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GENETIC CONTROL OF RESIDUAL VARIANCE FOR TEAT NUMBER IN PIGS

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SUMMARY

The genetic improvement in litter size in pigs has been substantial during the last 10-15 years. The number of teats on the sow must increase as well to meet the needs of the piglets, because each piglet needs access to its own teat. We applied a genetic heterogeneity model on teat number in sows, and estimated medium-high heritability for teat number (0.5), but low heritability for residual variance (0.05), indicating that selection for reduced variance might have very limited effect. A numerically positive correlation (0.8) between additive genetic breeding values for mean and for variance was found, but because of the low heritability for residual variance, the variance will increase very slowly with the mean.

INTRODUCTION

For pigs the genetic improvement in litter size has been substantial during the last 10-15 years. The number of teats on the sow must increase as well to meet the needs of the piglets, because each piglet needs access to its own teat (Chalkias *et al.* 2013).

Genotypes differ not only in mean for a trait but also in variation around the mean (Mulder *et al.* 2007). The possibility to select for uniform individuals by selecting animals expressing a small response on environment has been studied extensively in animal breeding. Considerable support for a heritable component in the environmental variation has been found (Hill and Mulder 2010).

The term genetic heterogeneity is used for models including genetically structured differences in the residual variance. It is difference in residual variance among individuals maintained in similar environments, caused by genetic interaction with unknown environmental differences. Having fitted fixed effects such as herd and sex, the remaining unknown environmental differences among individuals are assumed to be negligible, therefore referred to as micro-environmental changes (Mulder *et al.* 2013, Rönnegård *et al.* 2013). Genetic heterogeneity is not to be confounded with the topic of robustness; reaction on macro environmental differences.

Rönnegård *et al.* (2010) and Felleki *et al.* (2012) proposed an algorithm for estimation of genetic heterogeneity, which builds on the theory of Double Hierarchical Generalized Linear Models (Lee and Nelder 2006). The algorithm has previously been used for analysing data on litter sizes in pigs, and for analysing data on milk yield and somatic cell counts in dairy cattle (Rönnegård *et al.* 2013).

The aim for this paper is to study genetic heterogeneity for teat numbers in pigs, and thereby discuss the feasibility for genetic increase of number of teats in sows, that is, the possibility to select for an increasing stabile number of teats.

MATERIAL AND METHODS

Data were obtained from the Swedish pig breeding organisation Nordic Genetics, and included data on teat number (recorded at three weeks of age, both genders) on 47866 purebred Yorkshire pigs and their pedigree (in total 52817 individuals). The teat number is total teat number including non-functional teats. The pigs were born between January 2007 and April 2009. Variables in the data set were number of teats at three weeks of age, litter identity, year-month of birth, herd, gender, litter size, and birth parity number. Analyses were restricted to nucleus herds with at least

a thousand animals recorded during the time period considered. Teat number observations below ten and above nineteen (totally 25 observations) were removed from the data set.

The mean of teat number was 14.49, and the standard deviation was 0.94. Most pigs (24147) had 14 teats, 12355 had 15 teats, 6708 had 16, 3017 had 13, 825 had 12, 642 had 17 teats, and the rest (totally 172) had 10, 11, 18 or 19 teats. Number of dams was 3403 and number of sires was 337. Dams had between 1 and 67 offspring with median 11, and sires had between 2 and 717 offspring with median 87.

Four models were fitted. For the first model, the Animal model, teat numbers *y* were modelled

$$y = \mu + X\beta + Za + Wpe + e,$$

where μ was an intercept, β was a vector of fixed effects of year-month of birth, herd, gender, and birth parity number, X was a known design matrix, $a \sim N(0, A\sigma_a^2)$ was the random effect of animal, A was the additive genetic relationship matrix, $pe \sim N(0, I\sigma_{pe}^2)$ was the random effect of litter identity, Z and W were known coincidence matrices, and $e \sim N(0, I\sigma_E^2)$ was the residual.

Three models included individually structured genetically differences in the residual variance. Same additive genetic structure, either sire, dam, or sire-dam, was used for mean and variance, and the models were named Sire, Dam, and Sire-dam referring to the common structure of the additive genetic effects s for the mean model and s_d for the variance model. The coincidence matrix Z had a 1 in the column for sire, dam or both, and the mean part was otherwise similar to the animal model, $y = \mu + X\beta + Zs + Wpe + e$.

The residuals were assumed to be heterogeneous, $e \sim N(0, \Phi)$, Φ was a diagonal matrix with diagonal φ, and it was assumed that φ was linear on logarithmic scale, $\log \varphi = \log \sigma_{E,exp}^2 + X\beta_d + Zs_d + Wpe_d$.

It was moreover assumed that s and s_d were correlated,

$$\begin{pmatrix} s \\ s_d \end{pmatrix} \sim N(0, \begin{pmatrix} \sigma_s^2 & \rho\sigma_s\sigma_{s_d,exp} \\ \rho\sigma_s\sigma_{s_d,exp} & \sigma_{s_d,exp}^2 \end{pmatrix} \otimes A),$$

while the random effects for litter identity pe and pe_d were assumed independent, $pe_d \sim N(0, I\sigma_{pe_d,exp}^2)$. Fixed effects, β_d, were same as for the mean model.

The genetic heterogeneity models were fitted using the algorithm from Felleki *et al.* (2012). The statistical principle used is that of extended likelihood, or hierarchical likelihood. The joint likelihood of trait values and random effects is used for estimation of mean effects, and adjusted profile likelihoods are used for estimation of effects for the residual variance, and for estimation of the variance components. The resulting algorithm is feasible for large data sets, and necessary commands are implemented in ASReml 4.0.

Mulder *et al.* (2007) gave formulas for the heritability for residual variance, which is modified to be used for the sire, dam, and sire-dam models with permanent environmental effect,

$$h_v^2 = \frac{4\sigma_{s_d}^2}{2\sigma_P^4 + 3(\sigma_{s_d}^2 + \sigma_{pe_d}^2)},$$

where

$$\sigma_P^2 = \sigma_a^2 + \sigma_{pe}^2 + \sigma_E^2,\ \sigma_E^2 = \sigma_{E,exp}^2 \exp\left(\frac{\sigma_{a_d,exp}^2}{2}\right) \exp\left(\frac{\sigma_{pe_d,exp}^2}{2}\right),$$

$$\sigma_{s_d}^2 + \sigma_{pe_d}^2 = \sigma_{E,exp}^4 \exp\left(2\sigma_{s_d,exp}^2\right) \exp\left(2\sigma_{pe_d,exp}^2\right) - \sigma_E^4,\ \sigma_{s_d}^2 = (\sigma_{s_d}^2 + \sigma_{pe_d}^2) \cdot \left(\frac{\sigma_{s_d,exp}^2}{\sigma_{pe_d,exp}^2 + \sigma_{s_d,exp}^2}\right).$$

The genetic coefficient of correlation was calculated by $\mathrm{GCV_E} = \sqrt{4\sigma_{s_d}^2}/\sigma_E^2$.

RESULTS AND DISCUSSION

Estimated variance components with standard errors for the four models are found in Table 1. The genetic variance component, σ_a^2, for the animal effect for the mean part of the genetic

heterogeneity models is calculated by $\sigma_a^2 = 4\sigma_s^2$, and these values are between 0.33 and 0.38 in agreement with 0.35 for the animal model.

Table 1. Estimate(standard error) of variance components for an animal model, and variance components and correlations for three genetic heterogeneity models with identical genetic structure for mean and variance (sire, dam, or sire-dam)

Model name	σ_{pe}^2	σ_a^{2*}	$\log \sigma_{E,exp}^2$	$\sigma_{pe_d,exp}^2$	$\sigma_{s_d,exp}^2$	ρ
Animal[†]	0.03(0.003)	0.35(0.017)	-0.67(0.008)			
Sire	0.10(0.003)	0.33(0.036)	-0.64(0.064)	0.12(0.008)	0.03(0.005)	0.85(0.047)
Dam	0.09(0.004)	0.38(0.026)	-0.59(0.068)	0.09(0.008)	0.07(0.008)	0.86(0.039)
Sire-dam	0.02(0.003)	0.34(0.018)	-0.55(0.074)	0.07(0.008)	0.04(0.004)	0.81(0.035)

[*] For the three latter models, $\sigma_a^2 = 4\sigma_s^2$.

[†] Residual variance for Animal model is estimated on logarithmic scale, $\sigma_E^2 = \exp(\log \sigma_{E,exp}^2)$, where $\log \sigma_{E,exp}^2$ is estimated.

The correlation ρ is positive and numerically high (0.81-0.86) indicating a close connectedness between breeding values for mean and for residual variance, hence a Poisson model for teat data might be more appropriate.

Phenotypic variance, σ_P^2, is 0.89 for the animal model, and between 0.72 and 0.78 for the genetic heterogeneity models (Table 2). The difference in values among models might be due to the assumption that the random effects are independent, or the lower values for the genetic heterogeneity models might be caused by the fixed effects in the variance part.

Heritability, h^2, for teat number is found in the medium-high range between 0.39 and 0.48, as previously reported (Chalkias *et al.* 2013). For the animal model, h^2 is 0.39, while h^2 is slightly higher for the genetic heterogeneity models (0.45-0.48).

The heritability for residual variance, h_d^2, takes the values 0.03, 0.05, and 0.07. These are in the higher range of common reported values (Hill and Mulder 2010). As heritability values, however, these values are negligible. The closely connected genetic coefficients of variation GCV_E, with values between 0.34 and 0.59, are also found in the higher range of common values.

Table 2. Heritability and genetic coefficient of variation

Model name	σ_P^2	h^2	$\sigma_{a_d}^2$	h_d^2	GCV_E
Animal	0.89(0.009)	0.39(0.016)			
Sire[‡]	0.75	0.45	0.04	0.03	0.34
Dam[‡]	0.78	0.48	0.10	0.07	0.54
Sire-dam[‡]	0.72	0.48	0.06	0.05	0.39

[‡] Standard errors could not be found.

Inferences under the genetically structured heterogeneous variance model can be misleading when the data are skewed (Yang *et al.* 2011). Therefore data should be checked for scale effects before fitting a genetic heterogeneity model, which has not been done in this study.

Functionality (not inverted, blind, small or inserted) of the teats is a necessity. In this study the genetic components for mean and for variance of total number of teats are estimated, leaving out correlation between functional, non-functional, and total teat number. The data for this study is collected at three weeks of age; hence the counts of non-functional teats might not be accurate.

Chalkias *et al.* (2013) found a favourable (that is positive) correlation between number of functional and total number of teats, and concluded that the genetic increase of teats, will give

increase in functional teats as well. They did, however, mention the possible consequence of a non-functional teat for a piglet using the crucial first hours of life suckling it. We suppose that also the sow could be stressed of this with consequences for nursing behaviour. 13% of all tested pigs had at least one non-functional teat.

Traits important for pig production are many: litter size and uniformity, piglet survival, weight and growth, milk production, teat number, ability to become pregnant, and behaviour (Rydhmer 2000). Many of these traits are genetically connected such that selection on one, as practised on teat number, might give undesired results for other traits (Chalkias *et al.* 2013). These correlations are to be studied.

The heritability for the residual variance, and the correlation between breeding values for mean and variances, can be tools to determine if a trait can be controlled under selection, or if fluctuation of the trait values will increase. In this study we find a considerable correlation, thus variances are expected to increase with increased mean values, and we also find a low value for heritability of residual variance, indicating that selection for reduced variance might have very limited effect. Hill and Mulder (2010) reported that no convincing results have been reported this far on selection for reduced variance in any study. It would be interesting to repeat such an experiment on a trait with a numerically small mean-variance correlation (close to zero) and high variance heritability, if such a trait is found.

CONCLUSION

For teat number in pigs, we find breeding values for mean and variance to be highly correlated indicating a Poisson distribution. Hence selecting for an increased mean number, the variance might increase as well. We also find heritability of breeding values for residual variance to be low; hence selection for decreased residual variance might give negligible response.

As long as the new teats are mainly functional, one way to go around the problem is selection of sows with many functional teats for production as already practised. The low heritability for residual variance indicates that the variance will increase very slowly with the mean. However the piglet's and sow's reactions on non-functional teats are to be investigated.

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