MACE for Ayrshire Conformation: Impact of Different Uses of Prior Genetic Correlations

Thomas Mark¹, Per Madsen², Just Jensen² and Freddy Fikse¹ ¹Interbull Centre, Uppsala, Sweden ²Danish Institute of Agricultural Sciences, Foulum, Denmark

Introduction

This study is a continuation of the study by Mark and Madsen (2002), who compared Ayrshire across country genetic correlation estimates for conformation traits using REML analysis with estimates from Gibbs sampling using three different prior beliefs. Previous results concerning the length of the burnin period were too pessimistic. Convergence of the Gibbs chain was assessed by the method of batching without accounting for the auto-correlation among samples. Taking the auto-correlation into account reduces the number of rounds needed for burnin from more than 200,000 to less than 10,000.

We believe that the main issue, which determines the feasibility of Multiple-trait Across Country Evaluations (Mace) for Ayrshire conformation, is the availability of proper genetic correlations, and that a crude way of accounting for the relative uncertainty of prior information can be almost as good as the theoretically more elegant, but more computing intensive Gibbs sampling approach. The main aim of this study was to test this hypothesis on Ayrshire conformation data. More specifically the aim was to sample dispersion parameters, breeding values and reliabilities using Gibbs sampling, and compare those results with more simple ways of using prior information from Holstein correlations.

Material

The exact same data and edits as in Mark and Madsen (2002) were used for all analysis in this study. Data comprised national fore udder evaluation results from nine Ayrshire populations. Genetic ties were generally weak for the Ayrshire data, whereas the corresponding Holstein populations always had more bulls with evaluations in multiple countries (common bulls), except for Norway for which no Holstein data were available and for a couple of country combinations involving Finland (Table 1).

Table 1. Number of Ayrshire bulls included in Mace and average number of common bulls (CB) for Ayrshire and Holstein, respectively.

	AUS	CAN	DNK	FIN	GBR	NOR	NZL	SWE	USA
Bulls incl.	148	478	864	1453	189	1732	288	586	175
Avg. CB _{AYS}	2.3	14.3	2.9	5.7	5.4	1.6	6.1	7.8	11.4
Avg. CB _{HOL}	66.8	114.4	22.0	5.7	74.7	0.0	36.9	17.8	121.6

Methods

National evaluation results were deregressed within country (Jairath et al., 1998). The deregressed national proofs were used as dependent variable in the Mace model (Schaeffer, 1994), which was assumed for all analysis. Two different approaches were used to obtain genetic correlations. First, separate Ayrshire and Holstein correlation estimates were weighted together using a crude, but very simple way of accounting for the uncertainty of each set of correlation estimates. The separate set of correlations were each estimated with an EM-REML algorithm applied to a reduced set of Mace equations for a well connected subset of the respective data sets (Klei and Weigel, 1998). Secondly, the Gibbs sampling procedure described by Jensen and Madsen (2002) was used to simultaneously sample international breeding values and genetic correlations. This procedure will be referred to as "Bayesian Mace" in this paper.

Weighted average of Ayrshire and Holstein correlation estimates (crude weighting)

It was assumed that the standard error of the genetic correlation coefficient (SE_{rG}) could be approximated as being proportional to the reciprocal of the square root of the number of common bulls (CB) between the two countries (i and j) of interest: $SE_{r_{cii}} = k/\sqrt{CB_{ij}}$, where zero CB was set to one and k was a constant, which was assumed to be equal for all country combinations regardless of breed in this study. This implied that the influence on SE_{rG} from all other factors such as different heritabilities, the total number of observations per country, the size of the true correlation, genetic ties other than number of common bulls were assumed similar for both the Ayrshire and Holstein data considered here. However, for the purpose of this study a crude approximation was considered to be sufficient. Prior information in the form of Holstein genetic correlations $p(\theta)$ were combined with information from the Ayrshire data $p(y|\theta)$ via Bayes formula: $p(\theta|y) = p(\theta) \times p(y|\theta)$, where the probability distributions were assumed to be Gaussian, i.e. $p(\theta|y) \sim N(r_G, \sigma^2_{rG}), p(\theta) \sim$ $N(r_{Ghol},d^2 \sigma^2_{rGhol})$ and $p(y|\theta) \sim N(r_{Gays}, \sigma^2_{rGays})$, where d was a constant that can be varied in order to reduce the weight that should be put on the Holstein (prior) information relative to the information from the Ayrshire data.

Then the posterior (weighted) genetic correlation (r_G) was given by the following equation:

$$r_{G} = \frac{\frac{r_{G_{ays}}}{\sigma_{r_{G_{ays}}}^{2}} + \frac{r_{G_{hol}}}{\sigma_{r_{G_{hol}}}^{2}}}{\frac{1}{\sigma_{r_{G_{hol}}}^{2}} + \frac{1}{\sigma_{r_{G_{hol}}}^{2}}} = \frac{CB_{ays}r_{G_{ays}} + \frac{CB_{hol}r_{G_{hol}}}{d^{2}}}{CB_{ays} + \frac{CB_{hol}}{d^{2}}}$$

Description of Mace runs

In this study three different values were used for d, namely 2, 4 and 8 representing high, medium and low prior belief, respectively. These correlations were then used to predict breeding with international values the "traditional" MACE procedure as outlined by Schaeffer (1994). These three runs were denoted Run 1, 2 and 3 respectively. Similarly three Gibbs sampling chains with different prior belief (i.e. 5, 10 and 100 degrees of freedom, respectively) were run (Run 10-12). For all Bayesian Mace runs, 10,000 samples were discarded as burn-in and 500,000 additional rounds with an interleave of 10 rounds were used for inferences, i.e. a total of 50,000 samples were available for inferences in each Bayesian Mace run.

Posterior means of parameters from Bayesian Mace were also used in the traditional Mace for comparison. First three runs using only genetic correlations from Bayesian Mace (assumed heritabilities and EM-REML sire variances as in Run 1-3) were conducted (Run 4-6), and finally three runs using both genetic correlations, sire variances and heritabilities from Bayesian Mace were conducted (Run 7-9). Thus a total of 12 Mace runs were conducted (Table 2).

Table 2. Description of Mace runs.

Run	Approach	r _G prior weight
1^{1}	$Mace^{2}$ (crude r_{G} weighting)	d=8
2	$Mace^2$ (crude r_G weighting)	d=4
3	$Mace^{2}$ (crude r_{G} weighting)	d=2
4	$Mace^2$ (r _G from Gibbs)	df=5
5	$Mace^2$ (r _G from Gibbs)	df=10
6	$Mace^2$ (r _G from Gibbs)	df=100
7	Mace ² (all (co)var from Gibbs)	df=5
8	Mace ² (all (co)var from Gibbs)	df=10
9	Mace ² (all (co)var from Gibbs)	df=100
10	Full Bayesian Mace	df=5
11	Full Bayesian Mace	df=10
12	Full Bayesian Mace	df=100

1) Reference run; 2) Traditional Mace.

All results were de-standardized to the sire transmitting ability scale relative to the sire standard deviation EM-REML estimate (σ_{sire}) for the country in question to ease interpretation and enable comparison of results across country scales.

Pearson correlations between international proofs (proof correlations) and international rankings (rank correlations) in different Mace runs were computed for the top 100 bulls in Run 1. Bulls with data and a minimum reliability of 40% in Run 1 was considered in each run to compute these correlations. Comparisons of results from different Mace runs were often done separately for foreign and domestic bulls. Foreign bulls were defined as bulls included in Mace with zero effective daughter contributions (EDC) in the country in question, whereas domestic bulls were defined as bulls with one or more EDC in the country in question.

Reliability and prediction error variance

Reliabilities (REL) were approximated according to Harris and Johnson (1998) for traditional Mace (run 1-9). Reliabilities were not available from the Bayesian Mace. Instead prediction error variances (PEV) were compared with PEV from traditional Mace (PEV_{Mace}) to get an indication of the underestimation of PEV due to the assumption of known parameters: $PEV_{Mace} = (1-REL_{Mace})$ σ^2_{sire} , where σ^2_{sire} is the sire variance.

Predictive ability

The 12 Mace runs (Table 2) were repeated with selected subsets of bulls national proof set to missing to access the predictive ability of the alternative Mace approaches. Three different subsets were created for this purpose. All 12 approaches were run for each of the following three data sets: 1) The youngest 5 percent of bulls with data were set to missing in each country; 2) 5 percent of bulls with data were randomly set to missing in each country; and 3) The youngest 25 percent of import bulls with at least 40 daughters in 20 herds were set to missing in each country. The three different data sets were formed to investigate the predictive ability with respect

to each of these three particular types of bulls. The two first data sets had 300 bulls with their national proof set to missing and the third only had 27 bulls with their proof set to missing due to relatively few bulls identified as imports (type of proof = 21). Only one common bull was set to missing of the 5% youngest bulls. For the two other data sets 25 and 33 pair-wise links were lost by setting certain bull proofs missing (some pairwise links were due to the same common bull). The predicted breeding values were compared with national breeding values, which were assumed unbiased. However predicted breeding values were also compared with predicted values from the corresponding full Mace run to access the stability of predictions with and without certain data included.

Results and Discussion

The 50,000 samples corresponded to 58-522, 119-1573 and 1077-5036 effective samples for covariances for Run 10, 11 and 12, respectively. Effective sample sizes were larger for residual and sire variances. Each Bayesian Mace run took approximately 4.5 days on an Intel Pentium IV 2Ghz running Linux.

(Co)variance components

Genetic correlations were larger for Holsteins compared with Ayrshire when estimated with EM-REML, and correlations used in Run 2 and Run 3 were therefore higher compared with those used in Run 1 (Table 3). Posterior mean of genetic correlations from Bayesian Mace were substantially higher than EM-REML estimates. For Bayesian Mace, posterior means of genetic correlations were larger on average (+0.02), when the prior belief were low (df=5) compared with high prior belief (df=100). Genetic correlations varied generally much more across countries when the prior belief was low than when prior belief was high, and they varied less for Bayesian Mace estimates compared with those used in Run 1-3. Mean posterior standard deviations of genetic correlations were less than 0.1 for 5 degrees of freedom and decreased with increasing prior belief as expected.

Run	Mean	\pm SE ¹	Range
1	0.56		0.99
2	0.60		0.85
3	0.64		0.69
4, 7, 10	0.79	± 0.094	0.46
5, 8, 11	0.79	± 0.075	0.43
6, 9, 12	0.77	± 0.032	0.42

Table 3. Mean and range of genetic correlations used in Run 1-12.

In comparison, the mean genetic correlation when no weight was given to the Holstein estimates (i.e. pure Ayrshire estimates) was identical to the mean genetic correlation in Run 1 (0.56), and the mean genetic correlation for Holstein was 0.72. Thus posterior means of genetic correlations were on average larger than the prior correlations used for the Bayesian Mace. Posterior distributions of genetic correlations were often left skewed, but were closer to normal when the prior belief increased (results not shown).

1) Mean posterior standard deviation of genetic correlation.

Table 4. Comparison of assumed¹ and mean posterior² heritabilities for the nine countries in Run 2-12.

Run	AUS	CAN	DNK	FIN	GBR	NOR	NZL	SWE	USA
1-6	0.240	0.190	0.240	0.280	0.260	0.061	0.211	0.300	0.260
7 & 10	0.202	0.237	0.438	0.120	0.130	0.017	0.221	0.179	0.209
8 & 11	0.216	0.219	0.358	0.127	0.161	0.021	0.205	0.183	0.226
9 & 12	0.242	0.196	0.267	0.180	0.235	0.040	0.200	0.242	0.264

1) The heritability provided by respective countries were assumed and used to approximate residual variances; 2) All genetic and residual (co)variance components are estimated (prior equal to assumed heritabilities in Run 1-6).

Run	AUS	CAN	DNK	FIN	GBR	NOR	NZL	SWE	USA
10	0.076	0.074	0.120	0.019	0.048	0.004	0.074	0.049	0.051
11	0.071	0.057	0.086	0.018	0.050	0.005	0.060	0.047	0.051
12	0.035	0.024	0.029	0.019	0.032	0.005	0.027	0.031	0.032

Table 5. Posterior standard deviation of heritabilities for Bayesian Mace.

1) The heritability provided by respective countries were assumed and used to approximate residual variances; 2) All genetic and residual.

The differences between heritabilities assumed in Mace run 1-6 and those estimated by Bayesian Mace were surprisingly large (Table 4). But it is not known what the correct values should be. Some national genetic evaluation units seldom estimate genetic parameters, and the parameters do not necessarily correspond to the data used for national genetic evaluation. Posterior standard deviations of heritabilities for Bayesian Mace ranged between 0.004 and 0.120 (Table 5) and decreased with increasing prior beliefs. Posterior distributions of heritabilities and variances were approximately normal (results not shown).

Impact on international proofs

The impact of using different genetic correlations in traditional Mace (Run 2-6) were small for domestic bulls (Table 6). Using variances from Bayesian Mace seemed to have a larger impact on the spread of international proofs and on differences on individual bulls than when only genetic correlations from Bayesian Mace were used in traditional Mace, which agreed with the results of Schaeffer et al. (1996). Changes from individual bull proofs in Run 1 were largest for Run 10-12, but on average proofs from Run 7-9 deviated just as much. Generally there were good agreement between international proofs for domestic bulls, when different Mace approaches were used, and the correlation of proofs in Run 1 with proofs in another Mace run were always higher than 0.98 for domestic bull.

Table 6. Comparison of Mace proof for *domestic* bulls from Run1 with Mace proofs in Run 2-9. Mean statistic across all nine countries are shown.

	Differe	ence		
Run	Mean	SD	b^1	Corre- lation
2-3	0.000	0.04	1.00	1.00
4-6	0.000	0.11	1.00	1.00
7	0.001	1.15	0.90	0.99
8	0.001	1.02	0.91	0.99
9	0.001	0.35	0.98	1.00
10	0.001	1.17	0.90	0.98
11	0.001	1.04	0.92	0.99
12	0.000	0.56	0.97	1.00

1) Regression coefficient for regression of proofs from Run x on proofs from Run 1.

There was only minor differences between international proofs of foreign bulls from traditional Mace, when different genetic correlations were used (Table 7). However, the spread of international proofs were clearly larger for Run 10-12 compared with traditional Mace. Differences of individual bull proofs from those in Run 1 were also larger for Bayesian Mace compared with Run 2-9 (differences between proofs in Run 10-12 and proofs in Run 1 were 0.4_{sire} units on average). The use of parameters from Bayesian Mace in traditional Mace (Run 7-9) had only minor impact on foreign bulls, but the impact was substantially larger when the uncertainty about the same parameters were accounted for in Bayesian Mace (Run 10-12). Thus the correlation between Bayesian Mace proofs and proofs from Run 1 were only 0.62 to 0.66 and regressions from 1.32 to 1.35 for foreign bulls.

Table 7. Comparison of Mace proof for *foreign* bulls from Run 1 with Mace proofs in Run 2-9. Mean statistics across all nine countries are shown.

	Differe	ence		
Run	Mean	SD	b^1	Corre- lation
2	0.009	0.21	1.03	0.99
3	0.024	0.42	1.07	0.98
4	0.089	1.07	1.20	0.94
5	0.077	1.01	1.19	0.94
6	0.062	0.95	1.17	0.95
7	0.101	1.16	1.10	0.92
8	0.093	1.09	1.10	0.93
9	0.072	0.95	1.17	0.95
10	0.414	6.82	1.32	0.62
11	0.425	6.81	1.32	0.63
12	0.364	6.78	1.35	0.66

1) Regression coefficient for regression of proofs from Run x on proofs from Run 1.

Table 6 and 7 summarized the mean impact across all countries of different Mace runs on results from Run 1. Although the main aim of this study was not to investigate differences in impact among countries, it is of interest to get an idea of how much specific impacts ranged between countries for the different Mace runs and especially so for foreign bulls. Deviations between countries of various statistics measuring the change of proofs in comparison with Run 1 were larger for Bayesian Mace compared with Run 2-9 (results not shown). Changes from Run 1 were largest for Australia and New Zealand, which both had relatively few bulls and relatively few genetic ties (especially with the large Nordic Ayrshire populations). The mean proof difference between Run 12 and Run 1 were 2.97 and 1.30 sire SD units for Australia and New Zealand, respectively.

Previously (Table 6-7) all Mace runs were only compared with Run 1, which differed substantially from other Mace runs in some situations. It is also of interest to do pair-wise comparisons among all runs. There was good agreement within the different Mace approaches (Table 8). Rank correlations differed substantially between Bayesian Mace and traditional Mace runs (0.47-0.80). Proof correlations were generally higher than rank correlations and ranged from 0.62 to 1.00. Varying weight given to the prior correlation did not have a large impact on rankings and rank correlations ranged from 0.96 to 1.00 among Run 1-3, but they ranged from 0.75 to 1.00 among Run 1-6. Regression coefficients ranged from 0.46 to 1.21 among all runs and deviated most between Bayesian Mace and traditional Mace runs (results not shown).

Table 8. Rank (above diagonal) and proof (below diagonal) correlations between different Mace runs for top 100 ranking bulls¹. Mean correlation across all nine countries are shown.

						Ru	n					
Run	1	2	3	4	5	6	7	8	9	10	11	12
1		0.98	0.96	0.75	0.78	0.78	0.62	0.65	0.80	0.47	0.48	0.52
2	1.00		0.99	0.78	0.81	0.81	0.63	0.67	0.82	0.48	0.49	0.53
3	0.99	0.99		0.81	0.84	0.84	0.67	0.71	0.85	0.52	0.53	0.56
4	0.87	0.88	0.90		0.99	0.97	0.87	0.88	0.92	0.77	0.77	0.79
5	0.88	0.90	0.91	1.00		0.99	0.86	0.88	0.95	0.74	0.75	0.77
6	0.89	0.90	0.92	0.98	1.00		0.83	0.87	0.96	0.72	0.73	0.75
7	0.82	0.83	0.84	0.92	0.91	0.91		0.99	0.84	0.80	0.80	0.78
8	0.84	0.85	0.66	0.92	0.93	0.92	1.00		0.87	0.80	0.79	0.78
9	0.87	0.88	0.90	0.97	0.98	0.98	0.92	0.94		0.68	0.69	0.70
10	0.62	0.63	0.64	0.81	0.80	0.77	0.83	0.82	0.79		1.00	0.98
11	0.64	0.64	0.66	0.82	0.81	0.79	0.83	0.82	0.80	1.00		0.98
12	0.67	0.68	0.69	0.84	0.83	0.81	0.82	0.82	0.82	0.98	0.99	

1) The top 100 bulls with data and at least 40% reliability in the reference file (Run 1) was considered.

The large deviations between Bayesian Mace and Run 1 was primarily for bulls with little information about their breeding values (results not shown). The correlation between international proofs in Run 1 and Run 10 were 0.62, 0.68, 0.81 and 0.88 when considering foreign bulls with a reliability in Run 1 of at least 0%, 20%, 40% and 60%, respectively.

Impact on genetic trends

Trends in mean international proof differed for the different Mace approaches (Figure 1). The genetic trends for Run 2 and 3 were very similar to that of Run 1, trends for Run 5 and 6 were very similar to that of Run 4 and so forth. The genetic trends estimated with Bayesian Mace differed noticeably from trends estimated by traditional Mace. This was the case for all country scales (results only shown for the Swedish scale).



Figure 1. Genetic trend of mean international predicted transmitting ability (PTA) on Swedish scale for Run 1, 4, 7 and 10 ($\sigma_{sire}=0.26$).

Impact on reliability and prediction error variance

Reliabilities for domestic bulls were only slightly affected by the use of different genetic correlations in traditional Mace, when genetic correlations increased (Table 3) as expected. The largest difference in mean reliability for foreign bulls was 12% between Run 4 and Run 1. Furthermore the spread and range of reliabilities decreased when genetic correlations increased and the spread of genetic correlations decreased. Reliabilities for Run 7-9 were smaller than those for Run 4-6 for both foreign bulls (mean reliability was 41-42) and for domestic bulls (mean reliability was 68-72).

Traditional Mace and reliabilities for traditional Mace results did not account for the uncertainty about residual and genetic parameters, and as a result reliabilities for traditional Mace were overestimated. Posterior prediction error variances from Bayesian Mace were substantially higher (often more than one σ_{sire}^2 unit) compared with those obtained for traditional Mace (Table 9). The overestimation of reliabilities for traditional Mace reliabilities was on average larger for foreign bulls compared with domestic bulls.

Table 9. Difference between Bayesian Mace and traditional Mace runs in standard deviation of prediction errors¹ for domestic (Dom) and foreign (For) bulls, respectively.

	Me	an	SI	D
Run	Dom	For	Dom	For
10 vs 4	1.07	1.64	0.65	1.14
11 vs 5	1.03	1.64	0.53	1.15
12 vs 6	1.08	1.70	0.53	1.15

1) Square root of (PEV_{Gibbs}-PEV_{Mace})/ σ^2_{sire} .

Predictive ability

in ability Differences predictive between alternative Mace approaches (Table 10) were in most cases small and the results did not clearly and consistently favour any of these approaches in comparison with others. The largest difference in mean absolute value of difference between national and predicted Mace proof between two runs were 3.4%, 1.7% and 19,3% for the subset of 5% youngest, 5% random and 25% youngest imports, respectively. Mean absolute bias were always less than 0.65 σ_{sire} units, but single bulls had larger deviations between their national and predicted international proof (up to 2.6 σ_{sire} units mean absolute bias). The predictive ability of the Bayesian Mace were slightly better compared with traditional Mace for the data sets with 5% youngest and 5% randomly missing bulls, whereas it was worst for the data set with 25% youngest import bulls missing.

For young bulls differences between predictive information mainly comes through the additive

genetic relationship matrix (i.e. basically the within country parent average). Predictions for randomly chosen and especially import bulls are not only through the additive genetic relationship matrix, but also through genetic correlations (G^{-1}) . This could have some influence on the difference in predictive ability for different types of bulls. Another (and perhaps more likely) reason why Bayesian Mace performed poorer for the data set with import bulls set to missing can be because Bayesian Mace re-sampled genetic parameters, whereas the same genetic parameters as in the full Mace was used for traditional Mace. In the data set with import bulls set to missing, relatively many genetic ties were lost and this makes it more difficult to sample proper covariances. Although differences were slightly higher for the data set with bull proofs randomly and especially import bulls set to missing then the differences in posterior mean genetic correlations between the full and reduced Bayesian Mace runs were always very small and typically smaller than the posterior standard deviations (Table 3).

Table 10. Standard deviation (SD) of difference and mean and maximum of absolute value of difference between national and predicted Mace proof for three different sets of bulls set to missing in 12 different Mace runs.

		5% young	gest		5% random	1	25% youngest imports			
Run	Mean ¹	SD	Max	Mean	SD	Max	Mean	SD	Max	
1	0.5907	0.7391	2.3398	0.6404	0.8088	2.6130	0.5437	0.6409	1.4032	
2	0.5905	0.7386	2.3401	0.6409	0.8088	2.6118	0.5496	0.6415	1.3932	
3	0.5907	0.7385	2.3397	0.6418	0.8093	2.6136	0.5609	0.6452	1.3941	
4	0.5922	0.7403	2.3334	0.6437	0.8116	2.6418	0.5806	0.6730	1.5496	
5	0.5919	0.7398	2.3362	0.6445	0.8124	2.6430	0.5809	0.6738	1.5374	
6	0.5917	0.7397	2.3383	0.6451	0.8129	2.6376	0.5770	0.6715	1.5242	
7	0.5956	0.7490	2.3281	0.6381	0.8020	2.6382	0.5582	0.6454	1.4024	
8	0.5947	0.7470	2.3320	0.6396	0.8039	2.6394	0.5639	0.6503	1.4037	
9	0.5912	0.7395	2.3363	0.6439	0.8109	2.6364	0.5752	0.6630	1.4661	
10	0.5824	0.7371	2.3649	0.6341	0.7909	2.2085	0.6474	0.7360	1.5802	
11	0.5806	0.7349	2.3723	0.6345	0.7917	2.2109	0.6415	0.7312	1.5697	
12	0.5762	0.7270	2.3663	0.6366	0.7939	2.2194	0.6488	0.7471	1.6230	

1) Mean = $\Sigma_n(|\text{proof}_{\text{predicted}} - \text{proof}_{\text{national}}|)/n\sigma_{\text{sire.}}$

Also, national genetic evaluations for import bulls are possibly biassed in some cases and may therefore not serve as a good reference in determining predictive ability. Furthermore, only 27 import bulls were set to missing in that data set, and differences in predictive ability between different Mace alternatives may be attributed to chance.

The slightly superior ability of Bayesian Mace to predict international proofs close to national proofs for bulls with their national proof set to missing did not mean that Bayesian Mace proofs corresponded better with national proofs than traditional Mace proofs. Contrarily, Bayesian Mace results deviated more from national genetic evaluation results than traditional Mace results (results not shown). The correlation between proofs from national genetic evaluations and the corresponding ones from Bayesian Mace (full data) ranged between 0.91 and 0.97. In comparison proofs from national genetic evaluations and the corresponding ones from Run 1-6 were essentially unity, whereas those for Run 7-9 were in the same range as for Bayesian Mace (ranged between 0.90 and 0.98).

The difference in variance components alone could not explain why Bayesian Mace predictions were closer to national evaluations compared with traditional Mace predictions. Predictions from Run 7-9, which used the posterior means of variance components inferred with Bayesian Mace, deviated most from initial national evaluations. The only difference between Run 7-9 and Bayesian Mace was that uncertainty in variance components were considered in the latter, and this could be the reason for the slightly better predictive ability Bayesian Mace.

Bayesian Mace is fundamentally different from traditional Mace not only because it accounts for the uncertainty of all parameters, but also because it resample all parameters, i.e. posterior mean of all genetic and residual variances and covariances are not necessarily equal to that used in traditional Mace and to that used in national genetic evaluations. When different genetic parameters (i.e. ratio between sire and residual variance) are used in Bayesian Mace compared with the national evaluation it could be speculated that it would be more difficult to predict exactly the national evaluation results. However, the predictive ability of Bayesian Mace were in most cases better than traditional Mace in this study. It would be interesting to investigate the impact of fixing the ratio between sire and residual variances in Bayesian Mace to that used in the national evaluation to see if this would further improve the predictive ability. However, the question is whether it is desirable to assume national evaluations to be unbiased as is current practise for international genetic evaluations?

What is the best practical Mace alternative for Ayrshire conformation?

The best option of the Mace alternatives investigated in this study seemed to be either the crude weighting (Run 1-3) or the full Bayesian Mace (Run 10-12). Run 4-9 requires running Bayesian Mace in any case, and since Bayesian Mace seemed to perform slightly better in terms of predictive ability in most cases and have better theoretical properties, Run 4-9 should not be considered. Of course Bayesian Mace could be run during test-runs and parameters could subsequently be used in traditional Mace during routine runs, but since Run 4-9 did not perform better than Run 1-3 this would not be worthwhile. The main benefit of Bayesian Mace seemed to be its ability to be able to account for the uncertainty of genetic parameters, while breeding values were sampled simultaneously.

Based on the slightly superior predictive ability and better theoretical properties, Bayesian Mace would be preferred over the crude weighting approach, but Bayesian Mace has some practical drawbacks. Bayesian Mace is much more computer intensive compared with the crude weighting. It would require 81 days to predict international breeding values for 18 conformation traits in the current setting (unless traits are analysed parallel) plus additional time for data preparation and checks. Furthermore, there is no practical experience with using Bayesian methods for routine genetic evaluations to our knowledge, and it would be hard to predict the outcome of routine runs and resolve potential problems (e.g. with input data) within the short time window that is usually allowed for routine runs.

Considering these practical drawbacks of Bayesian Mace together with the fact that the

predictive performance was only slightly (2-3%) better compared with traditional Mace, we recommend traditional Mace for international genetic evaluations of Ayrshire conformation of the alternatives considered in this study.

The question that remains, is whether it would be appropriate to introduce traditional Mace given the large changes observed especially when comparing with Bayesian Mace - and if it is deemed appropriate which weight to use for the prior (Holstein) correlations relative to the Ayrshire ones. Introducing Mace for Ayrshire conformation is probably better than doing nothing (proof and rank correlations were always positive, and genetic correlations differed from zero). It is likely that additional genetic ties have accumulated since data was collected for this study that would warrant a pilot run using traditional Mace. Furthermore, the main differences between the different Mace alternatives were for bulls with low reliability. There was only little impact on international proofs when different relative prior weights were used (i.e. d equal to 2, 4 or 8). Using d equal to four seems to be a good practical choice, and would yield more meaningful genetic correlations than pure Ayrshire estimates.

Conclusion and recommendation

Parameters and predicted international proofs for especially foreign bulls were substantially different for Bayesian Mace compared with traditional Mace, even when posterior means of (co)variance components from Bayesian Mace were used in traditional Mace. Using different genetic correlations for traditional Mace had little impact on sire rankings and predictive ability, but influenced reliabilities of especially foreign bulls. Prediction error variances for traditional Mace proofs were substantially underestimated and reliabilities were thus overestimated due to the assumption of known parameters. Predictive ability favoured Bayesian Mace over traditional Mace although differences in predictive ability were small and not consistent for all groups of bulls investigated. Considering this and the practical drawbacks of Bayesian Mace, we recommend to collect new data and to do a pilot run for Ayrshire conformation traits using the crude weighting of Ayrshire and Holstein genetic correlation estimates (with d=4).

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