Genetic parameters for a joint genetic evaluation of production and reproduction traits in pigs

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ABSTRACT: The covariance structure was estimated by REML for a joint genetic evaluation of production and reproduction traits for Czech Landrace (58 258 records) and Czech Large White (167 161 records) pigs using four-trait animal models. The following traits were analysed: lean mean percentage at the end of the performance test in the field, estimated from ultrasonic measurements unadjusted for live weight (LM), average daily gain in field test (in g/day) calculated as weight at the end of the test divided by age at the end of the test (ADG), number of piglets born alive in parity 1 (NBA1) and number of piglets born alive in parity 2 and subsequent parities (NBA2+). The heritabilities were in the range from 0.30 to 0.37 for LM, from 0.13 to 0.18 for ADG, from 0.09 to 0.13 for NBA1 and from 0.10 to 0.14 for NBA2+, depending on the breed and on the model (herd-year-season random or fixed). Genetic correlations between production and reproduction traits were estimated to be non-zero. Correlations between traits caused by the herd-year-season effect were mostly positive. As a general conclusion, the joint genetic evaluation of production and reproduction traits is recommended. The herd-year-season effect should be preferably considered as random.

Keywords: pig; production traits; reproduction traits; multi-trait animal model; genetic parameters

Mainly for historical reasons, genetic evaluation for pigs is carried out separately for production and reproduction traits in most pig breeding associations. As a rule, the animal model for production traits was developed first and reproduction traits were added later to genetic evaluation. Computer resources were limited in the starting phase of animal model based genetic evaluation, which was probably another reason for separate analyses.

Recently, the joint evaluation of production and reproduction traits has become possible and should be used as the method of choice being a logical extension. Joint genetic evaluation of production and reproduction traits has been implemented in the Czech Republic and in Slovakia since 1999 (Wolf *et al*., 1999; Peškovičová *et al*., 2002). Currently, in the Czech Republic routine testing has shifted completely from station to large-scale field testing with only a small number of animals being tested on station for monitoring the development of carcass and meat quality traits. Therefore, a revision of the models used and a new estimation of genetic parameters became necessary.

MATERIAL AND METHODS

The analyses were based on performance test data for the breeds Czech Landrace and Czech Large White. The time period considered was 1995 to 2004, both for production and reproduction traits. The analysed traits were as follows:

LM – Lean mean percentage at the end of the performance test, estimated from ultrasonic measurements unadjusted for live weight

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ADG – Average daily gain in field test (in g/day) calculated as weight at the end of the test divided by age at the end of the test

NBA1 – Number of piglets born alive in parity 1

NBA2+ – Number of piglets born alive in parity 2 and subsequent parities

All data were collected under field conditions. The field test for production traits started at an age of 80 to 88 days and lasted between 56 and 70 days (from 1 January 2003 on this interval was changed to 49 to 63 days for gilts, young boars were not affected). The weight at the beginning of the test was approximately 30 kg. No editing of production data was required as all records were in the required range. For reproduction data the following editing was carried out:

– The gestation length was expected to be in the interval between 105 and 125 days
– The minimal age for farrowing was 300 days
– Parities higher than 10 were not considered
– The age of the sow for parities 1 to 10 had to be in the following intervals: 300–500 d, 450 to 750 d, 600–950 d, 750–1 150 d, 1 050–1 550 d, 1 200–1 750 d, 1 350–1 850 d, 1 500–2 050 d and 1 650–2 250 d, respectively
– The total number of piglets born should not be lower than 4
– The difference between the number of piglets weaned and the number of piglets born alive should not be larger than 4
– The farrowing interval should be between 130 and 300 days

When applying these restrictions, about 10% of the reproduction records were excluded.

The herd-year-season effect was defined in the same way for production and reproduction traits. A flexible allocation of records to herd-year-season classes was applied. For this purpose, a Fortran

Table 1. Number of observations, means and standard deviations for individual traits for the breeds Czech Landrace and Czech Large White

Trait	*n*	Mean	SD
Czech Landrace			
Lean meat percentage (%)	37 780	61.5	2.12
Average daily gain from birth to test end (g/d)	37 780	626	73.40
Number of piglets born alive in parity 1	6 790	10.4	2.20
Number of piglets born alive in parity 2 and subsequent parities	13 688	11.1	2.35
Start weight in the field test (kg)	37 780	30.1	4.47
End weight in the field test (kg)	37 780	92.8	11.29
Age at the beginning of the test (d)	37 780	84.1	2.37
Age at the end of the test (d)	37 780	148.3	4.88
Age at parity 1 (d)	6 790	369	36.30
Farrowing interval before parity 2 and higher (d)	13 688	168	26.10
Czech Large White			
Lean meat percentage (%)	106 596	61.3	2.27
Average daily gain from birth to test end (g/d)	106 596	592	64.70
Number of piglets born alive in parity 1	17 815	10.2	2.17
Number of piglets born alive in parity 2 and subsequent parities	42 750	11.0	2.30
Start weight in the field test (kg)	106 596	29.6	4.82
End weight in the field test (kg)	106 596	87.7	9.83
Age at the beginning of the test (d)	106 596	84.2	2.43
Age at the end of the test (d)	106 596	148.2	4.92
Age at parity 1 (d)	17 815	375	38.60
Farrowing interval before parity 2 and higher (d)	42 750	165	24.8

n – number of records, SD – phenotypic standard deviation program was written. The principles for forming herd-year-season classes were as follows. Herd-year-season classes were preferably formed according to natural seasons and normally had a length of three months: March to May, June to August, September to November and December to February of the following year. The minimal total number of records (for production and reproduction traits) for each herd-year-season class was 20. At least three of these records had to be on the number of piglets born alive in parity 1, four of these records had to be on the number of piglets born alive in parity 2 and subsequent parities and at least five of these records had to be on production traits. As it could happen that in certain time intervals no records were available in a herd, it was ensured that the minimal time interval between the first and the last record in the herd-year-season class was not shorter than 30 days.

The number of records, the phenotypic mean and standard deviation for all four traits and some further characteristics are summarized in Table 1. The mean performance of both breeds was very similar. The data set for Czech Large White was about three times as large as the data set for Czech Landrace.

A four-trait animal model was used for the estimation of the covariance components. The structure of the model is given in Table 2. For the factor "parity" in the model, 1 to 4 was used for parities 1 to 4, the code 5 summarized parities 5 and 6 and the code 6 summarized parities 7 to 10. This was done to keep the number of records for the higher parity orders reasonably high. Linear regression on live weight was only included for lean meat content, not for daily gain. A quadratic regression on age at farrowing was used for the number of piglets born alive in parity 1 whereas for the subsequent parities a quadratic regression on the farrowing interval was included. The model for the number of piglets born alive in parity 2 and subsequent parities is a repeatability model and includes therefore the effect of parity and the permanent effect of the sow.

For each of both data sets (i.e. both breeds) two calculations were carried out differing in treating the herd-year-season effect as random or as fixed. All available pedigree information was used. That means the pedigree was traced back approximately to the year 1980.

Restricted maximum likelihood (REML) and optimisation by a quasi Newton algorithm with analytical gradients (Neumaier and Groeneveld, 1998) as implemented in VCE 4.0 program (Groeneveld and Garcia Cortes, 1998) were used to estimate the

Table 2. Structure of the four-trait animal model

Factor	Type of factor	LM	ADG	NBA1	NBA2+
Live weight at the beginning of the test	C	x	–	–	–
Live weight at the end of the test	C	x	–	–	–
Age at parity 1 linear and squared	C	–	–	x	–
Farrowing interval linear and squared	C	–	–	–	x
Animal	A	x	x	x	x
Sex	F	x	x	–	–
Herd-year-season	F or R	x	x	x	x
Litter the animal is from	R	x	x	–	–
Mating type (AI or natural mating)	F	–	–	x	x
Breed of the boar	F	–	–	x	x
Parity	F	–	–	–	x
Permanent effect of the sow	R	–	–	–	x

Type of factor: C – covariable, A – random with relationship matrix, R – random, F – fixed

Traits: LM – lean meat content, ADG – average daily gain from birth to the end of the field test, NBA1 – number of piglets born alive in parity 1, NBA2+ – number of piglets born in parity 2 and subsequent parities

x – factor is used in the model

variances and covariances. Approximate standard errors of the covariance components representing the lower bound of the real standard errors were calculated from the Hessian matrix. The number of estimated covariances was 34 for the model with herd-year-season random and 24 for the model with herd-year-season fixed. The number of equations was in the range of 250 000 for Czech Landrace and around 700 000 for Czech Large White.

RESULTS

The estimated genetic parameters for the Czech Landrace and the Czech Large White breeds are presented in Tables 3 and 4, respectively. The estimate for the model with herd-year-season random is given in the first row and the estimate for herd-year-season fixed in the second row of each cell of the respective table. The covariance estimates for

Table 3. Genetic parameters for the Czech Landrace breed. Estimates for herd-year-season random (1st row) and fixed (2nd row) with approximate standard errors

	LM	ADG	NBA1	NBA2+
Heritabilities and genetic correlations				
LM	0.30 ± 0.005 0.32 ± 0.009	0.16 ± 0.018 0.03 ± 0.012	0.26 ± 0.023 0.10 ± 0.021	0.22 ± 0.018 0.01 ± 0.017
ADG		0.13 ± 0.005 0.16 ± 0.008	–0.06 ± 0.023 –0.32 ± 0.061	0.01 ± 0.017 –0.12 ± 0.029
NBA1			0.12 ± 0.007 0.09 ± 0.014	0.996 ± 0.003 0.96 ± 0.046
NBA2+				0.14 ± 0.006 0.11 ± 0.009
Proportions of variance and correlations caused by the litter of origin of the animal				
LM	0.08 ± 0.003 0.11 ± 0.004	0.11 ± 0.016 0.12 ± 0.020		
ADG		0.17 ± 0.003 0.24 ± 0.005		
Proportions of variance caused by the permanent environmental effect of the sow				
NBA2+				0.04 ± 0.006 0.05 ± 0.009
Proportions of variance and correlations caused by the herd-year-season effect				
LM	0.23 ± 0.006 –	0.12 ± 0.033 –	–0.003 ± 0.048 –	–0.11 ± 0.038 –
ADG		0.29 ± 0.005 –	0.55 ± 0.031 –	0.58 ± 0.027 –
NBA1			0.07 ± 0.005 –	0.96 ± 0.028 –
NBA2+				0.05 ± 0.003 –
Proportions of variance and correlations caused by residual effects				
LM	0.39 ± 0.005 0.57 ± 0.011	0.06 ± 0.011 0.09 ± 0.012		
ADG		0.42 ± 0.005 0.60 ± 0.007		
NBA1			0.81 ± 0.007 0.91 ± 0.014	
NBA2+				0.78 ± 0.006 0.84 ± 0.009

For the abbreviations of traits see Table 2

Table 4. Genetic parameters for the Czech Large White breed. Estimates for herd-year-season random (1st row) and fixed (2nd row) with approximate standard errors

	LM	ADG	NBA1	NBA2+
Heritabilities and genetic correlations				
LM	0.33 ± 0.003 0.37 ± 0.006	–0.14 ± 0.009 –0.23 ± 0.010	0.09 ± 0.009 –0.002 ± 0.009	0.08 ± 0.010 –0.007 ± 0.013
ADG		0.15 ± 0.003 0.18 ± 0.005	–0.11 ± 0.014 –0.19 ± 0.023	–0.20 ± 0.010 –0.26 ± 0.027
NBA1			0.13 ± 0.007 0.09 ± 0.009	0.80 ± 0.021 0.88 ± 0.035
NBA2+				0.13 ± 0.003 0.10 ± 0.005
Proportions of variance and correlations caused by the litter of origin of the animal				
LM	0.07 ± 0.001 0.09 ± 0.002	–0.07 ± 0.011 –0.06 ± 0.012		
ADG		0.17 ± 0.002 0.22 ± 0.002		
Proportions of variance caused by the permanent environmental effect of the sow				
NBA2+				0.04 ± 0.003 0.05 ± 0.005
Proportions of variance and correlations caused by the herd-year-season effect				
LM	0.21 ± 0.002 –	0.19 ± 0.006 –	0.13 ± 0.021 –	0.17 ± 0.018 –
ADG		0.20 ± 0.003 –	0.29 ± 0.016 –	0.25 ± 0.015 –
NBA1			0.08 ± 0.003 –	0.85 ± 0.020 –
NBA2+				0.05 ± 0.002 –
Proportions of variance and correlations caused by residual effects				
LM	0.39 ± 0.003 0.54 ± 0.007	–0.09 ± 0.006 –0.07 ± 0.006		
ADG		0.47 ± 0.004 0.60 ± 0.004		
NBA1			0.79 ± 0.006 0.91 ± 0.009	
NBA2+				0.79 ± 0.002 0.85 ± 0.005

For the abbreviations of traits see Table 2

Czech Landrace and Czech Large White were in close agreement for each of the models, differences of some practical importance occurred mainly in the estimates of correlations.

The highest heritability (between 0.30 and 0.37 depending on the breed and the model used) was estimated for lean meat content. The heritability for average daily gain was relatively low (between 0.13 and 0.18). The heritabilities for both production traits were somewhat higher in Czech Large White than in Czech Landrace. The heritability for the number of piglets born alive in parity 1 was between 0.09 and 0.13, the corresponding value for parity 2 and subsequent parities was between 0.10 and 0.14. Whereas the heritabilities for production traits were always higher in the model with the fixed herd-year-season effect compared to the model with random herd-year-season, the situation was reverse for the heritability estimates of both reproduction traits.

The highest genetic correlations were observed between both reproduction traits. They were close to 1 in Czech Landrace and between 0.80 and 0.88 in Czech Large White. On the other hand, the genetic correlations between both production traits were relatively low (less than 0.25 in their absolute value) and even differed in the sign between breeds – negative correlations were found for Czech Large White and positive correlations for Czech Landrace. The genetic correlations between average daily gain and the reproduction traits were mostly negative. Between lean meat content and the reproduction traits, zero or slightly positive genetic correlations were estimated.

The proportion of variance caused by the environmental litter effect was about 0.1 for lean meat content and 0.2 for average daily gain. The permanent effect of the sow caused about 5% of the total variance of the number of piglets born in parity 2 and subsequent parities.

As the herd-year-season effect was defined in the same manner for all traits, the full covariance matrix could be estimated when considering herd-year-season random. The proportion of variance caused by herd-year-season was similar for both production traits and in the range from 0.20 to 0.29. Considerably lower values (0.05 to 0.08) were estimated for the reproduction traits. The estimates of the correlations caused by the herd-year-season effect were mostly positive. The highest values were reached between the reproduction traits (0.85 to 0.96). Considerably high values were observed for the correlations between average daily gain and reproduction traits.

DISCUSSION

In the present paper, the covariance components were jointly estimated for production and reproduction traits. Until recently, the genetic evaluation of pigs in most countries and breeding associations was carried out separately for production and reproduction traits (Wolfová and Wolf, 1999). When analysing the international literature by 2001, it was found that on average the correlations between production and reproduction traits were near zero (Peškovičová *et al.*, 2002). This was also confirmed by Noguera *et al.* (2002a,b), who conducted a large-scale selection experiment in order to study the responses to selection for the number of piglets born alive. The results of this study, which successfully improved litter size, indicated that correlated responses in performance-tested traits (body weight and backfat thickness at the end of the test) were negligible.

According to Estany *et al.* (2002a), these results, however, are not sufficient to preclude the existence of an underlying pattern of correlated changes in production traits. These authors concluded that in the long term, selection for litter size could result in pigs with lower capacity of lean growth. In a related paper, Estany *et al.* (2002b) found evidence that pigs selected for litter size had less polyunsaturated fatty acids in intramuscular fat. This highlights the fact that the major effects of selection for litter size on carcass and meat traits would be associated with fat metabolism. Overall, the pattern of correlated changes could be interpreted as selected pigs being more mature at the same age, though the underlying genetic and physiological processes are unknown.

Chen *et al.* (2003) stated that unfavourable genetic correlations between lean growth and litter traits indicated that long-term selection for lean growth traits could harm litter traits if selection was practised for many generations and these relationships were ignored. Although breed-specific estimates for genetic correlations between lean growth and litter traits were found to be low, including them in maternal-line evaluations using a multiple-trait model within breed could increase the accuracy of the genetic evaluation for litter traits. These relationships should be evaluated periodically, however, if selection for lean growth continues. Serenius *et al.* (2004) also came to the conclusion that the accuracy of estimated breeding values might be improved by accounting for genetic associations between prolificacy, carcass and performance traits in a multiple-trait analysis.

When discussing joint or separate analyses of two blocks of traits considered in selection, it should be noted that only a joint analysis is theoretically correct, no matter what the covariances are. Accordingly, separate analyses have to be considered shortcuts and therefore they need justification. Furthermore, the breeding values from a joint genetic evaluation can be combined to the aggregate genotype simply by multiplying each breeding value by its economic value and summing up the products. This would be operationally much simpler compared to two separate analyses.

Unlike done in earlier joint analyses of production and reproduction traits (Ducos and Bidanel, 1996; Crump *et al*., 1997; Hermesch *et al*., 2000; Peškovičová *et al*., 2002; Chen *et al*., 2003), a joint herd-year-season effect for production and reproduction traits was defined. The reason for this was that both production and reproduction data were collected under the same conditions. Though production and reproduction data for the same animal are collected normally in two different herd-year-classes, a connection is given through related animals. For this reason, correlations between production and reproduction traits caused by the herd-year-season effect can be estimated. With two exceptions only positive estimates of correlations caused by the herd-year-season effect were calculated. This seems to be reasonable. It is expected in herds with good (bad) management that the values of all traits increase (decrease).

An important question is the way contemporary groups are treated – as fixed or as random effects. Frey *et al*. (1997) confirmed the results of Estany and Sorensen (1995) that the model with a random contemporary group effect yields more accurate predictions than the model with fixed contemporary group effects. Though a non-random distribution of contemporary groups over families leads to biased genetic evaluations, the authors could show that the prediction of observations was in general more accurate using a model with random herd-year-season effects. Therefore, the bias of predicted breeding values with random models was probably small. It is important to emphasise that this result was achieved on the basis of field data, where a significant non-random distribution of contemporary groups over families should be expected.

Oikawa and Sato (1997) compared the robustness of prediction with random and fixed herd models in a simulation study. No difference in empirical accuracy was observed between the prediction models if data included only large herds, whereas for data with small herds, the random herd model had a higher accuracy than the fixed herd model in general. This superiority of the random herd model did not change under selection. The authors concluded that under realistic conditions, the random herd model was superior to the fixed herd model in general.

Furthermore, taking the herd-year-season effect random has an operational advantage in genetic evaluation. If herd-year-season subclasses have very few animals, the regression on the population mean that is implicit in BLUP as opposed to BLUE implies that the herd-year-season solutions will be close to zero instead of being close to the average of a (small) number of observations in a herd-year-season cell in the fixed case.

According to Babot *et al*. (2003) the impact of the definition and treatment of contemporary groups in the evaluation model on the genetic response of a pig nucleus is expected to be small. This conclusion has been obtained using the contemporary group size from eight to 100 sows. These sizes are common for most of the private breeding companies, but can differ from the situation in national pig breeding programmes or in multinational breeding companies. The results of the authors illustrate that treating the herd-year-season effect as random improves the predictive ability of the evaluation model for litter size. However, this does not necessarily lead to significant changes in the selection decisions and in the genetic response achieved. The existence of environmental trends within a population increases the risk of obtaining biased estimators of the genetic means.

Summarizing the discussion, it is concluded that a joint evaluation of production and reproduction traits will be advantageous compared with a separate genetic evaluation. The treatment of contemporary groups as random effects seems to be favourable under realistic conditions. Though possible disadvantages cannot be fully ignored, they should be of minor importance under practical conditions. Correlations between production and reproduction traits caused by herd-year-season effects can be taken into account in models with random contemporary groups.

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