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Modelling non-genetic correlations between animal- and litter-recorded traits affect genetic covariances

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Introduction

In pig breeding, both animal-recorded traits, such as growth and feed efficiency, and litter-recorded traits, such as litter size and piglet survival, are of interest. When combining traits of interest into an index, the use of a multi-trait model is the best methodology, since it takes into account the relationships between the traits (Mrode, 2013). Relationships between traits are determined by both genetic and non-genetic correlations.

Non-genetic correlations between traits are incorporated by having random environmental effects that are shared across traits. For animal-recorded traits, the unit of observation is the individual, and shared environmental effects could be e.g. litter, pen and residual effects. For litter-recorded traits, the unit of observation is the litter, and shared random environmental effects could be e.g. permanent environmental effect of the sow and residual effects. However, incorporating non-genetic correlations between animal- and litter-recorded traits is not straight-forward, since traits are recorded on different units of observation, i.e. individual and litter, and residuals therefore cannot be shared random effects. In practice, non-genetic correlations between animal- and litter-recorded traits are therefore often ignored, but as demonstrated by Walter and Mao (1985), in the presence of selection, ignoring non-genetic correlations can bias the estimates of genetic parameters.

For both animal- and litter-recorded traits, there is selection on which animals obtain records, and to incorporate non-genetic correlations between animal- and litter-recorded traits, Ostersen *et al.* (2022) proposed a modeling framework with non-genetic correlations between litter effects for animal-recorded traits and residual effects for litter-recorded traits and non-genetic correlations between residual effects for animal-recorded traits and permanent environmental sow effects for litter-recorded traits, and proposed how to fit the model using standard genetic evaluation software.

The aim of our study was to investigate the hypothesis that genetic parameter estimates are biased when ignoring non-genetic correlations between animal- and litter-recorded traits. The hypothesis was investigated in DanBred Landrace by estimating parameters in multi-trait models with or without non-genetic correlations between animal- and litter-recorded traits.

Materials & Methods

Experimental design and data. We estimated (co)variance parameters for two multi-trait models with six animal-recorded traits and two litter-recorded traits in DanBred Landrace pigs. The animal-recorded traits were: average daily gain until 30kg (G1; g/day; 207,184 records), average daily gain from 30 to 100kg (G2; g/day; 218,094 records), feed conversion ratio (FCR; feed units per kg gain; 10,885 records), lean meat percentage (LMP; 218,094 records), and conformation (CON; 218,076 records). The litter-recorded traits were: piglet survival (PS; 55,589 records) and total number born (TNB; 248,875 records), both recorded on multiple litters of sows. The pedigree included 368,422 pigs. Animal-recorded traits were recorded in nucleus herds and included pigs born from 2018 to 2023, while ensuring complete contemporary groups. Litter-recorded traits were recorded in both nucleus herds and multiplier herds and were from farrowings from 2018 to 2023.

Models. The joint model for animal- and litter recorded traits is:

$\mathbf{y}_{anim}=\mathbf{X}_1\mathbf{b}_1+\mathbf{Z}_1\mathbf{a}_1+\mathbf{H}_1\mathbf{d}_1+\mathbf{W}_1\mathbf{l}_1+\mathbf{F}_1\mathbf{e}_1$, (animal)

$\mathbf{y}_{lit}=\mathbf{X}_2\mathbf{b}_2+\mathbf{Z}_2\mathbf{a}_2+\mathbf{V}_2\mathbf{s}_2+\mathbf{F}_2\mathbf{p}_2+\mathbf{W}_2\mathbf{e}_2$, (litter)

where $\mathbf{y}_x$ are vectors of records, $\mathbf{b}_x$ are vectors of fixed and regression effects, $\mathbf{a}_x$ are vectors of random genetic effects (direct genetic effects on all traits, maternal genetic effects on G1 and PS, denoted G1-m and PS-m), $\mathbf{d}_1$ is the vector of random pen effects, $\mathbf{s}_2$ is the vector of random non-genetic sire effects, $\mathbf{l}_1$ is the vector of random birth litter effects, $\mathbf{p}_2$ is the vector of random permanent environment effect of the sow, and $\mathbf{e}_x$ are vectors of random residual effects; matrices $\mathbf{X}_x$, $\mathbf{Z}_x$, $\mathbf{H}_1$, $\mathbf{V}_2$, $\mathbf{W}_x$ and $\mathbf{F}_x$ are design matrices assorting phenotypes with random effects. Details on fixed and regression effects are omitted here for shortness of the presentation. Random genetic, and non-genetic animal and litter effects are independent and distributed:

$$\begin{bmatrix}\mathbf{a}_1\\ \mathbf{a}_2\end{bmatrix}\sim MVN(\mathbf{0},\mathbf{G}\otimes\mathbf{A}),\begin{bmatrix}\mathbf{e}_1\\ \mathbf{p}_2\end{bmatrix}\sim MVN\left(\mathbf{0},\begin{bmatrix}\mathbf{R}_{11} & \mathbf{R}_{12}^{a}\\ . & \mathbf{R}_{l}\end{bmatrix}\otimes\mathbf{I}\right),\begin{bmatrix}\mathbf{l}_1\\ \mathbf{e}_2\end{bmatrix}\sim MVN\left(\mathbf{0},\begin{bmatrix}\mathbf{R}_{\text{pe}} & \mathbf{R}_{12}^{l}\\ . & \mathbf{R}_{22}\end{bmatrix}\otimes\mathbf{I}\right),$$

where matrix $\mathbf{G}$ is the genetic covariance matrix, matrix $\mathbf{A}$ is the pedigree-based additive genetic relationship matrix, $\mathbf{R}_{11}$ is the covariance matrix of residual effects for animal-recorded traits, $\mathbf{R}^{a}_{12}$ is the matrix of covariances between residual effects for animal-recorded traits and permanent environmental sow effects for litter-recorded traits, $\mathbf{R}_{pe}$ is the covariance matrix of permanent environmental sow effects for litter-recorded traits, $\mathbf{R}_l$ is the covariance matrix of litter effects for animal-recorded traits, $\mathbf{R}^{l}_{12}$ is the matrix of covariances between litter effects for animal-recorded traits and residual effects for litter-recorded traits, $\mathbf{R}_{22}$ is the covariance matrix of residual effects for litter-recorded traits, and $\mathbf{I}$ is an identify matrix. Details on the multivariate normal distribution of random pen and sire effects are omitted here for shortness of the presentation. The full model is denoted *M* and the model without non-genetic correlations between animal- and litter-recorded traits, i.e. with $\mathbf{R}^{a}_{12}=\mathbf{R}^{l}_{12}=\mathbf{0}$, is denoted M_0.

Parameter estimation. The parameters were estimated using restricted maximum likelihood implemented in software APEX (https://ghpc.ai/). Standard genetic evaluation software, such as APEX, require that residual effects are independent of each other and independent of other random effects. In order to fit the models, a computational trick was used, as suggested by Ostersen *et al.* (2022) and Romé *et al.* (2022, 2023). The trick consists of adding dummy residual effects $\boldsymbol{\varepsilon}_x$ to the model:

$\mathbf{y}_{anim}=\mathbf{X}_1\mathbf{b}_1+\mathbf{Z}_1\mathbf{a}_1+\mathbf{H}_1\mathbf{d}_1+\mathbf{W}_1\mathbf{l}_1+\mathbf{F}_1\mathbf{e}_1+\boldsymbol{\varepsilon}_1$, (animal)

$\mathbf{y}_{lit}=\mathbf{X}_2\mathbf{b}_2+\mathbf{Z}_2\mathbf{a}_2+\mathbf{V}_2\mathbf{s}_2+\mathbf{F}_2\mathbf{p}_2+\mathbf{W}_2\mathbf{e}_2+\boldsymbol{\varepsilon}_2$, (litter)

where variance parameters of these effects are fixed to small values (smaller than the residual variances to be estimated).

Results

Estimates of the non-genetic correlations between animal- and litter-recorded traits from *M* are shown in Table 1 and 2. In Table 1, we see that more than half the correlations between residual effects for animal-recorded traits and permanent environmental effects of sows for litter-recorded traits are statistically significantly different from 0, and in Table 2, we see that all the correlations between litter effects for animal-recorded traits and residual effects for litter-recorded traits are statistically significantly different from 0. In addition, we see a general pattern of opposite signs of the correlations in the two tables, i.e. negative in one table and positive in the other table.

Table 1. Non-genetic correlations between residual effects for animal-recorded traits and permanent environmental sow effects for litter-recorded traits[1].

	G1	G2	FCR[2]	LMP	CON
PS	-0.04	-0.05		0.03	-0.08*
TNB	0.22*	0.18*		0.08*	0.05*

[1] G1: early growth, G2: finisher growth, FCR: feed conversion ratio, LMP: lean meat percentage, CON: conformation, PS: piglet survival, TNB: litter size.

[2] No correlations for FCR, since this is only recorded on males.

* Statistically significantly different from 0.

Table 2. Non-genetic correlations between birth litter effects for animal-recorded traits and residual effects for litter-recorded traits[1].

	G1	G2	FCR	LMP	CON
PS	0.19*	0.17*	-0.14*	0.11*	0.11*
TNB	-0.43*	-0.21*	0.22*	-0.12*	-0.15*

[1] Trait definitions as in Table 1.

* Statistically significantly different from 0.

Variances for all genetic effects in the two models are shown in Table 3. We see that variances are larger in M_0 than in M for the effects on litter-recorded traits and the trait G1, whereas for the effects on the remaining animal-recorded traits, variances are almost identical for the two models.

Table 3. Genetic variances in models with (M) and without (M_0) non-genetic covariances between animal- and litter-recorded traits[1].

	G1	G1-m^2	G2	FCR	LMP	CON	PS	PS-m^2	TNB
M	173	42	2570	0.00440	0.338	1.57	0.00265	0.00237	2.03
M_0	204	70	2548	0.00439	0.338	1.57	0.00273	0.00284	2.35

[1] Trait definitions as in Table 1.

[2] Maternal genetic effect.

Correlations between genetic effects for animal-recorded and litter-recorded traits are shown in Table 4 for M and M_0, where differences between elements for M and M_0 are of interest. Several of these differences are substantial.

Table 4. Genetic correlations between animal- and litter-recorded traits in models with (M) and without (M_0) non-genetic covariances between animal- and litter-recorded traits[1].

M	G1	G1-m^2	G2	FCR	LMP	CON
PS	-0.01	0.00	-0.04	0.10	-0.05	0.24
PS-m^2	-0.04	0.29	-0.16	0.26	-0.14	0.21
TNB	-0.02	-0.35	-0.10	0.11	-0.03	-0.05
M_0						
PS	0.10	-0.06	0.01	0.06	-0.02	0.23
PS-m^2	-0.11	0.58	-0.08	0.13	-0.07	0.21
TNB	0.25	-0.76	-0.05	0.13	-0.02	-0.09

[1] Trait definitions as in Table 1.

[2] Maternal genetic effect.

Concerning the genetic correlations between animal-recorded traits and between litter-recorded traits (results not shown), then these are in general similar between the two models (differences below

0.05), with the exception of the correlation between direct and maternal genetic effects for G1, which is -0.08 in M and -0.28 in M_0.

Discussion

Results show that including non-genetic covariances between animal- and litter-recorded traits changes the genetic parameter estimates, with several changes being substantial, which confirms our hypothesis that genetic parameter estimates are biased in models without such non-genetic covariances. It is therefore important to incorporate such non-genetic covariances into the genetic model.

Walther and Mao (1985) showed that the bias in the estimation of genetic parameters was caused by a combination of selection and ignoring strong non-genetic covariances. The selection in our study is both related to animal- and litter-recorded traits. For example, it is not random which females become sows, since females with high value of the index tend to be selected, where G2 plays a big role. Another example of selection is that animals born in small litters or litters with high mortality tend not be chosen for phenotyping of animal-recorded traits. Non-genetic correlations being statistically significantly different from zero are also seen in our study, and we also see an interesting general pattern in these non-genetic correlations, where the sign of the correlation between residual effects for animal-recorded traits and permanent environmental effects of sows for litter-recorded traits is the opposite of the sign of the correlation between litter effects for animal-recorded traits and residual effects for litter-recorded traits. We believe that both types of non-genetic correlations are important, and that ignoring either one or both of them will result in biased genetic parameter estimates.

Conclusions

The findings show that ignoring non-genetic covariances between animal- and litter-recorded traits changes the estimates of genetic parameters, where several of the changes are substantial, which is a strong indication of biased parameter estimates. The model should cater for both genetic and non-genetic covariances between animal- and litter-recorded traits for accurate parameter estimation, and we believe that this is important for obtaining genetic progress in a pig breeding program.

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