Multiple-Trait-Multiple-Country Genetic Evaluations for Udder Health

T. Mark[1] and P. G. Sullivan[2]
[1]Interbull Centre, SLU, Uppsala, Sweden
[2]Beef Improvement Ontario and Canadian Dairy Network, Guelph, Canada

Introduction

Multiple-trait-multiple-country genetic evaluation (**MT-Mace**) methods can be used for both national and international purposes to combine different genetically and residually correlated evaluations. Presently, the theory of different MT-Mace models has been described (e.g. Schaeffer, 2001; Liu *et al.,* 2004) and different MT-Mace strategies have been compared by simulation (Sullivan *et al.,* 2005). The simulation study by Sullivan *et al.* confirmed the theoretical expectation that MT-Mace methods should be preferred over methods that only allow one trait per country (ST-Mace; Schaeffer, 1994) when assuming true genetic parameters. However, investigations on field data are of interest before MT-Mace is applied in practise.

International genetic evaluation for udder health traits is one example where MT-Mace could be beneficial. Currently, this Interbull service comprises two separate evaluations due to the limitations of the applied ST-Mace method; one including milk somatic cell (**SC**) from all participating countries and the other including clinical mastitis (**CM**) from the Nordic countries and SC from the non-Nordic countries (Mark *et al.,* 2002). This practice does not use all available information in an optimal way and it is therefore of interest to extend the current method to allow more than one trait per country.

The aim of the present study was to apply MT-Mace to udder health field data and quantify the benefits in terms of reliability and predictive ability of predicted international genetic merit of MT-Mace compared with ST-Mace.

Material

National genetic evaluation results for Holstein bulls for CM and SC from Denmark (**DNK**), Finland (**FIN**) and Sweden (**SWE**) as well as SC from Canada (**CAN**), Austria-Germany (**DEA**), Estonia (**EST**), France (**FRA**) and the United States (**USA**) were considered. These were a subset of the data used in the February 2004 Interbull routine evaluation for udder health traits, and included populations with different recorded traits, number of animals, progeny group sizes, degree of genetic exchange with other populations and national genetic evaluation methods (Interbull, 2004A&B; Table 1). The Swedish and Finnish national genetic evaluations were single trait, whereas a multi trait model including both SC and CM was used in Denmark (Nielsen *et al.,* 2000). In the Danish national genetic evaluation, a residual correlation of 0.11 and a genetic correlation of 0.509 were assumed between CM and SC.

Table 1. Number of national breeding values (n), average EDC (AVG_{EDC}), standard deviation of EDC (SD_{EDC}) and heritabilities (h^2) per trait.

Country	n	AVG_{EDC}	SD_{EDC}	h^2
Clinical mastitis:				
DNK	4338	491	2750	0.04
FIN	635	446	863	0.05
SWE	1381	250	841	0.02
Milk somatic cell:				
DNK	4747	205	1329	0.11
FIN	656	351	661	0.17
SWE	1402	213	720	0.08
CAN	5581	230	1653	0.27
DEA	12207	342	1789	0.23
EST	273	316	762	0.12
FRA	8658	668	4350	0.15
USA	18549	228	1030	0.10

In addition to the data described in Table 1, similar data used in the November 2003 Interbull routine evaluation were used to assess the consistency of consecutive international evaluations. There were no changes in the national genetic evaluation models between November 2003 and February 2004, but for all countries additional daughter records were included. There were 1616 new bull records across all 11 traits in February 2004 compared with November 2003, and the average EDC and number of daughters of the bulls considered for both evaluations increased by 13.9 and 12.1, respectively. While the amount of available information increased for all countries, the relative increase in the number of qualifying records differed between countries, e.g., the increase ranged from 0.5 percent in CAN to 5.4 percent in EST.

The data edits used in this study were identical to those applied for Interbull routine evaluations. The data were standardised within country so that each set of national genetic evaluations had equal mean (10) and standard deviation (1) and so that a high breeding value was desirable. This did not change the traits genetically, but eases interpretation of results and can be computationally advantageous.

Methods

ST-Mace was as applied for Interbull routine evaluations (Mark *et al.,* 2002). MT-Mace was similar to ST-Mace, except that effective independent weighting factors (Sullivan and Wilton, 2001) were used, and observations were based on a multivariate deregression procedure (Schaeffer, 2001). The following steps were performed to implement MT-Mace:

Step 1. *Create effective independent weighting factors for correlation estimation.* The original weighting factors provided by the countries (EDC) were transformed (Sullivan and Wilton, 2001) to effective independent weighting factors (MTi-EDC). This transformation allowed residual correlations to be zero in the following steps. The national heritabilities and within country residual and genetic correlations were used for the transformations.

Step 2. *Multivariate deregression of national genetic evaluations for correlation estimation.* National genetic evaluations were deregressed across traits and within country (Schaeffer, 2001) using the MTi-EDC from step 1, national heritabilities and genetic correlations. This step ensured that genetic information within a country, from related individuals and from correlated traits, was not double-counted between the national and international evaluations.

Step 3. *Estimation of genetic correlations.* Genetic correlations were estimated based on MTi-EDC and deregressed national genetic evaluations from steps 1 and 2 using an EM-REML algorithm applied to a reduced set of MACE equations (Klei and Weigel, 1998). Subsequently, the estimated within country genetic correlation between CM and SC for Denmark was replaced by the correlation used in the national evaluation and the blended correlation matrix was bended (Jorjani *et al.,* 2004) to ensure positive definiteness. In this bending procedure, the diagonal elements and the within country correlation for Denmark were not allowed to change, whereas the allowed changes for the remaining genetic correlations were inverse-proportional to the number of common bulls.

Step 4. *Create effective independent weighting factors for prediction of breeding values*. As step 1, except that the bulls included corresponded to the bulls considered for prediction of breeding values.

Step 5. *Multivariate deregression of national genetic evaluations for prediction of breeding values.* As step 2, except that the bulls included corresponded to the bulls considered for prediction of breeding values.

Step 6. *Estimation of sire variances.* Sire variances were estimated using a single-trait EM-REML algorithm (Sullivan, 1999) using weights and dependent variables from steps 4 and 5.

Step 7. *Prediction of international genetic merit*. International genetic merits were predicted based on national heritabilities, and the parameters, weights and dependent variables from step 3 to 6. Solutions were obtained by both direct inverse (FSPAK90; Misztal and Perez-Enciso, 1998) and Gauss-Seidel iteration.

Step 8. *Approximation of reliabilities*. Reliabilities for international genetic evaluations were approximated using a multivariate approach to combine information sources (Sullivan and Mark, 2005; Appendix).

Genetic groups were treated as random effects throughout the process and a minimum group size of 30 was required for the across country data set. The same genetic group definitions were used in the deregression as in Mace. Steps 1 and 4 were only necessary for Denmark and the deregression was only multivariate for Denmark as this was the only country that analysed CM and SC simultaneously.

Analyses and comparisons

Results from two ST-Mace analyses, each involving eight traits, were combined to resemble current Interbull practice. The first ST-Mace considered SC evaluations from all eight countries. The second ST-Mace considered CM evaluations from the three Nordic countries (DNK, FIN, SWE) and SC data from the other five countries. The international genetic evaluations for SC in all countries from the first ST-MACE, and for CM in the Nordic countries from the second ST-Mace, were compared with evaluations from MT-Mace applied to all 11 traits simultaneously.

The cross-reference and pedigree files from the February 2004 data, and the genetic correlations estimated for MT-Mace based on February 2004 data, were used in all analyses. However, within country sire variances were re-estimated for each data set in step 6.

Three different groups of bulls were studied: 1) *Young bulls*, i.e. bulls that were born in 1997 or later and had daughters in only one country (studied on both domestic and foreign country scales); 2) *Export bulls*, i.e. bulls with daughters in at least two countries and most daughters in the given country; 3) *Import bulls*, i.e. bulls with daughters in at least two countries and most daughters in a country other than the given country. The number of export bulls ranged from one in Finland to 584 in the United States. The number of import bulls was usually higher than the number of export bulls, and ranged from 37 for CM in Finland to 777 in the United States. Bulls with both ST-Mace and MT-Mace evaluations, for a given trait, were considered for comparisons of the two methods.

Results and Discussion

Genetic correlations

The genetic correlations between SC in one country and SC in another country ranged from 0.80 to 0.96, the across country genetic correlation between SC and CM ranged from 0.51 to 0.73, and the genetic correlations between CM in one country and CM in another country ranged from 0.71 to 0.86 (Table 2).

The estimated genetic correlation between CM and SC in Denmark was 0.65, but the correlation used in MT-Mace was the correlation used in the national evaluation (i.e., 0.51). The discrepancy between the national and estimated correlation can be due to different models, data and pedigrees used at national and international levels as well as bias in residual Mace (co)variances due to imperfect national weighting factors and heritabilities. The national correlation was used to ensure that, for bulls with local information only, local evaluations and reliabilities from MT-Mace would align with the corresponding national values. Aligning these results was considered more important in practice than possible improvements in predictive ability of MT-Mace with the use of new parameters within a country.

Table 2. Genetic correlations used for the Mace runs.

	Clinical mastitis			Milk somatic cell							
	DNK	FIN	SWE	DNK	FIN	SWE	CAN	DEA	EST	FRA	USA
DNK		0.71	0.86	0.51	0.51	0.61	0.61	0.62	0.63	0.62	0.68
FIN			0.80	0.57	0.60	0.63	0.70	0.73	0.70	0.63	0.63
SWE				0.60	0.52	0.68	0.65	0.64	0.64	0.57	0.64
DNK					0.93	0.96	0.84	0.80	0.86	0.89	0.87
FIN						0.91	0.85	0.81	0.87	0.90	0.83
SWE							0.86	0.81	0.87	0.87	0.88
CAN								0.89	0.82	0.93	0.93
DEA									0.95	0.93	0.86
EST										0.91	0.84
FRA											0.91
USA											

Bending of the blended correlation matrix of national and estimated correlations was necessary, but the impacts were small. All changes between the correlation before and after bending were 0.01 or lower, except for the correlation between EST and FIN that decreased 0.03 units and the correlation between CAN and FIN that increased 0.02 units. Both of these estimated correlations were based on relatively few common bulls.

Estimates of genetic correlation with CM in DNK increased from 0.84 to 0.86 for CM in SWE and decreased 0.03 to 0.07 units for SC in the non-nordic countries. These differences are likely due to the addition of, or the techniques used to add, SC in DNK to the MT-Mace model. While different parameters for ST-Mace relative to MT-Mace may be the most suitable, the correlations used for ST-Mace in this study were the correlations used in MT-Mace, to remove the impacts of different genetic correlations from the comparisons.

International genetic merits

Impact of prediction method

The international genetic evaluations were essentially the same regardless of whether they were predicted by direct inversion or Gauss-Seidel iteration. This was the case for all traits and Mace runs. The Pearson product-moment correlations between international genetic evaluations from the two methods of prediction were consistently 0.9999 or higher for all traits. Similarly, overall means and standard deviations of the international genetic evaluations differed between each method of prediction by less than 0.44 percent across all country scales.

This means that either approach can be used to solve the MT-Mace equations. The direct inversion appears to be faster for udder health traits, but requires more memory. For very large applications, where memory is a limitation, Gauss-Seidel iteration may be a viable alternative. Only predicted genetic merits from the direct inverse will be considered for the remainder of this paper.

Impact of ST versus MT-Mace

Predicted international genetic merits generally did not differ much depending on whether ST-Mace or MT-Mace was used (Table 3). Predictions were essentially the same for SC whereas minor differences were observed for CM, in Sweden and to a lesser extend in Finland, for young domestic bulls. The standard deviation of predicted international genetic merits were also essentially the same regardless of method of prediction. The reason for the high consistency of results for foreign bulls is that the vast majority of bulls only had daughters in non-Nordic countries (i.e. only SC records). When only young bulls with most daughters in Sweden were considered, Pearson product-moment correlations between ST-Mace and MT-Mace results on foreign scales were 0.994 for CM in FIN, 0.996 for CM in DNK and ranged between 0.999 and 1.000 for the SC traits.

Table 3. Pearson product-moment correlations between international genetic evaluations from ST-Mace and MT-Mace for clinical mastitis (CM) and milk somatic cell (SC) scales, respectively.

Bulls	CM	SC
Young (d)	0.994-1.000	0.999-1.000
Young (f)	1.000	1.000
Import	0.993-0.996	0.999
Export	0.988-0.999	0.998-1.000
All	0.998-0.999	0.999-1.000

Predictive ability

International genetic merits were unbiased and very consistent between consecutive evaluations for both ST-Mace and MT-Mace on all trait-within-country scales and for both domestic and foreign bulls (Table 4). The predictive ability of MT-Mace was always equal to or slightly better than the predictive ability of ST-Mace for the CM traits, whereas there were essentially no differences in predictive ability between ST-Mace and MT-Mace for the SC traits. Similar results were found for import and export bulls. For import bulls $b_{04|03}$ and $r_{04,03}$ were 0.996 and 0.995, respectively, for ST-Mace, whereas they were 0.997 and 0.995 for MT-Mace across all scales. For export bulls $b_{04|03}$ was 0.995 and $r_{04,03}$ was 0.996 for both ST and MT-Mace across all scales.

The comparisons in Table 4 were based on bulls that had an evaluation for both ST-Mace and MT-Mace in both November 2003 and February 2003 in order to compare the two methods fairly. However, additional predictions were available for MT-Mace that were not available for the applied ST-Mace, e.g. bulls with a national CM breeding value, but no SC breeding value, received MT-Mace predictions for SC on all country scales. With ST-Mace such bulls did not receive breeding values for the Nordic SC scales and the SC breeding values for the non-Nordic scales would in practice be disregarded (as they were in this study).

Table 4. Regression coefficient from regressions of predicted international genetic merit of February 2004 data on predicted international genetic merit of November 2003 data ($b_{04|03}$) and correlation between predicted genetic merit in February and November data ($r_{04,03}$) for **young**[1] bulls on the domestic (d) and foreign scale (f).

	ST-Mace				MT-Mace			
Country	$b^d_{04\|03}$	$b^f_{04\|03}$	$r^d_{04,03}$	$r^f_{04,03}$	$b^d_{04\|03}$	$b^f_{04\|03}$	$r^d_{04,03}$	$r^f_{04,03}$
Clinical mastitis:								
DNK	0.998	0.999	0.999	0.999	0.998	1.000	0.999	0.999
FIN	1.002	1.005	0.999	0.999	1.002	1.003	0.999	0.999
SWE	1.001	1.001	0.999	0.999	1.000	1.001	1.000	0.999
Milk somatic cell:								
DNK	1.000	1.000	0.999	0.998	1.000	1.000	0.999	0.998
FIN	1.003	0.998	0.999	0.999	1.003	0.998	0.999	0.999
SWE	1.000	1.000	1.000	0.998	1.000	1.000	1.000	0.998
CAN	1.001	1.001	0.997	0.999	1.002	1.001	0.997	0.999
DEA	1.002	1.002	0.998	0.999	1.002	1.002	0.998	0.999
EST	0.997	1.001	0.997	0.999	0.997	1.001	0.997	0.999
FRA	1.000	1.001	0.998	0.998	1.000	1.001	0.998	0.998
USA	0.998	1.000	0.998	0.998	0.998	1.000	0.998	0.998
All	1.000	1.001	0.998	0.999	1.000	1.001	0.998	0.999

[1]Bulls born after 1996 with daughters in only one country (the no. domestic bulls ranged from 43 in EST to 3360 in USA).

Reliabilities

Reliabilities were generally higher for MT-Mace than ST-Mace (Table 5), but overall impacts were small. The impact of ST-Mace versus MT-Mace differed depending on the group of bulls studied and the impact was largest for young bulls, since they typically have less information. The relative increase in reliability between consecutive evaluations was slightly higher for ST-Mace than MT-Mace for young bulls, because bulls obtain a given reliability earlier in life with MT-Mace. For each type of bull, and for young bulls on foreign scales in particular, average reliabilities from either data set were higher with MT-Mace.

Table 5. Percent increase[1] in average reliability from November 2003 to February 2004 for ST-Mace (ΔREL_{ST}) and for MT-Mace (ΔREL_{MT}) and percent increase[1] from ST-Mace to MT-Mace (ΔREL_{04})[2] for different groups of bulls[3].

Bulls	ΔREL_{ST}	ΔREL_{MT}	ΔREL_{04}
Young (d)	5.15	5.12	0.30
Young (f)	4.59	4.55	0.78
Import	0.66	0.66	0.24
Export	0.56	0.56	0.14
All	0.84	0.84	0.77

[1] $100(REL_x\text{-}REL_y)/REL_y$
[2] Based on data from February 2004
[3] refers to domestic and f to foreign scales

The impact of switching from ST-Mace to MT-Mace, on international reliabilities, was largest for the Swedish CM scale (1.83 percent increase on average for all bulls), followed by the Finish CM scale (1.58 percent increase on average for all bulls). Heritabilities were lower for CM than SC and neither Sweden nor Finland utilized correlated information from SC in their national CM evaluations. The average increase was lowest for the Danish SC scale (0.08 percent), because CM information from DNK was incorporated into the national Danish SC evaluations that were used in ST-Mace. The largest increase for a non-Nordic scale was 0.96 percent on the USA-scale, which can be explained by the relatively high correlation (0.68) between SC in USA and CM in DNK, which is the largest of the Nordic populations. The bulls with most daughters in Sweden had much higher increases in average reliability when going from ST-Mace to MT-Mace, between 16 to 23 percent for the three CM scales and 0.5 to 3.7 percent for the eight SC scales.

General discussion

In this application, MT-Mace was implemented using the modified weighting factor approach of Sullivan and Wilton (2001). While MTi-EDC can always be derived, there may be situations where MTi-EDC do not produce the same reliabilities as multivariate weighting factor blocks, which include information about residual correlations in off-diagonal elements of a matrix (Schaeffer, 2001). This is because of a required constraint to avoid negative MTi-EDC and hence negative definite weighting blocks per animal, which could occur due to problems with weighting factors provided by the countries.

The advantages of MT-Mace over ST-Mace for udder health traits may be reduced when the Nordic countries introduce a joint multi-trait genetic evaluation including both clinical mastitis and milk somatic cell. However, MT-Mace opens up many other possibilities. For example, multiple lactation-specific traits per country could be considered, and reliabilities could be improved by considering udder conformation traits (e.g. udder depth) and milking speed evaluations simultaneously with CM and SC. The main practical limitation is the total number of traits that can be accommodated and hence the number of correlations to be estimated. However, at least three traits per country appears to be feasible with the current correlation estimation procedure. MT-Mace is computationally more demanding than a single ST-Mace run, but less demanding than multiple ST-Mace runs. For udder health traits, only one simultaneous analysis is needed with MT-Mace instead of the two separate ST-Mace runs used currently.

Conclusion

Both MT-Mace and ST-Mace yielded unbiased and consistent consecutive predictions. There was essentially no difference in predictive ability for the milk somatic cell traits, whereas MT-Mace had either slightly superior or equal predictive ability compared with ST-Mace for th clinical mastitis traits. MT-Mace results

were the same when direct inversion and Gauss-Seidel were used to solve the equations. Reliabilities were higher for MT-Mace than for ST-Mace predictions, especially on the Swedish and Finnish mastitis scales and especially for young bulls with most daughters in Sweden and Finland.

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Appendix
Extension of the information source reliability method to multiple-trait MACE

(extracted from Sullivan and Mark, 2005)

In the reliability approximation methods of Harris and Johnson (1998a,b) (HJ), progeny information is included in reliabilities of parents based on single-trait reliability equations that are not easily extended to multiple traits, as needed for multiple-trait MACE. Equivalent equations based on effective records, however, are easily extended. Effective record contributions to a sire and maternal grandsire (mgs), for an animal with p observations, can be approximated by absorbing row 1 of the following matrices;

$$\text{sire}: \begin{bmatrix} p+\frac{4}{3}k & -\frac{2}{3}k \\ -\frac{2}{3}k & \frac{1}{3}k \end{bmatrix} \quad \text{mgs}: \begin{bmatrix} p+\frac{16}{15}k & -\frac{4}{15}k \\ -\frac{4}{15}k & \frac{1}{15}k \end{bmatrix}$$

The resulting effective records, which can be accumulated for multiple progeny, are;

$$\text{sire}: \frac{pk}{3p+4k} \quad \text{mgs}: \frac{pk}{15p+16k}$$

Reliabilities for each ancestor, after combining the progeny contribution with their own observations (s and m), are;

$$\text{sire}: R_s = \frac{n_{s+p}}{n_{s+p}+k},\ n_{s+p} = \frac{3sp+4sk+pk}{3p+4k}$$

$$\text{mgs}: R_m = \frac{n_{m+p}}{n_{m+p}+k},\ n_{m+p} = \frac{15mp+16mk+pk}{15p+16k}$$

Substituting $s = \frac{kR_s}{1-R_s}$, $m = \frac{kR_m}{1-R_m}$ and $p = \frac{kR_p}{1-R_p}$ into the above equations, and cancelling from the numerator and denominator the common terms; $\frac{k^2}{(1-R_s)(1-R_p)}$ for the sire and $\frac{k^2}{(1-R_s)(1-R_p)}$ for the mgs, yields:

$$R_{s+p} = \frac{R_s + \frac{1}{4}R_p - \frac{1}{2}R_sR_p}{1 - R_s\,\frac{1}{4}R_p}$$

$$R_{m+p} = \frac{R_m + \frac{1}{16}R_p - \frac{1}{8}R_mR_p}{1 - R_s\,\frac{1}{16}R_p}$$

These are identical to the corresponding equations of Harris and Johnson (1998b). Therefore, to extend the procedure to multiple traits, replace p with $\mathbf{Z_p'MZ_p}$ and k with $\mathbf{G}^{-1}$ in the above matrices and follow the above steps. Absorb the progeny equations to derive progeny contribution matrices, instead of effective records (n), which can be added to information matrices of sire ($\mathbf{Z_s'MZ_s}$) and mgs ($\mathbf{Z_m'MZ_m}$) observations, respectively, to form combined information matrices ($\mathbf{E}$). Combine information from all r trait groups as follows;

$$\text{Let } \mathbf{B} = \left[\begin{pmatrix} \mathbf{E}_1 & \cdots & \mathbf{0} \\ \vdots & \ddots & \vdots \\ \mathbf{0} & \cdots & \mathbf{E}_r \end{pmatrix} + \mathbf{G}^{-1} \right]$$

Then for trait t; $R_t = 1 - \frac{\left[\mathbf{B}^{-1}\right]_{tt}}{\mathbf{G}_{tt}}$.

The last step of Harris and Johnson can be applied without modification, as only minor improvements are expected from extending the parent absorption step to multiple traits.

The software was tested for both ST and MT-Mace, and approximate reliabilities for ST-Mace were essentially equal to the corresponding HJ reliabilities.

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