Prediction Of Breeding Values For Mean And Environmental Variance With An Iterative BLUP-Procedure

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Introduction

Animals may not only differ genetically in phenotypic trait values, but also in their response to environmental factors, which would lead to genetic variation in environmental variance. Several studies have shown the existence of genetic variation in environmental variance (e.g. Sorensen and Waagepetersen (2003); review Mulder *et al.* (2007); Wolc *et al.*, (2009)). Genetic variation in environmental variance can be used to breed for increased robustness and uniformity (Mulder *et al.* (2007, 2008)).

Mulder *et al.* (2007) proposed a selection index framework to predict breeding values for mean and environmental variance in the presence of genetic variation in environmental variance. In principle this idea can be easily extended to a mixed model framework using the phenotype and squared trait values adjusted for fixed effects. However, in the presence of genetic trend it is theoretically better to use squared residuals instead of squared trait values adjusted for fixed effects, which means that a bivariate iterative BLUP-procedure is required to update the squared residuals. Updating the squared residuals is important when the breeding value for mean and the breeding value for environmental variance are correlated and to account for heterogeneous residual variance in phenotype. Such an iterative BLUP-procedure has not been tested before, but has the advantage that it can be implemented in software for routine genetic evaluation, such as MiXBLUP (Lidauer and Stranden (1999)).

The aim of this paper was to test an iterative BLUP-procedure to predict breeding values for mean and environmental variance. Bivariate models for phenotype and squared residuals with and without accounting for heterogeneous residual variance in phenotype were compared using simulation. In addition, a univariate analysis was studied where the bivariate mixed model was split into two independent univariate models.

Material and methods

The model. The bivariate mixed model used for the iterative BLUP-procedure was:

 $\begin{bmatrix} \mathbf{p} \\ \mathbf{e}_p^2 \end{bmatrix} = \begin{bmatrix} \mathbf{X}\mathbf{b}_p \\ \mathbf{X}\mathbf{b}_{e^2} \end{bmatrix} + \begin{bmatrix} \mathbf{Z}\hat{\mathbf{a}}_m \\ \mathbf{Z}\hat{\mathbf{a}}_v \end{bmatrix} + \begin{bmatrix} \mathbf{e}_p \\ \mathbf{e}_{e^2} \end{bmatrix}, \text{ where } \mathbf{p} \ (\mathbf{e}_p^2) \text{ is a vector with phenotypes (squared})$

residuals of phenotypes), X and Z are incidence matrices for fixed effects and additive

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genetic effects respectively, \mathbf{b}_{p} ($\mathbf{b}_{e^{2}}$) is a vector with solutions for fixed effects for phenotype (squared residual), in this case we a have only the overall mean as fixed effect, $\hat{\mathbf{a}}_{m}$ ($\hat{\mathbf{a}}_{v}$) is a vector with additive genetic effects for the mean (environmental variance), $\mathbf{e}_{p}(\mathbf{e}_{2})$ is a vector with residuals for phenotype (squared residuals). The additive genetic

effects were assumed to be
$$\begin{bmatrix} \hat{\mathbf{a}}_m \\ \hat{\mathbf{a}}_v \end{bmatrix} \sim N(\mathbf{0}, \mathbf{A} \otimes \mathbf{G})$$
 with $\mathbf{G} = \begin{bmatrix} \sigma_{a_m}^2 & r_A \sigma_{a_m} \sigma_{a_v} \\ r_a \sigma_{a_m} \sigma_{a_v} & \sigma_{a_v}^2 \end{bmatrix}$, where $\sigma_{a_m}^2$ is the additive genetic variance of \hat{a}_v and r_a is the correlation between \hat{a}_m and \hat{a}_v . The residuals were assumed to be

$$\begin{bmatrix} \mathbf{e}_p \\ \mathbf{e}_{e^2} \end{bmatrix} \sim N(\mathbf{0}, \mathbf{R} \otimes \mathbf{I}) \text{ with } \mathbf{R} = \begin{bmatrix} \sigma_{e_p,i} & \sigma \\ 0 & \sigma_{e_p^2}^2 \end{bmatrix}, \text{ where } \sigma_{e_p,i}^2 \text{ is the residual variance of } e_p$$

for animal *i*, $\sigma_{e_e^2}^2$ is the residual variance of e_p^2 . With heterogeneous residual variance

 $\sigma_{e_p,i}^2 = \sigma_e^2 + \hat{a}_{v,i}$, i.e. the random additive genetic effect acts additively on the residual variance.

The iterative BLUP-procedure: The MiXBLUP software was used to predict breeding values using preconditioned gradient method to solve the mixed model equations (Lidauer and Stranden (1999)). The true simulated variance components were used in the BLUP-procedure. First a univariate BLUP run was performed with homogeneous residual variance for phenotype. Secondly, an iterative bivariate BLUP-procedure was performed either with homogeneous (*hom*) ($\sigma_{e_{p},i}^2 = \sigma_e^2$ is constant) or heterogeneous residual variance (*het*), in which $\sigma_{e_{p},i}^2 = \sigma_e^2$ is constant) or heterogeneous residual variance (*het*), in

which $\sigma_{e_p,i}^2$ was updated each iteration using weights $(k = (\sigma_e^2 + \hat{a}_{v,i}) / \sigma_e^2)$ in MiXBLUP.

The squared residuals were updated each iteration for both models. Ten iterations were performed to reach convergence. For comparison, one additional procedure was studied: a *univariate* analysis where the bivariate mixed model was split into two independent univariate models.

Simulation: The iterative BLUP-procedure was tested with data from a simulated population in which 4 generations of cows were generated from 50 test-bulls and 2500 cows (50 daughters per sire). The 50 test-bulls were offspring of 10 bull-sires and 50 dams. No selection was performed. In total 10,000 phenotypic records were generated according to the quantitative genetic model in Mulder *et al.* (2007). The simulated variance components were $\sigma_{a_m}^2 = 0.3$, $\sigma_e^2 = 0.7$ and $\sigma_{a_v}^2 = 0.05$. The genetic correlation r_a was varied (0, 0.25, 0.50 and 0.75). Accuracies were calculated as correlations between true and estimated breeding values. In addition, regressions of true on estimated breeding values were calculated. Results were based on averages of 50 replicates.

Results and discussion

Table 1 shows accuracies of \hat{a}_m and \hat{a}_v for bulls and cows using *univariate* BLUP or bivariate iterative BLUP with either homogeneous residual variance for phenotype (*hom*) or heterogeneous (*het*) residual variance for different values of r_a . The accuracy of \hat{a}_v increased with the bivariate iterative BLUP in comparison to univariate BLUP, when $r_a > 0$. Differences in accuracy between homogeneous and heterogeneous iterative BLUP were very small. Due to pedigree information the accuracy of \hat{a}_v for cows was at a reasonable level and much higher than solely based on phenotype (Mulder *et al.* (2007)). For bulls the accuracy was slightly higher than expected based on 50 offspring due to additional pedigree information (Mulder *et al.* (2007)).

Table 1. Accuracies of \hat{a}_m and \hat{a}_v for bulls with 50 daughters and cows with phenotype using univariate BLUP or bivariate iterative BLUP with either homogeneous (hom) or heterogeneous (het) residual variance for different values of r_a .

		Accuracy ¹							
		\hat{a}_m				\hat{a}_v			
Bull/cow	r _a	univariate	hom	het		univariate	hom	het	
Bulls with	0	0.899	0.899	0.900		0.567	0.567	0.562	
50 daughters	0.25	0.899	0.899	0.900		0.578	0.600	0.598	
Cows with phenotype	0.5	0.907	0.906	0.907		0.587	0.657	0.656	
	0.75	0.905	0.905	0.905		0.561	0.741	0.737	
	0	0.633	0.633	0.634		0.336	0.336	0.335	
	0.25	0.635	0.635	0.636		0.344	0.364	0.364	
	0.5	0.632	0.632	0.634		0.340	0.418	0.419	
	0.75	0.635	0.636	0.638		0.340	0.510	0.510	

 $^{\scriptscriptstyle 1}$ standard errors were 0.002 – 0.004 for $\, \hat{a}_m^{\phantom i}$, 0.004 - 0.017 for $\, \hat{a}_\nu^{\phantom i}$.

The accuracy varied only slightly between iterations of the iterative BLUP-procedure. However, it improved the regression of true on estimated a_v substantially when assuming heterogeneous variance (Figure 1). With homogeneous residual variance, the variance of \hat{a}_v was biased downwards. Although the regression coefficients for \hat{a}_m were always close to 1.0, the iterative BLUP-procedure with heterogeneous variance decreased the bias in \hat{a}_m for cows with extreme phenotypes (results not shown).

The model presented here assumed normally distributed residuals, which is clearly violated for squared residuals. The next step would be to investigate whether using a transformation or gamma distributed residuals (e.g. Rönnegård *et al.* (2010); Felleki and Chalkias (2010)) can further improve the accuracy of breeding values. Results of this study help to improve statistical modeling and quantitative genetic understanding of genetic variation in environmental variance.



Figure 1. The regression of true on estimated a_v (= Av) of cows with the iterative BLUP-procedure assuming either homogeneous (left) or heterogeneous (right) residual variance for phenotype for different values of the genetic correlation (r_a =ra).

Conclusion

The iterative BLUP-procedure developed in this study improved the accuracy of breeding values for environmental variance in comparison to univariate BLUP, when breeding values for mean and environmental variance are correlated. Accounting for heterogeneous residual variance in phenotype improved the regression of true on estimated breeding values for environmental variance, but did hardly change the accuracies. The iterative BLUP-procedure allows the use of existing BLUP-software to predict breeding values for phenotype and environmental variance in practical breeding programs.

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