to present results on the original scale.

All parameters were estimated using the average information residual maximum likelihood algorithm (Jensen et al., 1997) as implemented in the DMU software (http://dmu.agrsci.dk; Madsen and Jensen, 2008). Standard errors of heritabilities and genetic and phenotypic correlations were calculated from the average information matrix at convergence by means of the delta method (e.g., Dodenhoff et al., 1998). The genetic parameter estimates were considered significantly different from 0 when the estimate deviated by more than \(1.96 \times \text{SE}\) from 0.

RESULTS

Boar Taint Compounds

The raw averages of skatole-equivalent and androstenone concentrations are 0.197 and 1.080 μg/g back fat (Table 1). Variation is also substantial as the CV is close to 100% for both traits. The concentrations of the 2 boar taint compounds are plotted against each other in Fig. 1 with suggested sensory thresholds added (Mortensen et al., 1986). Within the sensory thresholds (or “safe box”), a carcass can be declared free of boar taint (Mortensen et al., 1986). This means that the concentrations of skatole and androstenone in carcass back fat are below 0.25 and 1.0 μg/g back fat, respectively, for both compounds (Mortensen et al., 1986). Based on this classification, only 35% of all carcasses will be declared free of boar taint.

A significant proportion of the variation in boar taint is of genetic origin, which is confirmed by the moderate to high heritabilities for both compounds (Table 2). These amount to 0.33 (SE = 0.05) and 0.59 (SE = 0.14) for \(\log(\text{skatole})\) and \(\log(\text{androstenone})\), respectively. The litter variance account for a smaller (≤5%) but significant proportion of the phenotypic variance in \(\log(\text{skatole})\). The genetic correlation (based on the bivariate animal model) between \(\log(\text{skatole})\) and \(\log(\text{androstenone})\) is 0.37 (SE = 0.15), positive and significantly different from 0 (Table 2).
Production Traits and Boar Taint Compounds

Heritabilities of ADG30, ADG100, MP, and FCR and genetic correlations to boar taint compounds, which are estimated in either bivariate or multivariate animal model analyses, are presented in Tables 2 and 3. In general, the multitrait estimates presented in Table 3 yield minor differences to those estimates present in Table 2. The heritabilities of ADG30 and ADG100 are moderate (i.e., 0.22 and 0.30) whereas MP is a highly heritable trait where the heritability is estimated to 0.48. The contribution of the litter variance to the phenotypic variance is small for most traits but significant whereas its contribution to the ADG30 phenotypic variance is substantial (i.e., 0.17). The heritability of FCR is estimated to 0.17 and 0.16 in the bivariate and multivariate analyses, respectively.

The genetic correlations (rg) between production traits and boar taint compounds are generally small and tend to be favorable but in most cases not significantly different from 0. The exception is the ADG30 trait where low unfavorable correlations were estimated (0.17 < r_g < 0.28). Meat percentage and Log(skatole) are correlated genetically (−0.22 < r_g < −0.20), pointing in a favorable direction. Hence, selection for increasing MP will result in decreasing skatole concentrations. Consequently, moderate selection emphasis on boar taint in Danish Landrace is expected to have limited effects on the production traits and vice versa.

Litter Size Traits and Boar Taint Compounds

The genetic parameters for litter size traits and boar taint compounds are presented in Table 4. The heritability based on the sow component is 0.09 (SE = 0.01) and 0.06 (SE = 0.01) of TNB and LP5, respectively, and the heritability of SV5 was 0.09 (SE = 0.01) and at the same level as TNB. The genetic correlation between boar taint and litter size (based on the sow component) are low (−0.18 < r_g < 0.06) and not significantly different from 0. Genetic correlations between boar taint and piglet survival are low (0.01 < r_g < 0.03).

DISCUSSION

Boar Taint Compounds

The average skatole-equivalent level was substantially greater in the current data compared with the previous investigations reported by Pedersen (1998). The data collection scheme for the current study differed from the scheme described by Pedersen (1998) because slaughter boars from all Landrace nucleus herds were sampled and not only those that were reared and performance tested at the national test station. Different management procedures in nucleus herds may have affected the phenotypic skatole concentrations. In addition, the carcass weight was greater in the current study compared with the study

Table 2. Heritability of Log(skatole) and Log(Andro-stenone), growth traits (ADG from birth to 30 kg BW [ADG30] and ADG from 30 to 100 kg [ADG100]), meat percentage (MP), and feed conversion ratio (FCR) and additive genetic correlations with boar taint compounds estimated from pairwise bivariate animal model analyses

<table>
<thead>
<tr>
<th>Trait</th>
<th>h²</th>
<th>l²</th>
<th>Genetic correlations</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>Log(skatole)</td>
</tr>
<tr>
<td>Log(skatole)</td>
<td>0.33 ± 0.05</td>
<td>0.05 ± 0.02</td>
<td>1.00</td>
</tr>
<tr>
<td>Log(Androstenone)</td>
<td>0.59 ± 0.14</td>
<td>0.03 ± 0.06</td>
<td>0.37 ± 0.15</td>
</tr>
<tr>
<td>ADG30</td>
<td>0.22 ± 0.03</td>
<td>0.17 ± 0.01</td>
<td>0.26 ± 0.11</td>
</tr>
<tr>
<td>ADG100</td>
<td>0.30 ± 0.03</td>
<td>0.04 ± 0.01</td>
<td>−0.06 ± 0.09</td>
</tr>
<tr>
<td>MP</td>
<td>0.48 ± 0.03</td>
<td>0.03 ± 0.01</td>
<td>−0.22 ± 0.08</td>
</tr>
<tr>
<td>FCR</td>
<td>0.17 ± 0.08</td>
<td>0.02 ± 0.05</td>
<td>0.24 ± 0.19</td>
</tr>
</tbody>
</table>

1l² = ratio of litter variance to phenotypic variance

Table 3. Heritabilities of traits1, genetic correlations (above diagonal) and phenotypic correlations (below diagonal; ±SE) among growth traits, feed conversion ratio, meat percentage, and boar taint compounds

<table>
<thead>
<tr>
<th>Item</th>
<th>ADG30</th>
<th>ADG100</th>
<th>FCR</th>
<th>MP</th>
<th>Log(skatole)</th>
<th>Log(androstenone)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Trait</td>
<td>0.22 ± 0.03</td>
<td>0.30 ± 0.03</td>
<td>0.16 ± 0.07</td>
<td>0.48 ± 0.03</td>
<td>0.33 ± 0.04</td>
<td>0.59 ± 0.14</td>
</tr>
<tr>
<td>ADG30</td>
<td>0.25 ± 0.07</td>
<td>−0.19 ± 0.21</td>
<td>−0.13 ± 0.07</td>
<td>0.17 ± 0.09</td>
<td>0.28 ± 0.13</td>
<td></td>
</tr>
<tr>
<td>ADG100</td>
<td>0.09 ± 0.01</td>
<td>−0.04 ± 0.18</td>
<td>−0.42 ± 0.05</td>
<td>−0.04 ± 0.08</td>
<td>0.10 ± 0.11</td>
<td></td>
</tr>
<tr>
<td>FCR</td>
<td>−0.04 ± 0.04</td>
<td>−0.32 ± 0.03</td>
<td>−0.24 ± 0.16</td>
<td>0.18 ± 0.19</td>
<td>−0.04 ± 0.26</td>
<td></td>
</tr>
<tr>
<td>MP</td>
<td>−0.01 ± 0.01</td>
<td>−0.27 ± 0.01</td>
<td>−0.10 ± 0.03</td>
<td>−0.20 ± 0.07</td>
<td>−0.18 ± 0.10</td>
<td></td>
</tr>
<tr>
<td>Log(skatole)</td>
<td>0.02 ± 0.02</td>
<td>−0.01 ± 0.02</td>
<td>0.04 ± 0.04</td>
<td>−0.12 ± 0.02</td>
<td>0.35 ± 0.14</td>
<td></td>
</tr>
<tr>
<td>Log(androstenone)</td>
<td>0.08 ± 0.04</td>
<td>0.05 ± 0.04</td>
<td>0.14 ± 0.10</td>
<td>−0.15 ± 0.03</td>
<td>0.25 ± 0.03</td>
<td></td>
</tr>
</tbody>
</table>

1Average daily gain from birth to 30 kg BW (ADG30), ADG from 30 to 100 kg BW (ADG100), feed conversion ratio (FCR), and meat percentage (MP).
Genetic parameters for boar taint

Log(skatole) show medium to high heritability values ranging from 0.19 to 0.54 and hence the current estimate was close to the average reported range. The estimate in the present study was somewhat less than reported by Tajet et al. (2006) who estimated a heritability of 0.55 whereas Grindflek et al. (2011) reported 0.41 for skatole in the same population of Norwegian Landrace. Heritability of skatole has been reported on several occasions in Dutch populations (e.g., Engelsma et al., 2007) and Windig et al. (2012) recently reported a heritability of 0.41, which was slightly greater than our estimate.

The heritability of Log(androstenone) has been previously estimated in Danish Landrace. Jonsson and Andresen (1979) computed the heritability of Log(androstenone) to 0.54, but the estimate had limited precision (i.e., the SE was 0.32). The point estimate agreed very well with the estimate derived herein. The authors also developed a boar taint index, which was a linear combination of Log(androstenone) and an olfactory measurement, showing a heritability of 0.46. The literature survey of Robic et al. (2008) reported heritabilities ranging from 0.25 to 0.88 for Log(androstenone) and the current estimate was close to the average reported estimate in the literature. Tajet et al. (2006) and Grindflek et al. (2011) reported heritabilities of 0.54 and 0.49, respectively, for Norwegian Landrace. The average androstenone concentration in back fat in the Danish Landrace was comparable to the phenotypic level observed in Norwegian Landrace (i.e., 1.14 vs. 1.08 μg/g), suggesting that the 2 breeds are quite comparable in the androstenone trait. Based on the current investigation and previously published work in Denmark and other European countries, it can be stated that Log(skatole) and Log(androstenone) were moderately to highly heritable, which was expected.

The genetic correlation between the 2 boar taint compounds in Danish Landrace has not previously been estimated. Estimates for the genetic correlation between Log(skatole) and Log(androstenone) were reported to be 0.32 to 0.36 in Norwegian Landrace (Tajet et al., 2006; Grindflek et al., 2011), which corresponds very well with the current estimates of 0.35 to 0.43 based on the different models that were fitted. Windig et al. (2012) reported a genetic correlation of 0.37 between the 2 traits in the Dutch populations, a blend of different breeds and lines. We chose to use the carcass weight as a fixed effect even though the variation in carcass is in part genetic. We explored the consequence of this approach by treating carcass weight as a third trait and obtained a heritability of 0.15 (SE = 0.04), confirming our assumption. However, it did not change the estimate of the genetic correlation between boar taint compounds significantly as the estimate was 0.42 (SE = 0.14). In addition, other recent genetic analyses of boar taint traits in other populations have included age at slaughter and carcass weight as fixed effects (Baes et al., 2012; Windig et al., 2012).

These results suggest that selection emphasis should probably be placed on both compounds if the selection is to be based directly on the chemical components. This would also result in a significant reduction in indole, because the trait (skatole-equivalent) was a mixture of skatole and indole. Moreover, there has been a report of a high genetic correlation between the pure substances indole and skatole in back fat of boars (Grindflek et al., 2011; Windig et al., 2012) and hence collecting indole as a separate trait

### Table 4

The proportion of phenotypic variance that is due to sow and genetic effects on litter size traits and direct animal genetic effects on boar taint compounds are presented in bold on the diagonal. Genetic correlations between litter size traits and boar taint compounds are presented below the diagonal.

<table>
<thead>
<tr>
<th>Four-trait model</th>
<th>TNB</th>
<th>LP5</th>
<th>Log(skatole)</th>
<th>Log(Androstenone)</th>
</tr>
</thead>
<tbody>
<tr>
<td>TNB</td>
<td>0.09 ± 0.01</td>
<td></td>
<td>0.06 ± 0.01</td>
<td>0.33 ± 0.05</td>
</tr>
<tr>
<td>LP5</td>
<td>0.57 ± 0.06</td>
<td>0.05 ± 0.13</td>
<td>0.41 ± 0.14</td>
<td>0.59 ± 0.14</td>
</tr>
<tr>
<td>Log(skatole)</td>
<td>0.06 ± 0.11</td>
<td>0.18 ± 0.18</td>
<td>0.41 ± 0.14</td>
<td>0.59 ± 0.14</td>
</tr>
<tr>
<td>Log(Androstenone)</td>
<td>–0.12 ± 0.15</td>
<td>0.42 ± 0.14</td>
<td>0.59 ± 0.14</td>
<td></td>
</tr>
<tr>
<td>Three-trait model</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>SV5</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>SV5</td>
<td>0.09 ± 0.01</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Log(skatole)</td>
<td>0.01 ± 0.12</td>
<td>0.33 ± 0.05</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Log(Androstenone)</td>
<td>0.03 ± 0.17</td>
<td>0.42 ± 0.14</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

1 Total number born (TBN), live piglets at d 5 (LP5), and survival rate until d 5 (SV5) = LP5/TNB.

2 Estimation of genetic and environmental parameters for litter size and boar taint traits were performed in 4-trait [TNB, LP5, Log(skatole), and Log(androstenone)] or 3-trait [SV5, Log(skatole), and Log(androstenone)] linear mixed model analyses.
is not necessary in a future breeding scheme. Finally, it should be noted that in the literature the boar taint effect of indole is considered secondary to that of skatole and androstenone (Zamaratskaia and Squires, 2008).

**Genetic Correlations among Production Traits and Boar Taint Compounds**

The heritabilities for ADG30, ADG100, and MP were close to those used in routine genetic evaluations whereas the heritability of FCR was significantly lower than the estimate for the entire Landrace population. Two earlier studies conducted in Danish Landrace have estimated the genetic correlation between ADG100 and boar taint. Both studies found genetic correlations to be low and not significantly different from 0 (Jonsson and Andresen, 1979; Pedersen, 1998). Therefore, the current estimates were in agreement with these findings, which are also supported by Windig et al. (2012).

The genetic correlation between skatole and MP has been previously reported by Pedersen (1998), resulting in an estimate of \(-0.21\), which was close to our estimates. Meat percentage is approximately the inverse of back fat thickness. Windig et al. (2012) reported low positive genetic correlations between carcass fat depth and boar taint compounds, supporting the results obtained in this study. Selection to increase lean meat content in pigs may slowly decrease the concentration of skatole-equivalents and androstenone and hence prevalence of boar tainted carcasses. In Denmark, the average carcass weight has increased from 77 to 82 kg during the last 10 yr, and therefore the correlated response to selection for lean meat content may have had a very limited effect on boar taint prevalence due to the increased carcass weight. The genetic relationship between boar taint and FCR has not been previously reported in the literature. The genetic correlation points in a favorable direction although the estimates were estimated with low precision due to the small number of records for the trait. Hence, these estimates should be treated with some caution and more data is needed to improve the accuracy of these estimates. Nonetheless, these results suggest that feed efficient animals would tend to be low in skatole. Hence, continued selection for feed efficiency would slowly reduce the concentration of skatole in back fat. The biological mechanism behind this finding cannot be deduced from the current study, but possible links between rates of nutrient metabolism in the liver and its skatole clearance capacity may exist. Finally, selection against skatole would have positive effects in both males and females because it is associated with environmental conditions and bacterial digestion of tryptophan in the gut of the pig.

**Litter Size Traits and Boar Taint Compounds**

The heritability of TNB was greater than that of LP5, which was in agreement with Su et al. (2007). The heritability of SV5 was the same as that of TNB but lower than previously reported by Su et al. (2007). The genetic correlation between boar taint compounds and dam genetic effects on litter size and survival rate was low and not significantly different from 0. The literature estimates of these correlations are scarce, but Engelsma et al. (2007) reported similar estimates for TNB as presented here. Litter mortality and Log(androstenone) have been reported to be unfavorable genetically correlated \((r_g = –0.59)\) by Engelsma et al. (2007), which are contrary to our results, being an estimate of 0.03 between Log(androstenone) and SV5. It must be noted that the results of their analysis was based on a substantially smaller dataset (5,320 records) compared with the present investigation (35,715 records).

The precision of the genetic correlations could be improved if the service sire or AI boar had phenotypic records for boar taint. Therefore, obtaining boar taint information on AI boars seems to be a necessary step toward fully estimating the association between boar taint and both female and male fertility. Recently, Baes et al. (2012) presented a quantitative performance test for use in live male breeding candidates, which showed that the estimated heritabilities on the basis of data from small tissue samples obtained by biopsy were comparable to our estimates. The literature is scarce in terms of estimates of genetic correlations between economically important traits such as litter size and boar taint compounds. Further research is needed to quantify the genetic relationships between boar taint compounds and litter size traits in other breeds and especially dam lines.

In conclusion, skatole and androstenone can be reduced through selection without negatively affecting important economical production traits. The fertility of the boar may be of secondary importance in a general breeding scheme, because in practice, female fertility is the major trait of direct economic importance to pig producers. However, deterioration of male fertility should be avoided and genetic correlations between boar taint compounds and male fertility traits such as semen quality and libido may not be favorable. Hence future research should focus on estimating these correlations. Nonetheless, animal breeding seems to offer a sustainable solution to avoid surgical castration of male piglets. For an efficient eradication of boar taint, direct selection is necessary. This leads to an enhancement of sustainable pork production from both an animal welfare/ethics as well as an environmental perspective because intact males are 10 to 15% more feed efficient than their castrated counterparts.
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LITERATURE CITED