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ABSTRACT: Concerns have been raised regarding selection against the boar taint compounds, androstenone and skatole, due to potential unfavorable genetic correlations with important male fertility traits (i.e., selection of boars with low levels of these boar taint compounds might also reduce male fertility). Hence, the objective of this investigation was to study the genetic association between direct measures of male fertility and the boar taint compounds in Danish Landrace pigs. Concentrations of skatole and androstenone in the back fat were available for approximately 6000 and 1000 Landrace boars, respectively. The litter size traits, such as, total number born, live piglets at day 5 and piglet survival until day 5 on relatives of the slaughter boars were extracted from the Danish Landrace breeding program, yielding 35,715 records. Semen volume, sperm concentration, subjective sperm quality score, and total number of sperm were available from 95,267 ejaculates. These ejaculates were collected between 2005 and 2012 and originated from 3,145 Landrace boars from 12 AI stations in Denmark. The traits were analyzed using single and multi-trait animal models including univariate random regression models. Skatole and androstenone concentrations were moderate to highly heritable (i.e. 0.33 and 0.59, respectively). The genetic correlation between the two compounds was moderate (0.40). Genetic variance of sperm production per ejaculate increased during the productive life of the boar, resulting in heritability estimates increasing from 0.18 to 0.31. Genetic correlations between sperm production per ejaculate at different ages were high and generally larger than 0.8, indicating that later genetic merit can be predicted from records at an early age. The heritability (based on service-sire genetic component) of both total number of piglets born and survival to day 5 were 0.02 and the correlation between these effects and the additive genetic effect on boar taint ranged from 0.05 to -0.40 (none of these correlations were significantly different from zero). Most importantly, the genetic correlations between skatole and androstenone and the different semen traits tended to be more favorable with increase in age of the boars. In conclusion, these data suggest that concentrations of skatole and

androstenone can be reduced through genetic selection without negatively affecting important male fertility traits in Danish Landrace pigs.

Key words: Fertility, boar taint, breeding, random regression modeling

INTRODUCTION

Selection against boar taint is of interest in Europe as organizations within EU have signed a voluntary declaration to stop castration by 2018 (EU, 2012). Surgical castration is a routine procedure in most countries because it effectively removes the problem of boar tainted carcasses. Boar taint is caused primarily by skatole, indole and androstenone. Skatole and indole are the product of microbial metabolism of the amino acid tryptophan in the hindgut, while androstenone is produced by the Leydig cells of the testis and subsequently concentrated and converted in the salivary gland to an active sex pheromone. Androstenone is synthesized along with testosterone and estrogens, which are known to be important factors affecting male fertility. Highly unfavourable genetic correlations between androstenone (both plasma and fat) and the other sex steroids in plasma (i.e. estrone sulfate, 17β-estradiol, and testosterone) have recently been reported (Grindflek et al., 2011). Although sufficient plasma concentrations of testosterone are essential to maintain spermatogenesis and male fertility (e.g., Walker, 2010), plasma hormone concentrations are intermediate measures that do not explain all variation associated with male fertility. For instance, semen characteristics do not correlate strongly to plasma testosterone (Ren et al., 2009). Two alternative strategies for measuring male fertility that more directly capture variation of relevance to pig producers are: 1) direct measurements of semen characteristics such as semen volume, sperm concentration, sperm quality and total number of sperm per ejaculate which have been shown to be heritable (Grandjot et al., 1997; Oh et al., 2006), and 2) litter size (paternal effect). The 2nd measure is outcome based and directly relates the fertility to the economy of the pig producer, but both the male and female effect must be considered simultaneously to separate them appropriately. The 2nd measure reflects sire fertility and its contribution to fertilization and embryo survival and eventual piglet survival through the offspring's genotype (Van der Lende et al., 1999).

Today's pig production in Denmark relies strongly on the use of artificial insemination (AI) and AI-centers in Denmark are routinely collecting semen volume, sperm concentration and gross sperm morphology data for monitoring purposes. Also, litter size traits are routinely collected as part of the ongoing genetic improvement in female fertility. These data are available in large volume (as opposed to hormone serum concentrations) and they can be used to estimate genetic correlations to boar taint compounds. Moreover, the literature is scarce in terms of estimates of genetic associations between semen traits and skatole and androstenone concentrations and this is key knowledge, if a future selection scheme against boar taint is to be put into practice.

The objective of the current study was to estimate genetic parameters for semen characteristics and the paternal component of litter size traits, and to estimate genetic correlations between male fertility and concentrations of skatole and androstenone for Danish Landrace.

MATERIALS AND METHODS

Boar taint Compounds

The concentration of the boar taint compounds, androstenone and skatole-equivalents were measured in carcass fat samples. The fat samples were taken post-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. Levels of androstenone were analyzed by modified time-resolved fluoroimmunoassay (Tuomola et al., 1997), using an antibody (Andresen, 1974) produced at NVH. Additional details of measuring boar taint compounds and potential issues related to inter laboratory differences can be found in Ampuero Kragten et al. (2011). The original full 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. Data were discarded when either weight or age at slaughter was missing. Furthermore, each skatole-equivalent observation had to belong to a contemporary group containing at least five 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).

Semen traits

The current study included Landrace boars collected from January 2005 until May 2012. The boars were housed on 12 different Danish AI-stations. Boars were fed a commercial diet for pregnant sows. The following semen characteristics were recorded on each ejaculate: semen volume; sperm concentration using NucleoCounter SP100 (Hansen et al., 2006); subjective gross morphology/motility score (quality score). Sperm quality score was evaluated using microscopy with a 20x objective lens. The semen was assigned to either of the following quality score definitions: “90” was assigned when sperm motility appeared normal and only few morphological defects were observed; “80” was assigned when motility was moderately reduced or morphological defects was observed easily; lower scores were assigned in increments of 10 according to severity in the reduction of sperm quality.

Data were excluded from further analyses if one or more conditions were not fulfilled: The minimum number of ejaculates per AI-station-year-quarter groups was 50; a minimum of 5 ejaculates per boar collected between 30 – 100 weeks of age; semen volume was 25 to 600 mL;

sperm concentration between 100 to 1,000 million sperm per ml. Only ejaculates approved for commercial AI (i.e. normal ejaculates) were included in the analysis of semen quantity traits following the standard quality procedure at AI-stations in Denmark. The prevalence of abnormal ejaculates amounted to 5.8% and it was taken as a binary trait, i.e. 0 = normal ejaculate and 1 = abnormal ejaculate. The number of ejaculates was 95267, originating from 3145 Landrace boars. The average number of ejaculates per boar was 30.3, ranging from 5 to 123. Descriptive statistics for all semen traits in the final data set are presented in Table 2. Two additional traits were calculated, which were total number of sperm (concentration x volume) and number of functional sperm (concentration x volume x sperm quality score). In Figure 1, number of records (left y-axis) and average of functional sperm cells (right y-axis) is plotted against age of boar in weeks.

The combined dataset (i.e. semen and boar taint records) included 325 pairs of full siblings and 1902 pairs of half siblings, which had records on either semen or, boar taint traits. The pedigree for these animals was constructed. The pedigree was traced back 5 generations and it contained 15898 animals, including 8681 animals with phenotypic records.

Litter Size traits

Recordings on total number of born (**TNB**) piglets and live piglets at day five (**LP5**) were considered from sows which 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 bred pigs, and contemporary group sizes of at least five records. The survival rate until day five **(SV5)** was expressed as LP5/TNB. This yielded 35715, 34991 and 34991 records for TNB, LP5 and SV5, respectively.

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 contained 55047 animals including 43070 animals with phenotypic records.

Statistical Analysis

Random Regression Models for Semen Production Traits. The assumption of semen characteristics being the same trait genetically at different ages of the boar (i.e. univariate repeatability model) is often not appropriate, and a full multivariate model with the number of traits equal to the number of age-groups could result in an overparameterized model. A random regression model can be viewed as a powerful intermediate model between the univariate repeatability and the full multivariate model (Meyer and Hill, 1997; Kirkpatrick et al., 1990). Random regression models provide a method for analyzing independent components of variation that reveal specific patterns of change over time (Kirkpatrick et al., 1990) and it has been adopted for analyzing lifetime semen production in boars (Oh et al., 2006).

Let y_{ijklt} denote the measured semen trait on an ejaculate collected in the ith (i=1, 2, …310) AI-station-year-season (*AIYS*) group with the jth (j= 1, 2,… 11) interval between two subsequent semen collections (*INT*), at the kth (k = 30, 31, …, 100) week of age (*AGE*) for the lth (l=1, 2, … 3145) boar and on tth day on test. The following random regression model was fitted:

$$y_{ijklt} = \mu + AIYS_i + INT_j + AGE_k + \sum_{n=0}^{kp} p_{l,n}\Phi_n(w_t) + \sum_{n=0}^{ka} a_{l,n}\Phi_n(w_t) + e_{ijklt}$$

Where μ is the overall mean and $p_{l,n}$ and $a_{l,n}$ are random regression coefficients for the permanent environmental and additive genetic effects, which are related to the Legendre polynomials ($\Phi_n(\cdot)$) of orders *kp* and *ka*. The standardized time variable is denoted by w_t ($-1 \leq w_t \leq 1$) and the residual is

given by e_{ijklt}. In matrix notation, the model can be stated as $\mathbf{y} = \mathbf{Xb} + \mathbf{Z_{pe}p} + \mathbf{Z_a a} + \mathbf{e}$, where the expectations are given by $E(\mathbf{y}) = \mathbf{Xb}$ and the covariance structure for random effects is given by

$$\text{var}\begin{bmatrix}\mathbf{p}\\ \mathbf{a}\\ \mathbf{e}\end{bmatrix} = \begin{bmatrix}\mathbf{I}\otimes\mathbf{K_P} & \mathbf{0} & \mathbf{0}\\ \mathbf{0} & \mathbf{A}\otimes\mathbf{K_a} & \mathbf{0}\\ \mathbf{0} & \mathbf{0} & \mathbf{I}\sigma_e^2\end{bmatrix}$$

The matrices $\mathbf{K_p}$ and $\mathbf{K_a}$ are of order *kp* x *kp* and *ka* x *ka*, respectively, and **A** is the matrix of additive genetic relationships among animals in the pedigree and **I** is the identity matrix. The orders of the Legendre polynomials can be derived from data by fitting all combination of *kp* and *ka*. Oh et al. (2006) suggested that Legendre polynomials up to 8th order are required in order to give an adequate fit to the data, resulting in a total of 64 models per trait. Model selection indices (i.e. Bayesian, BIC and Akaike information criterion, AIC) are used to rank the different models within each analyzed trait. Methods for summarizing information from covariance functions (e.g. time-varying heritability) from random regression models have been described elsewhere (Veerkamp et al., 2001; Jamrozik and Schaeffer, 1996; Kirkpatrick et al., 1990) and are not repeated.

Repeatability Model for Binary Semen Quality Traits. Generalized linear mixed models (**GLMM**) have been developed to estimate effects on a continuous unobserved liability scale, on which linearity is imposed. The threshold (τ) provides the link between the observed abnormal ejaculate category and the underlying liability of abnormal ejaculate. The threshold and residual variance were set to $\tau = 0$ and $\sigma_e^2 = 1$, respectively. Both probit and logit link functions were used for modeling the probability that an ejaculate was abnormal [P(y = 1)]. The linear predictor (λ_{ijkl}) of the animal model was

$$\lambda_{ijkl} = \mu + AIYS_i + INT_j + AGE_k + p_l + a_l$$

where fixed effects are as described previously; p_l = the random permanent environment of the lth animal (l = 3145) with $\sim N(0, \mathbf{I}\sigma^2)$; a_l = the random additive genetic effect of the lth animal (l = 3145) with $\sim N(0, \mathbf{A}\sigma_a^2)$. Calculation of heritabilities on both liability and original scale were adapted from Robertson and Lerner (1949).

Multi-trait Model for Semen Production and Boar taint Traits. Once parsimonious models with high goodness of fit have been developed for semen production traits they are extended to include the two boar taint traits as two separate traits, i.e.

$$\begin{bmatrix}\mathbf{y}_1\\ \mathbf{y}_2\\ \mathbf{y}_3\end{bmatrix} = \begin{bmatrix}\mathbf{X}_1 & \mathbf{0} & \mathbf{0}\\ \mathbf{0} & \mathbf{X}_2 & \mathbf{0}\\ \mathbf{0} & \mathbf{0} & \mathbf{X}_3\end{bmatrix}\begin{bmatrix}\mathbf{b}_1\\ \mathbf{b}_2\\ \mathbf{b}_3\end{bmatrix} + \begin{bmatrix}\mathbf{Z}_{\mathbf{pe}} & \mathbf{0} & \mathbf{0}\\ \mathbf{0} & \mathbf{0} & \mathbf{0}\\ \mathbf{0} & \mathbf{0} & \mathbf{0}\end{bmatrix}\begin{bmatrix}\mathbf{p}\\ \mathbf{0}\\ \mathbf{0}\end{bmatrix} + \begin{bmatrix}\mathbf{0} & \mathbf{0} & \mathbf{0}\\ \mathbf{0} & \mathbf{Z}_{c_2} & \mathbf{0}\\ \mathbf{0} & \mathbf{0} & \mathbf{Z}_{c_3}\end{bmatrix}\begin{bmatrix}\mathbf{0}\\ \mathbf{c}_2\\ \mathbf{c}_3\end{bmatrix} + \begin{bmatrix}\mathbf{Z}_{a_1} & \mathbf{0} & \mathbf{0}\\ \mathbf{0} & \mathbf{Z}_{a_2} & \mathbf{0}\\ \mathbf{0} & \mathbf{0} & \mathbf{Z}_{a_3}\end{bmatrix}\begin{bmatrix}\mathbf{a}_1\\ \mathbf{a}_2\\ \mathbf{a}_3\end{bmatrix} + \begin{bmatrix}\mathbf{e}_1\\ \mathbf{e}_2\\ \mathbf{e}_3\end{bmatrix}$$

where $\mathbf{y}_1$, $\mathbf{y}_2$ and $\mathbf{y}_3$ are a vector of records for the semen trait, Log(skatole) and Log(androstenone), respectively; $\mathbf{X}_1$, $\mathbf{X}_2$, and $\mathbf{X}_3$ were design matrices relating fixed effects in $\mathbf{b}_1$, $\mathbf{b}_2$, and $\mathbf{b}_3$ to $\mathbf{y}_1$, $\mathbf{y}_2$, and $\mathbf{y}_3$, respectively. The fixed effects in the model involving the semen trait ($\mathbf{b}_1$), Log(skatole) ($\mathbf{b}_2$) and Log(androstenone) ($\mathbf{b}_3$) are:

$$\mathbf{b}_1 = \begin{bmatrix}\mu\\ AIYS\\ INT\\ AGE\end{bmatrix},\quad \mathbf{b}_2 = \begin{bmatrix}\mu\\ HYS\\ ASL\\ WSL\end{bmatrix},\quad \mathbf{b}_3 = \begin{bmatrix}\mu\\ Herd\\ ASL\\ WSL\end{bmatrix}$$

where μ = the overall mean; effects *AIYS*, *INT* and *AGE* are described above, Herd and herd-year-season effects HYS are treated as categorical variables; *ASL* and *WSL* denoted the continuous regression variables age (days) and carcass weight at slaughter (kg).

The vectors **p**, **c** and **a** contain permanent environmental, common litter of birth, and additive genetic effects, respectively. Design matrices $\mathbf{Z}_{pe}$, $\mathbf{Z}_c$, $\mathbf{Z}_a$ associate **p**, **c,** and **a** with **y** where $\mathbf{Z}_{pe}$ and $\mathbf{Z}_{a1}$ are matrices that contain the Legendre polynomials of appropriate order. The vector **e**

contains residuals. The random effects are assumed to be independent of each other and normally distributed, i.e.

$$\mathbf{p} \sim N(\mathbf{0},\ \mathbf{I} \otimes \mathbf{K_p});\ \mathbf{c} \sim N(\mathbf{0},\ \mathbf{I} \otimes \mathbf{C});\ \mathbf{a} \sim N(\mathbf{0},\ \mathbf{A} \otimes \mathbf{G});\ \mathbf{e} \sim N(\mathbf{0},\ \mathbf{I} \otimes \mathbf{R})$$

where $\mathbf{K_p}$, $\mathbf{C}$, $\mathbf{G}$, and $\mathbf{R}$ represent covariance matrices for permanent environmental effects, litter effects, additive genetic effects, and residuals, respectively. The covariance (in both permanent environmental and residual effects) between the semen trait and boar taint compounds are assumed to be zero because the semen traits are collected on the AI boars while boar taint compounds are measured on slaughter boars. In essence, there are no common observations across fertility and boar taint traits, but observations are connected through genetic relationships.

Multi-trait Model for Semen Quality and Boar taint Traits. The multi-trait animal model analysis of binary semen quality traits and boar taint compounds had similar structure as above with exception of $\mathbf{y}_1$, representing the vector of unobserved liabilities, and design matrices $\mathbf{Z}_{pe}$ and $\mathbf{Z}_{a1}$ were simple incidence matrices.

Multi-trait model for litter size and boar taint traits. Su et al. (2007) proposed a model for litter size with separate genetic effects of service sire and sow to obtain direct measures for male and female fertility based on actual number of piglets being born. We extended this model to investigate the genetic correlation between male fertility and boar taint compounds. Estimation of genetic and environmental parameters for litter size and boar taint traits are performed in three- [SV5, Log(skatole), Log(androstenone)] or four-trait [TNB, LP5, Log(skatole), Log(androstenone)] linear mixed model analyses. Model descriptions are limited to the four trait model because the two models are similar. The four-trait model to describe the observations for the *i*'th trait $i = \{1,...,4\}$ was,

$$\begin{bmatrix}\mathbf{y}_1\\ \mathbf{y}_2\\ \mathbf{y}_3\\ \mathbf{y}_4\end{bmatrix}=\begin{bmatrix}\mathbf{X}_1 & \mathbf{0} & \mathbf{0} & \mathbf{0}\\ \mathbf{0} & \mathbf{X}_2 & \mathbf{0} & \mathbf{0}\\ \mathbf{0} & \mathbf{0} & \mathbf{X}_3 & \mathbf{0}\\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{X}_4\end{bmatrix}\begin{bmatrix}\mathbf{b}_1\\ \mathbf{b}_2\\ \mathbf{b}_3\\ \mathbf{b}_4\end{bmatrix}+\begin{bmatrix}\mathbf{Z}_{ps_1} & \mathbf{0} & \mathbf{0} & \mathbf{0}\\ \mathbf{0} & \mathbf{Z}_{ps_2} & \mathbf{0} & \mathbf{0}\\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0}\\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0}\end{bmatrix}\begin{bmatrix}\mathbf{p}_{s_1}\\ \mathbf{p}_{s_2}\\ \mathbf{0}\\ \mathbf{0}\end{bmatrix}+\begin{bmatrix}\mathbf{Z}_{s_1} & \mathbf{0} & \mathbf{0} & \mathbf{0}\\ \mathbf{0} & \mathbf{Z}_{s_2} & \mathbf{0} & \mathbf{0}\\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0}\\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0}\end{bmatrix}\begin{bmatrix}\mathbf{s}_1\\ \mathbf{s}_2\\ \mathbf{0}\\ \mathbf{0}\end{bmatrix}$$
$$+\begin{bmatrix}\mathbf{Z}_{d_1} & \mathbf{0} & \mathbf{0} & \mathbf{0}\\ \mathbf{0} & \mathbf{Z}_{d_2} & \mathbf{0} & \mathbf{0}\\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0}\\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0}\end{bmatrix}\begin{bmatrix}\mathbf{d}_1\\ \mathbf{d}_2\\ \mathbf{0}\\ \mathbf{0}\end{bmatrix}+\begin{bmatrix}\mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0}\\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0}\\ \mathbf{0} & \mathbf{0} & \mathbf{Z}_{a_3} & \mathbf{0}\\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{Z}_{a_4}\end{bmatrix}\begin{bmatrix}\mathbf{0}\\ \mathbf{0}\\ \mathbf{a}_3\\ \mathbf{a}_4\end{bmatrix}+\begin{bmatrix}\mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0}\\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0}\\ \mathbf{0} & \mathbf{0} & \mathbf{Z}_{c_3} & \mathbf{0}\\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{Z}_{c_4}\end{bmatrix}\begin{bmatrix}\mathbf{0}\\ \mathbf{0}\\ \mathbf{c}_3\\ \mathbf{c}_4\end{bmatrix}+\begin{bmatrix}\mathbf{e}_1\\ \mathbf{e}_2\\ \mathbf{e}_3\\ \mathbf{e}_4\end{bmatrix}$$

where $\mathbf{y}_1$, $\mathbf{y}_2$, $\mathbf{y}_3$ and $\mathbf{y}_4$ are a vector of records for TNB, LP5, Log(skatole) and Log(androstenone), respectively; $\mathbf{X}_1$, $\mathbf{X}_2$, $\mathbf{X}_3$ and $\mathbf{X}_4$ are design matrices relating fixed effects in $\mathbf{b}_1$, $\mathbf{b}_2$, $\mathbf{b}_3$ and $\mathbf{b}_4$ to $\mathbf{y}_1$, $\mathbf{y}_2$, $\mathbf{y}_3$ and $\mathbf{y}_4$, respectively. The fixed effects in the model involving TNB ($\mathbf{b}_1$), LP5 ($\mathbf{b}_2$), Log(skatole) ($\mathbf{b}_3$) and Log(androstenone) ($\mathbf{b}_4$) are:

$$\mathbf{b}_1=\begin{bmatrix}\mu\\ HYQ\\ AFM\\ AFM^2\end{bmatrix},\ \mathbf{b}_2=\begin{bmatrix}\mu\\ HYQ\\ AFM\\ AFM^2\end{bmatrix},\ \mathbf{b}_3=\begin{bmatrix}\mu\\ HYS\\ ASL\\ WSL\end{bmatrix},\ \mathbf{b}_4=\begin{bmatrix}\mu\\ Herd\\ ASL\\ WSL\end{bmatrix}$$

where μ = the overall mean; HYQ (Herd-Year-Quarter) effects, Herd effects and HYS are categorical variables; *AFM* and AFM^2 was linear and quadratic effects of the continuous regression variable, age at first mating (days); *ASL* and *WSL* denoted the continuous regression variables age (days) and carcass weight at slaughter (kg).

The vectors $\mathbf{p_s}$ and **s** are permanent environments and genetic service-sire effects, respectively; **d** is the vector of genetic effects of the sow; **a** is the vector of direct animal genetic effects; **c** is the vector of litter effects; **e** is the vector of random residuals; and $\mathbf{Z}_{ps}$, $\mathbf{Z}_d$, $\mathbf{Z}_s$, $\mathbf{Z}_a$ are incidence matrices associating $\mathbf{p}_s$, **s, d**, and **a** with **y**. The random effects are assumed to be independent of each other, except for **s, 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 are assumed to be normally distributed. Thus,

$$\mathbf{p_s} \sim N(\mathbf{0}, \mathbf{I} \otimes \mathbf{S_0}),\ \mathbf{c} \sim N(\mathbf{0}, \mathbf{I} \otimes \mathbf{C_0}),$$
$$\begin{bmatrix} \mathbf{s} \\ \mathbf{d} \\ \mathbf{a} \end{bmatrix} \sim N(\mathbf{0}, \mathbf{A} \otimes \mathbf{G_0}),\ \mathbf{e} \sim N(\mathbf{0}, \mathbf{I} \otimes \mathbf{R_0})$$

where $\mathbf{S_0}$, $\mathbf{C_0}$, and $\mathbf{R_0}$ represented covariance matrixes for permanent effects of service-sire, litter effects and residuals, respectively, whereas $\mathbf{G_0}$ was the additive genetic covariance matrix for sow, service-sire and direct animal effects. Note that residual covariances between litter size traits and boar taint compounds are assumed to be zero 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 defined as $\sigma_p^2 = \sigma_{p_s}^2 + \sigma_s^2 + \sigma_d^2 + \sigma_e^2$ for litter size traits and $\sigma_p^2 = \sigma_c^2 + \sigma_a^2 + \sigma_e^2$ for boar taint compounds. The contribution to the phenotypic variance for litter size traits from twice the covariance between service-sire and dam genetic effects was dropped because the average relatedness between service-sire and dam was close to zero (Su et al., 2007).

An additional analysis was conducted for the SV5 trait on the arc-sine scale, $SV5_t = \arcsin(\sqrt{SV5})$, because it is often used for binomial proportions. In the transformation, a zero survival rate was counted as 1/4n and a 100% survival rate as (n-1/4)/n, where n is litter size at the start point. The inferences based on the transformed scale were almost identical to those based on the original scale and thus, 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 (Madsen and Jensen, 2008). For GLMMs, the GLMM option in DMU was evoked. Standard errors of heritabilities and genetic and phenotypic correlations were calculated from the average information matrix at convergence by means of the delta method. The genetic parameter estimates were considered significantly different when the estimate deviated with more than 1.96 x SE from zero.

RESULTS

Genetic parameters of Semen Traits

The average functional sperm count increased curvilinearly with age as depicted in Figure 1. Fluctuations were observed after approximately 70 wks of age due to the decreasing numbers of records. Fit statistics -2Log likelihood, AIC, and BIC values for different combinations of ka and kp are presented in Table 2. Based on BIC, orders of 4 to 7 for kp were necessary for modeling the permanent environmental variance while an order of 1 for ka was sufficient for describing the genetic variance along the age trajectory. Models with higher orders of ka than 1 did converge, but they did not improve BIC (Table 2). The heritabilities for the 4 traits are presented in Figure 2, where the heritabilities are plotted as a function of age with uncertainty around the curve given by the gray shaded area. The heritability estimates for semen volume were clearly increasing as the boar matured, while the total and functional sperm count were close to constant with increasing age. The heritability for sperm concentration was fluctuating somewhat over time. The heritabilities ranged from 0.23 to 0.26, 0.23 to 0.31, 0.18 to 0.20 and 0.17 to 0.19 for sperm concentration, semen volume and, total and functional sperm count in the ejaculate, respectively, excluding the edges of the curves. The genetic correlations (Table 3) across the different age classes for the traits sperm count and semen volume were high and ranged from 0.8 to almost 1, indicating that these traits do not undergo significant changes as the boar matures. Total and functional sperm counts were correlated even higher on the genetic level as the correlation ranged from 0.9 to almost 1.

The heritability of abnormal ejaculates on liability scale were 0.059 (0.02) and 0.062 (0.02) for the probit and logit link functions, respectively. The GLMM estimates of heritability on the logit

and probit scales were transformed to the observed scale. Heritability on the observed scale was 0.015 and quite similar to a univariate linear mixed model.

Genetic Parameters for Boar taint Compounds

A significant proportion of the variation in boar taint was of genetic origin, which was confirmed by the moderate to high heritabilities for both compounds. These amounted to 0.33 and 0.59 for Log(skatole) and Log(androstenone), respectively, across the different models (Tables 4 and 5). The genetic correlation between Log(skatole) and Log(androstenone) was approximately 0.4, positive and significantly different from zero.

Genetic Correlations between Boar taint and Male Fertility

The male genetic contribution to litter size and survival is much lower and amounting to approximately 0.02 of the phenotypic variance (Tables 4 and 5). The correlation between additive genetic effect on boar taint and the service-sire genetic effect on litter size was mainly favorable and ranged from 0.05 to -0.40, but none of the estimated genetic correlations were significantly different from zero. Genetic correlations between zero and first order coefficients of the Legendre polynomials, representing the genetic covariance along the trajectory, and boar taint compounds are presented in Table 6. The estimates ranged from 0.02 to -0.24 and from 0.24 to -0.70 for the zero and first order coefficients, respectively. Genetic correlations between functional sperm production at different ages and Log(skatole) and Log(androstenone) is presented in Figure 3 as an illustration of the consequence of modeling functional sperm production as continuously changing trait. If the genetic correlation between boar taint and first order coefficients is negative then genetic

correlation will evolve favorably with age and visa versa. Hence, the general trend across the different traits seems to be towards more favorable genetic correlations. The genetic correlation between Log(skatole) and abnormal semen cells were 0.09 (0.20) and 0.07 (0.21) for the models utilizing probit and logit link functions, respectively. The corresponding genetic correlations to Log(androstenone) were -0.39 (0.25) and -0.42 (0.25) for the models utilizing probit and logit link functions, respectively. Most genetic correlations were estimated with large standard errors as the numerical values were close estimates themselves. This is also indicated in Figure 3, especially for Log(androstenone).

DISCUSSION

Genetic Parameters for Semen Production

Although male fertility is not part of the breeding objectives in Danish pig breeds it is desirable to ensure that it is not negatively impacted by current selection and by inclusion of new traits in the breeding objective such as boar taint traits. Random regression models have been used in both pigs and cattle by Oh et al. (2006) and Carabano et al. (2007) to model semen production because these models allow environmental and genetic variance to continuously change as the boar matures. Based on the BIC, Oh et al. (2006) concluded that first-, and sixth-order Legendre polynomials for additive genetic and permanent environmental effects were desirable for modeling the variation in total sperm count along the age trajectory. This result is in accordance with our observation given in Table 2 for total sperm count. Both our and their approach assumed a homogeneous residual variance across ages of the boars. We plotted residuals as a function of age to check this assumption and did not reveal any deviation from the assumption (results not shown). Fitting the same order to all components allows for equal flexibility of both curves and avoids counterbalance effects.

Previous studies, applying random regression methodology to analyze semen traits, have all shown evidence of better performance of models by fitting a lower order for the genetic component than for the permanent environmental effect (Carabano et al., 2007; Oh et al., 2006). In fact, a lower order of polynomial for the genetic component would be biologically more sensible provided that larger orders of polynomials are likely to generate waving patterns, which might yield unexpected shapes for the genetic variance over time. Furthermore, rapid oscillatory behavior of the genetic merit of quantitative traits is not biologically understandable. On the other hand, given that semen traits measured during the lifetime of boars are usually quite oscillatory, environmental effects linked to individual boars could be expected to waver and should require larger order polynomials. Larger order polynomials are more flexible and can accommodate a wider variety of shapes for the permanent environmental effects.

Wolf (2009, 2010) estimated heritabilities of 0.19 to 0.25 and 0.18 to 0.19 for semen volume and sperm concentration, respectively, in Czech Landrace. The corresponding estimates from our investigation were 0.23 to 0.26 and 0.23 to 0.31, and thus slightly higher compared to both the studies. Grandjot et al. (1997) estimated heritabilities of 0.14 to 0.18, 0.17 to 0.26, and 0.17 to 0.25 for semen volume, sperm concentration, and the total number of sperm in the ejaculate, respectively. Heritability estimates for total number of sperm in the ejaculate ranged from 0.27 to 0.48 across ages and the heritability for the trait tending to increase with age (Oh et al., 2006), being substantially higher than the current estimates.

In summary, random regression models with Legendre polynomials are useful for analyzing semen characteristics because they can account for different environmental effects at different time points and because they provide information on both the level of production and its changes along time in a continuous manner. The genetic potential to produce semen changed with time, exhibiting different patterns among individuals. The semen traits showed a moderate heritability, ranging from

0.18 to 0.31, while ignoring edges with few observations. This indicates that selection for these traits may be effective at any stage.

Genetic Parameters for Boar taint Compounds

In an earlier investigation in Danish Landrace, the heritability of skatole concentration in back fat was reported as 0.27 (Pedersen, 1998), which was close to the current estimate. The estimate in the present study was somewhat lower than reported by Tajet et al. (2006) who estimated a heritability of 0.55, while 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 and Windig et al. (2012) recently reported a heritability of 0.41, which was slightly higher than our estimate. Heritability of androstenone in Norwegian Landrace has been reported to 0.54 and 0.49 by Tajet et al. (2006) and Grindflek et al. (2011), respectively. The genetic correlation between the two 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 – 0.36 in Norwegian Landrace (Grindflek et al., 2011; Tajet et al., 2006), which corresponds very well with the current estimates of approximately 0.4. Windig et al. (2012) reported a genetic correlation of 0.37 between the two traits in the Dutch populations, based on several sire and dam lines. Based on the current investigation and previously published work in Denmark and other European countries, it can be stated that Log(skatole) was moderately- and Log(androstenone) was highly heritable, which was expected. These results suggest that selection emphasis should be placed on both compounds if the selection is to be based directly on the chemical components.

Genetic Associations between Boar Taint Compounds and Male Fertility

The variance component associated with service-sire genetic effects was in line with previous estimates derived from Finnish and Danish Landrace populations (Serenius et al., 2004; Su et al., 2007). The variance component of service-sire genetic effects on litter size traits reflects sire fertility and its contribution to fertilization and embryo survival and eventual piglet survival through the genes passed on to the offspring. The correlation between sow genetic effects and service-sire genetic effects were small to moderate and positive and hence the continued selection on the sow component of the LP5 trait will improve service-sire fertility. These findings were consistent with Su et al. (2007). Our results did not indicate unfavourable relationship between the genetic effects of boar taint and service-sire genetic effects on litter size. Hence our results indicate that selection against boar taint compounds will not deteriorate service-sire fertility and embryo survival, since selection against boar taint would have limited effects on the service sire genetic component of litter size. Unfavorable genetic correlations between androstenone and serum sex hormone concentrations have been reported (Grindflek et al., 2011) and hence it was speculated that an unfavorable correlations existed between boar taint and semen and litter size traits. On the contrary, genetic correlations between boar taint and 8 traits all being indicators of reproductive performance pointed consistently in a favorable direction i.e., favourable estimates of genetic correlations. The explanation could be that different sets of genes control sex hormone concentrations compared with sperm characteristics as well as paternal effects of fertilization, embryo and offspring survival. However, one drawback of using litter size as measure of male and female fertility is that inseminations that do not result in pregnancy are ignored, which may lead to biased results. Also, it must be kept in mind that the correlations were estimated with large standard errors in our study which were partly due to lack of common observations on boar taint and fertility traits. Uzu and Bonneau (1980) concluded that androstenone level seemed to be independent from main parameters of the ejaculate: volume, concentration and total semen. Thus, there would be no relationship

between androstenone level of adipose tissue and boar's reproduction performances (Uzu and Bonneau, 1980), supporting the results in the current study. It must be mentioned that their conclusions were drawn from recordings on only 28 boars. The total sperm number per ejaculate was not correlated with the serum testosterone concentration in the study of Ren et al. (2009). Walker et al. (2004) demonstrated that serum testosterone concentrations of a high and a low testosterone production line differed by a two-fold and the sperm production by the boars under the divergent selection for testosterone production was unaffected. Ren et al. (2009) concluded that selection for the serum testosterone production should not be recommended for increasing the sperm production, and the serum testosterone concentration in mature boars could not be recommended as the indicator for sperm production. Additionally, the total sperm number per ejaculate was not correlated with boar libido, while serum testosterone concentration was moderately correlated to boar libido (Ren et al., 2009). Recording boar libido may be important for quantifying the effects of reducing boar taint by selection because a strong libido is desirable for AI-stations. In both studies (Ren et al., 2009; Walker et al., 2004), significant morphological changes were observed for boars displaying low serum testosterone concentrations because it was correlated with epididymis weight in both studies (Ren et al., 2009; Walker et al., 2004). The length of glandula bulbourethralis has been reported to be unfavorably correlated to both androstenone and skatole (Tajet et al., 2006). It is expected that breeding against boar taint should not affect sperm production, but morphological changes to the male reproductive system may occur.

In conclusion, selection for boar taint compounds does not seem to negatively affect semen production as well as survival of embryos and offspring. These results should be confirmed in other breeds and genetic correlations with libido and sexual maturity should be estimated before industry wide implementation.

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Figure 1. Number of ejaculates (left y-axis, as bars) and average number of functional sperm cells per ejaculate (right y-axis, dotted line) plotted as a function of the boar's age in weeks.

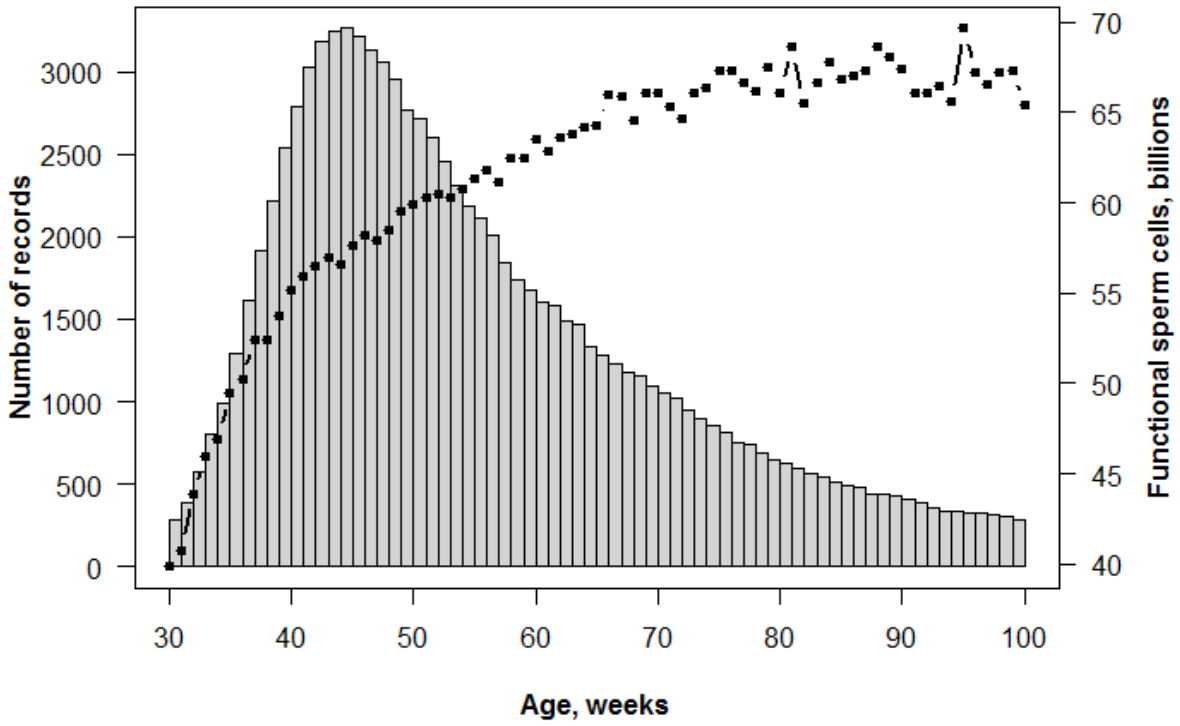

Figure 2. Heritability estimates of semen traits as a function of the age of the boar. Grey shaded areas represent estimate ±1.96 x standard error.

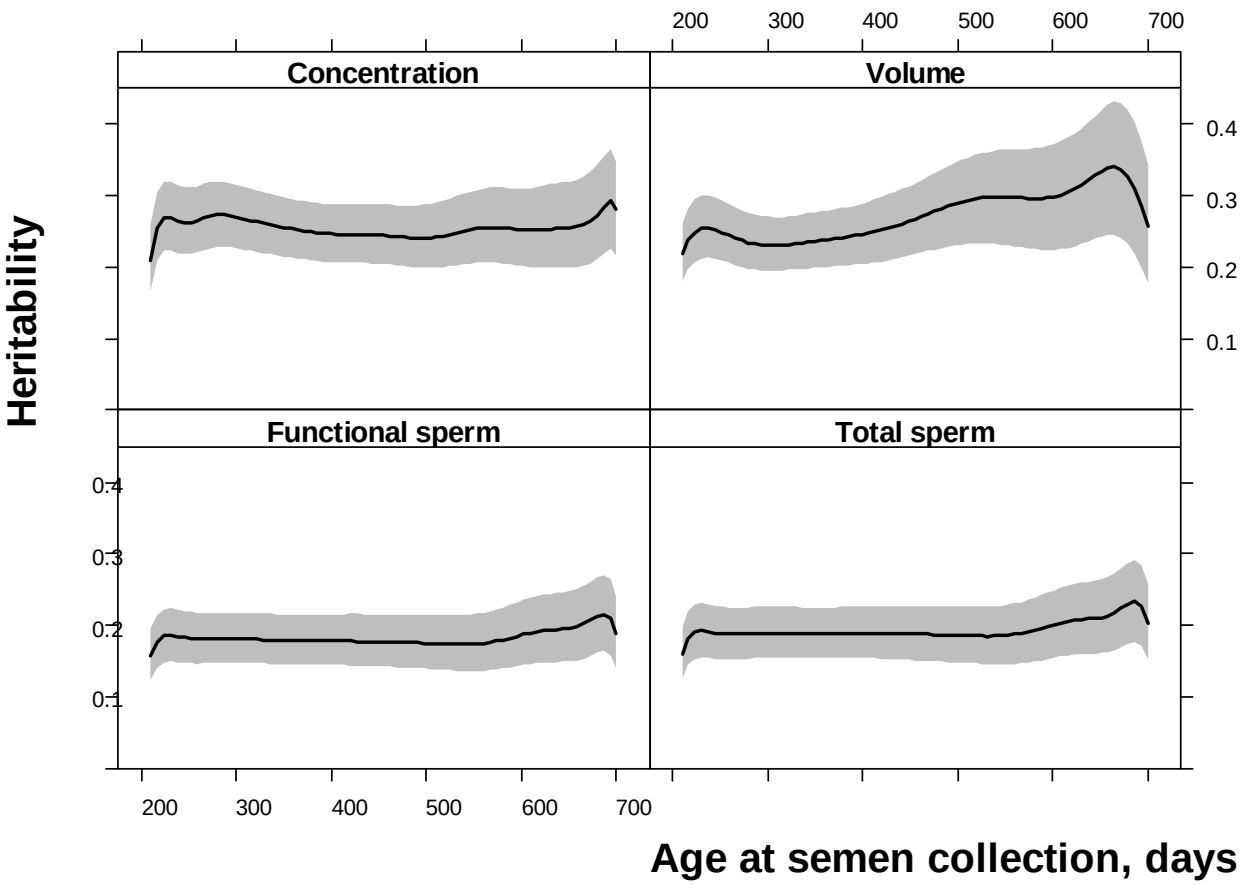

Figure 3. Genetic correlation between functional sperm at different ages and Log(skatole) and Log(Androstenone). Grey shaded areas represent estimate ±1.96 x standard error.

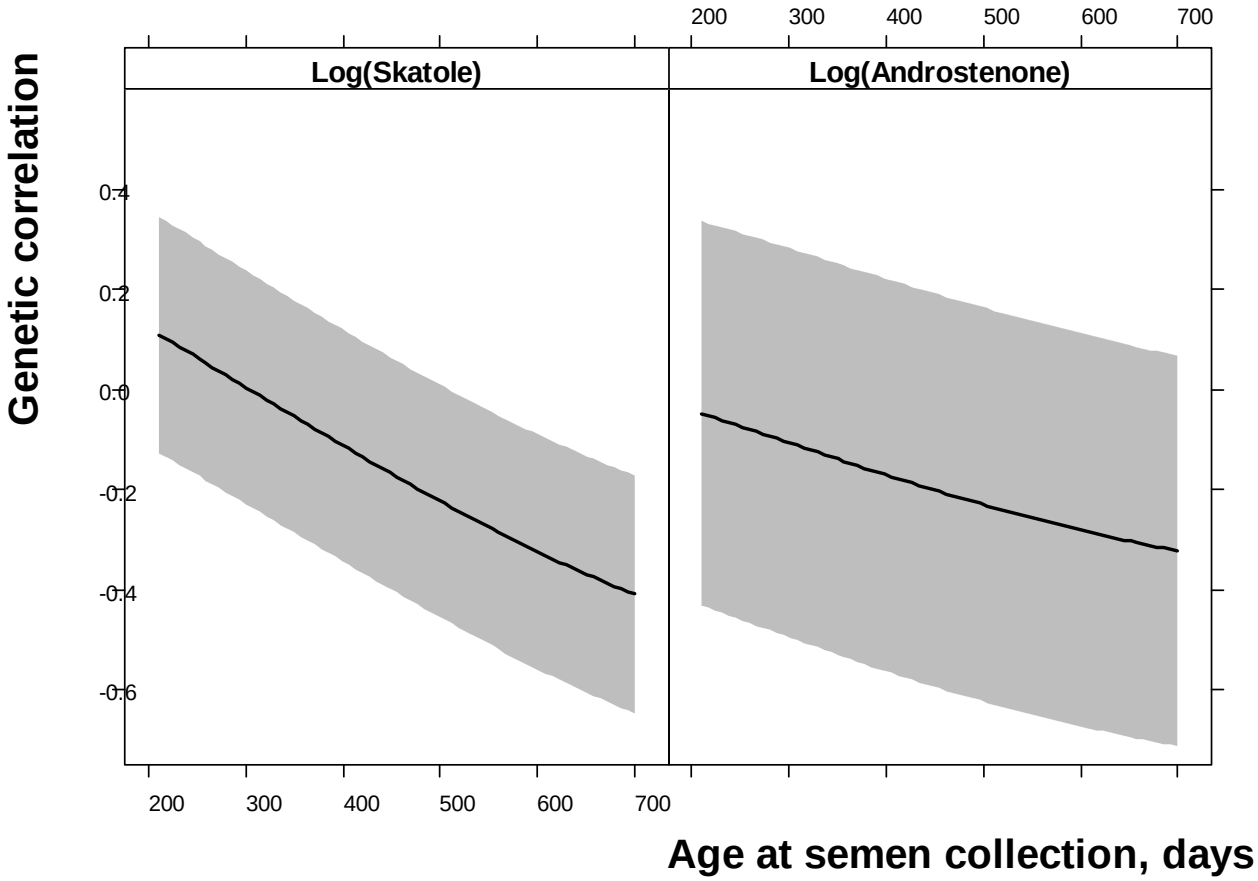

Table 1. Summary statistics for the traits[1] included in the dataset

Trait	No. records	Mean	Standard dev.	Minimum	Maximum
Boar taint					
Skatole, ug/g	5937	0.197	0.145	0.020	2.860
Androstenone, ug/g	920	1.080	0.985	0.010	10.60
Semen characteristics					
Volume, ml	95267	195	77.7	26.0	598
Concentration, 10^6/ml	95267	374	134	103	998
Total sperm, 10^9/ejaculate	95267	67.8	26.2	7.20	199
Functional sperm, 10^9/ejaculate	95267	60.3	23.4	5.76	179
Litter size					
TBN	35715	13.56	3.832	1.000	28.00
LP5	34991	10.47	3.453	0.000	22.00
SV5	34991	0.780	0.188	0.000	1.000

[1]Total number born (TBN), live piglets at day 5 (LP5) and survival rate until day 5 (SV5)

Table 2. Fit statistics (-2log likelihood, Bayesian and Akaike information criterion) for the top three random regression models. The superior model is identified, which is based on BIC and it represents the appropriate order (kp and ka) for the Legendre polynomials.

Trait	kp	ka	-2LogL	AIC	BIC
Volume	4	1	859027.3	859841.3	863691.6
	4	2	859006.2	859826.2	863704.9
	4	3	858980.4	859808.4	863725.0
Concentration	7	1	974279.1	975135.1	979184.1
	8	1	974176.7	975050.7	979184.9
	7	3	974204.0	975074.0	979189.2
Total sperm	6	1	129211.3	130051.3	134024.6
	6	2	129185.7	130031.7	134033.4
	5	1	129314.7	130140.5	134047.6
Functional sperm	6	1	120011.2	120851.2	124824.6
	6	2	119988.8	120834.8	124836.5
	5	1	120107.4	120933.4	124840.6

Table 3. Genetic correlations (below diagonal) and phenotypic correlations (above diagonal) between semen traits recorded between 40 to 90 weeks of age. The correlations are derived from the univariate random regression models and their corresponding covariance functions.

Sperm concentration:						
Age	40	50	60	70	80	90
40		0.37	0.32	0.30	0.29	0.29
50	0.99		0.40	0.32	0.28	0.30
60	0.97	0.99		0.38	0.29	0.29
70	0.93	0.96	0.99		0.38	0.29
80	0.87	0.92	0.96	0.99		0.39
90	0.80	0.86	0.92	0.96	0.99	
Semen volume:						
Age	40	50	60	70	80	90
40		0.41	0.31	0.27	0.29	0.34
50	0.99		0.46	0.38	0.30	0.31
60	0.95	0.99		0.49	0.37	0.31
70	0.91	0.97	0.99		0.50	0.42
80	0.86	0.93	0.98	0.99		0.58
90	0.81	0.90	0.95	0.98	0.99	
Total sperm cells:						
Age	40	50	60	70	80	90
40		0.30	0.26	0.26	0.26	0.25
50	0.99		0.34	0.29	0.28	0.28
60	0.98	0.99		0.37	0.30	0.30
70	0.96	0.98	0.99		0.40	0.33
80	0.94	0.97	0.99	0.99		0.38
90	0.90	0.94	0.97	0.99	0.99	
Functional sperm cells:						
Age	40	50	60	70	80	90
40		0.29	0.25	0.26	0.25	0.24
50	0.99		0.33	0.28	0.27	0.27
60	0.98	0.99		0.36	0.29	0.29
70	0.96	0.98	0.99		0.39	0.32
80	0.93	0.96	0.98	0.99		0.37
90	0.90	0.93	0.96	0.99	0.99	

Table 4. The proportion of phenotypic variance that is due to sow and service-sire genetic effects on litter size traits and direct animal genetic effects on boar taint compounds are presented in bold face on the diagonal. Genetic correlations between litter size traits and boar taint compounds are presented below the diagonal.

Trait		TNB[1]		LP5[1]		Log(skatole)	Log(androstenone)
		Sire	Dam	Sire	Dam		
TNB	Sire	**0.02 ± 0.01**					
	Dam	0.36 ± 0.14	**0.09 ± 0.01**				
LP5	Sire	0.70 ± 0.10	0.17 ± 0.12	**0.02 ± 0.01**			
	Dam	0.43 ± 0.05	0.58 ± 0.15	0.38 ± 0.13	**0.06 ± 0.01**		
Log(skatole)		0.05 ± 0.22	0.06 ± 0.11	-0.11± 0.18	0.03 ± 0.13	**0.33 ± 0.04**	
Log(androstenone)		-0.20 ± 0.27	-0.14 ± 0.15	-0.40 ± 0.22	-0.20 ± 0.17	0.41 ± 0.14	**0.59 ± 0.13**

[1]TNB: Total number of born piglets; and LP5: Live piglets at day 5

Table 5. The proportion of phenotypic variance that is due to sow and service-sire genetic effects on survival rate until day 5 (SV5[1]) and direct animal genetic effects on boar taint compounds are presented in bold face on the diagonal. Genetic correlations between SV5 and boar taint compounds are presented below the diagonal.

Trait		SV5[1]		Log(skatole)	Log(androstenone)
		Sire	Dam		
SV5[1]	Sire	**0.02 ± 0.004**			
	Dam	0.29 ± 0.10	**0.09 ± 0.01**		
Log(skatole)		-0.15 ± 0.14	0.00 ± 0.12	**0.33 ± 0.04**	
Log(androstenone)		-0.33 ± 0.18	0.02 ± 0.17	0.43 ± 0.14	**0.58 ± 0.14**

Table 6. Genetic correlations between coefficients of the Legendre polynomials, describing the genetic component of semen traits along the age trajectory, and boar taint components.

Trait (x)	Order	$r_{g(x, Log(skatole))}$	$r_{g(x, Log(androstenone))}$
Volume	0	0.01 ± 0.13	0.02 ± 0.18
	1	-0.05 ± 0.24	-0.22 ± 0.30
Concentration	0	-0.11 ± 0.13	-0.24 ± 0.16
	1	-0.30 ± 0.22	0.24 ± 0.25
Total sperm	0	-0.17 ± 0.13	-0.13 ± 0.18
	1	-0.68 ± 0.27	-0.11 ± 0.36
Functional sperm	0	-0.16 ± 0.17	-0.10 ± 0.18
	1	-0.70 ± 0.26	-0.10 ± 0.35