Short communication: Quantifying bias in a single-trait international model ignoring covariances from multiple-trait national models

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ABSTRACT

The current method in use for international genetic evaluations, called single-trait multiple across-country evaluation (ST-MACE), does not consider residual covariances among traits, making possible only the inclusion of one trait per country in an analysis. The aim of this study was to quantify the effect of bias resulting from treating traits from the same country as nationally independent in an international genetic evaluation. Data from the September 2007 Interbull test evaluation for Holstein female fertility traits were used. Data included were 1 trait from Belgium, Switzerland, Spain, and the United States of America, and 2 traits from Canada, Germany-Austria, and Denmark-Finland-Sweden. The biased results were obtained from a 10-variate ST-MACE analysis including all country traits. The unbiased results were obtained from 8 different 7-variate ST-MACE analyses, each including only 1 trait per country. Average absolute bias in the genetic correlations among 2-trait countries (0.11) was higher than for between 1-trait countries and 2-trait countries (0.07) and for among 1-trait countries (0.03). The results of the biased and the unbiased analyses were different, not only due to bias, but also because of different number of traits involved in the analyses. Differences were considerable (on average, 0.08 to 6.91) for reliabilities, which were higher for traits with lower heritability. Average differences were minor (−0.04 to 0.03 standard deviations) for predicted genetic merits. However, for the top 100 bulls in each country trait, these differences were important (on average, −0.26 to 0.11 standard deviation of predicted genetic merit), which caused considerable changes in bull rankings. The results of this study showed that the effect of bias, caused by ignoring covariances from multiple-trait national models in an ST-MACE analysis, is of such a magnitude that necessitates the use of another method

such as multiple-trait multiple across-country evaluation.

Key words: bias, multiple-trait, residual covariance, multiple across country evaluation

Short Communication

Multiple-trait models improve the accuracy of genetic evaluations (compared with single-trait models) through simultaneous utilization of records from multiple traits and using genetic and residual variance-covariance matrices incorporated in the mixed model equations (Schaeffer, 1984). Other features of multiple-trait models are accounting for the bias of selection on correlated traits (Pollak et al., 1984; Schaeffer, 1984) and for genotype by environmental interaction (Schaeffer, 1994), which is the main aspect for international genetic evaluations.

International genetic evaluations of bulls are performed under the auspices of Interbull (Interbull Centre, Uppsala, Sweden). The results on 6 breeds and 7 trait groups are widely in use by the dairy cattle breeding industry. The method used in Interbull genetic evaluations is the so-called single-trait multiple across-country evaluation (ST-MACE), originally proposed by Schaeffer (1994). One basic assumption of this method is that predicted genetic merit ($\hat{a}$) of bulls from different countries is measured on different daughter groups and, therefore, residually uncorrelated. In this method, the same traits (e.g., milk yield) submitted from different countries are considered to be different traits. As such, ST-MACE is a multiple-trait model. However, the usage of the term single trait signifies the fact that in each analysis only one trait per country can be included.

An ST-MACE can even be applied to the national data when no possibility exists for direct estimation of genetic correlations from the raw data (Larroque and Ducrocq, 1999). Because the assumption of nonzero residual correlations is not fulfilled by the national data, if residual correlations are moderately high, ST-MACE estimates may be substantially biased. However, ST-MACE can be used by forcing residual correlations to zero through an appropriate partitioning of the data

Received September 27, 2010.

Accepted January 12, 2011.

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Table 1. Number of bulls (born since 1970) in each country trait (on diagonal), number of common bulls between country traits (below diagonal), and heritabilities (h^2) for each country trait (bottom row)

Trait ¹	BEL _{DO}	CAN _{CF}	CAN _{FC}	CHE _{CF}	DEU _{CF}	DEU _{FL}	DFS _{CF}	DFS _{FL}	ESP _{DO}	USA _{DP}
BEL _{DO}	1,497									
CAN _{CF}	252	4,100								
CAN _{FC}	247	3,589	3,589							
CHE _{CF}	260	218	209	1,135						
DEU _{CF}	708	471	435	349	16,752					
DEU _{FL}	671	422	400	324	15,158	15,158				
DFS _{CF}	366	362	338	255	689	651	12,312			
DFS _{FL}	365	362	337	255	690	649	12,310	12,325		
ESP _{DO}	713	455	437	327	1,241	1,189	630	629	3,614	
USA _{DP}	523	1,026	906	343	1,099	993	718	718	1,139	35,125
h^2	0.040	0.072	0.077	0.059	0.039	0.010	0.040	0.020	0.045	0.040

¹BEL_{DO} = days open from Belgium; CAN_{CF} = calving to first insemination from Canada; CAN_{FC} = first insemination to conception from Canada; CHE_{CF} = calving to first insemination from Switzerland; DEU_{CF} = calving to first insemination from the joint Germany-Austria evaluation; DEU_{FL} = first to last insemination from the joint Germany-Austria evaluation; DFS_{CF} = calving to first insemination from the joint Nordic (Denmark-Sweden-Finland) evaluation; DFS_{FL} = first to last insemination from the joint Nordic evaluation; ESP_{DO} = days open from Spain; and USA_{DP} = daughter pregnancy rate from the United States.

set (Larroque and Ducrocq, 1999). Another difficulty with ST-MACE may arise when $\hat{\mathbf{a}}$ is obtained from the same multiple-trait national model rather than from independent national models (Larroque and Ducrocq, 1999).

In recent years, there has been a growing demand for including more than 1 trait per country in international genetic evaluations. One example is the demand for multiple-trait evaluation of several lactations (e.g., milk yield in the first 3 lactations). Another example is the demand for multiple-trait evaluation of several female fertility traits. In such cases, traits from the same country are residually correlated. Consequently, the current ST-MACE method cannot correctly handle such data.

Schaeffer (2001) extended his ST-MACE method to the so-called multiple-trait multiple across-country evaluation (**MT-MACE**), so that multiple traits from a country can be included in an analysis. Research has been ongoing on the implementation of MT-MACE (Sullivan et al., 2005; Jorjani, 2006; Mark and Sullivan, 2006; Tarrés et al., 2007; Liu et al., 2008; Nilforooshan et al., 2009, 2010). Although the technical difficulties of the implementation of MT-MACE are gradually being resolved, few attempts have been made to quantify bias resulting from analyzing correlated traits from the same country (especially if they are coming from a multiple-trait national model) in the framework of ST-MACE method.

The aim of this study was to quantify the effect of bias resulting from including traits from the same multiple-trait national model in ST-MACE as if those were from different national genetic evaluations. The effect of bias was measured for the estimated genetic correlations, $\hat{\mathbf{a}}$, and reliabilities for female fertility traits. The effect of bias on the evaluation of the top/bottom100 bulls (based on the unbiased evaluations) was also studied.

Data from the September 2007 Interbull test evaluation from 7 Holstein populations were used. Data were on 1 trait from 4 populations (1-trait countries), and 2 traits from 3 populations (2-trait countries), summing to a total of 10 traits. Traits were days open from Belgium (**BEL_{DO}**), days open from Spain (**ESP_{DO}**), calving to first insemination from Switzerland (**CHE_{CF}**), daughter pregnancy rate from the United States of America (**USA_{DP}**), intervals from calving to first insemination and first insemination to conception from Canada (**CAN_{CF}**, **CAN_{FC}**), calving to first insemination and first to last insemination from Germany-Austria (**DEU_{CF}**, **DEU_{FL}**), and calving to first insemination and first to last insemination from the Nordic countries including Denmark, Finland, and Sweden (**DFS_{CF}**, **DFS_{FL}**). Data quality was checked according to Jakobsen and Hjerpe (2006). Data structure and heritabilities (Interbull, 2007) of the studied country traits are shown in Table 1.

Germany and Austria have a joint genetic evaluation and were treated as a single Holstein population. The same was true for Denmark, Finland, and Sweden. The 2-trait populations were chosen because they all use a multiple-trait national genetic evaluation model for female fertility traits only. The reported within-country genetic and residual correlations were 0.274 and -0.047 for CAN, 0.370 and 0.278 for DEU, and 0.409 and -0.082 for DFS (Interbull, 2007).

Single-trait multiple across-country evaluation (Schaeffer, 1994) was used in this study. The model is as follows:

$$\mathbf{y}_i = \boldsymbol{\mu}_i + \mathbf{Z}_i \mathbf{Q} \mathbf{g}_i + \mathbf{Z}_i \mathbf{s}_i + \mathbf{e}_i,$$

where $\mathbf{y}_i$ is the vector of de-regressed national genetic evaluations (the de-regression procedure was according to Jairath et al., 1998); $\boldsymbol{\mu}_i$ is the vector of coun-

Table 2. Averages of the estimated genetic correlations by the unbiased analyses (below diagonal), and the estimated genetic correlations by the biased analysis (above diagonal)

Trait ¹	BEL _{DO}	CAN _{CF}	CAN _{FC}	CHE _{CF}	DEU _{CF}	DEU _{FL}	DFS _{CF}	DFS _{FL}	ESP _{DO}	USA _{DP}
BEL _{DO}		0.786	0.722	0.793	0.862	0.888	0.794	0.835	0.951	0.882
CAN _{CF}	0.749		0.546	0.899	0.891	0.743	0.937	0.793	0.816	0.785
CAN _{FC}	0.659			0.380	0.548	0.771	0.490	0.729	0.718	0.754
CHE _{CF}	0.759	0.928	0.244		0.913	0.740	0.937	0.770	0.807	0.763
DEU _{CF}	0.755	0.914	0.332	0.929		0.818	0.917	0.802	0.853	0.829
DEU _{FL}	0.780	0.516	0.832	0.493			0.780	0.941	0.922	0.946
DFS _{CF}	0.744	0.950	0.356	0.948	0.920	0.563		0.849	0.800	0.807
DFS _{FL}	0.799	0.656	0.811	0.625	0.603	0.925			0.860	0.914
ESP _{DO}	0.941	0.767	0.686	0.761	0.737	0.826	0.730	0.842		0.943
USA _{DP}	0.865	0.740	0.744	0.714	0.724	0.897	0.747	0.910	0.937	
Mean ²	0.835	0.831	0.639	0.778	0.827	0.841	0.808	0.831	0.852	0.847
Mean ³	0.783	0.778	0.583	0.771	0.739	0.729	0.745	0.771	0.803	0.809

¹BEL_{DO} = days open from Belgium; CAN_{CF} = calving to first insemination from Canada; CAN_{FC} = first insemination to conception from Canada; CHE_{CF} = calving to first insemination from Switzerland; DEU_{CF} = calving to first insemination from the joint Germany-Austria evaluation; DEU_{FL} = first to last insemination from the joint Germany-Austria evaluation; DFS_{CF} = calving to first insemination from the joint Nordic (Denmark-Sweden-Finland) evaluation; DFS_{FL} = first to last insemination from the joint Nordic evaluation; ESP_{DO} = days open from Spain; and USA_{DP} = daughter pregnancy rate from the United States.

²Upper diagonal values, excluding the 3 within-country genetic correlations.

³Lower diagonal values.

try means; $\mathbf{g}_i$ is the vector of phantom parent genetic groups, defined according to unidentified parents by the country of origin, breed, and birth year of the bull and the path of selection; $\mathbf{s}_i$ is the vector of random sire genetic effects in country i ; $\mathbf{e}_i$ is the vector of random residual effects; and $\mathbf{Z}$ and $\mathbf{Q}$ are the matrices that relate de-regressed national evaluations to sires, and sires to phantom parent groups, respectively. The effective daughter contributions (EDC) estimated from multiple-trait national genetic evaluations were used in the mixed model equations as elements of $\mathbf{R}^{-1}$ divided by the national residual variance. The estimation of genetic correlations was performed using an expectation maximization REML (EM-REML) algorithm (Klei and Weigel, 1998).

The unbiased estimates of genetic correlations, $\hat{\mathbf{a}}$, and reliabilities were obtained from 8 different 7-variate ST-MACE analyses, where all combinations of 1 trait per country were analyzed. From those analyses, each bull received 8 $\hat{\mathbf{a}}$ per country from the 1-trait countries and 4 $\hat{\mathbf{a}}$ per trait from the 2-trait countries. The $\hat{\mathbf{a}}$ per bull for each country trait with the highest reliability on that specific scale was retained and considered as the best unbiased estimate. The biased estimates were obtained from a single 10-variate ST-MACE analysis, including 2 traits from CAN, DEU, and DFS.

The bias in the 10-variate analysis resulted from ignoring within-country residual correlations for traits from CAN, DEU, and DFS, and single-trait de-regression of the national genetic evaluations, not taking into account the within-country genetic correlations. An additional source of bias stems from including more than 1 trait per country in the analysis, if EDC val-

ues had been estimated from a multiple-trait national model. Studying the French data for longevity and type traits, Larroque and Ducrocq (1999) neither found any important bias from ignoring residual correlations, nor important differences between using correlations from either single-trait or multiple-trait models in ST-MACE. However, they also mentioned that in different circumstances and for different data those assumptions should be rechecked.

All countries were moderately to highly correlated with each other. The USA_{DP} had the highest (0.809) and CAN_{FL} had the lowest (0.583) average of genetic correlation with the other country traits (Table 2; below diagonal). Average absolute deviation of genetic correlations estimated by the unbiased and biased analyses (Table 3), as expected, was the largest among 2-trait countries (0.11) and the smallest among 1-trait countries (0.03). Average absolute bias per country trait also showed higher values for 2-trait countries (Table 4).

Because the scales of evaluations were different for different country traits, average deviations for $\hat{\mathbf{a}}$ were not comparable across country traits. To make them comparable and also to consider different $\hat{\mathbf{a}}$ variances by the unbiased $\left(V_{\hat{a}_i}\right)$ and the biased $\left(V_{\hat{a}_i^*}\right)$ evaluations, standardized average deviations (SADV) of $\hat{\mathbf{a}}$ were used:

$$SADV_i = \frac{\sum_{j=1}^n (\hat{a}_{ij} - \hat{a}_{ij}^*)}{n \sqrt{\frac{V_{\hat{a}_i} + V_{\hat{a}_i^*}}{2}}},$$

Table 3. Average of genetic correlations from the unbiased analyses and average absolute bias (AAB) within different sets of genetic correlations from the biased analysis

Correlation	n	Mean	AAB
Among 1-trait countries	6	0.83	0.03
Between 1-trait and 2-trait countries	24	0.75	0.07
Among 2-trait countries	12	0.70	0.11
Total	42	0.77	0.07

where $\hat{a}_{ij}$ and $\hat{a}_{ij}^*$ are from the unbiased and biased analyses, respectively; n is the number of observations; i corresponds to the country trait; and j corresponds to the individual bull.

Decreasing prediction error variances through keeping the $\hat{\mathbf{a}}$ with the highest reliability for each bull in each country trait (i.e., compared with each single 7-variate analysis or taking the average of $\hat{\mathbf{a}}$ from the 7-variate analyses) was associated with increases in $V_{\hat{a}_i}$.

However, $V_{\hat{a}_i}^*$ (results are not shown) were, on average, 10% higher than $V_{\hat{a}_i}$, ranging from 4% higher for CAN_{FC} to 17% higher for ESP_{DO}. The larger $V_{\hat{a}_i}^*$ was probably

due to the fact that the residual covariances that could not be taken into account by the model increased prediction error variances. The *SADV* was in a range of -0.04 to 0.03 standard deviation of $\hat{\mathbf{a}}$. The average deviations of reliabilities between the biased and unbiased analyses were considerable and different from one country trait to another, generally higher for traits with lower heritability (Table 4).

Average deviations of reliabilities and $\hat{\mathbf{a}}$ for the top 100 and the bottom 100 bulls for each country trait were considered to study the rate and the direction of bias in distribution tails. The results (Table 5) showed that both for $\hat{\mathbf{a}}$ and reliabilities, the bias was higher for the top 100 and bottom 100 bulls than for the whole data. Rank correlations between the biased and unbiased evaluations for the top 100 bulls in each country trait (Table 5) were low (average = 0.74). This shows that even though, on average, the effect of bias on $\hat{\mathbf{a}}$ was small, the biased evaluations may considerably change the rankings for the most important bulls.

Whereas for 6 of 10 country traits, the average $\hat{a}_{ij}^*$ was higher than the average $\hat{a}_{ij}$ for the top 100 bulls, for all country traits, the average $\hat{a}_{ij}^*$ was lower than the average $\hat{a}_{ij}$ for the bottom 100 bulls. This can be a consequence of larger $V_{\hat{a}_i}^*$. Except for CAN_{FC}, reliabilities from the biased analysis were higher than the reliabilities from the unbiased analyses, both for top 100 and bottom 100 bulls, for all country traits (Table 5). For the top 100 bulls, this difference was generally higher than for the bottom 100 bulls.

Schaeffer (1984) studied the effect of incorrect genetic and residual correlations on the prediction of genetic merit in a bivariate model and reported that prediction error variances are influenced. Using incorrect genetic and residual correlations increases prediction error variances of evaluations (Schaeffer, 1984), which decreases reliabilities. We speculate about 3 reasons for increasing reliabilities in the biased analysis (Table 4). The first, and the most important, reason was applying a 10-variate analysis instead of 7-variate analyses

Table 4. Average absolute deviations for genetic correlations (r_g) and average deviations for predicted genetic merits ($\hat{\mathbf{a}}$) and reliabilities (REL) of the biased analysis from the unbiased analyses for different country traits (corresponding number of observations in parentheses)

Trait ¹	r_g	$\hat{\mathbf{a}}^2$	REL
BEL _{DO}	0.05 (9)	0.03 (49,170)	6.52 (49,170)
CAN _{CF}	0.07 (8)	-0.01 (49,170)	1.30 (49,170)
CAN _{FC}	0.09 (8)	-0.04 (48,812)	0.08 (48,812)
CHE _{CF}	0.08 (9)	-0.04 (49,170)	0.76 (49,170)
DEU _{CF}	0.10 (8)	0.01 (49,170)	3.93 (49,170)
DEU _{FL}	0.13 (8)	-0.01 (47,885)	6.91 (47,885)
DFS _{CF}	0.07 (8)	-0.04 (49,155)	2.69 (49,155)
DFS _{FL}	0.08 (8)	-0.03 (49,168)	5.83 (49,168)
ESP _{DO}	0.05 (9)	-0.02 (49,170)	6.44 (49,170)
USA _{DP}	0.04 (9)	0.00 (49,170)	5.86 (49,170)

¹BEL_{DO} = days open from Belgium; CAN_{CF} = calving to first insemination from Canada; CAN_{FC} = first insemination to conception from Canada; CHE_{CF} = calving to first insemination from Switzerland; DEU_{CF} = calving to first insemination from the joint Germany-Austria evaluation; DEU_{FL} = first to last insemination from the joint Germany-Austria evaluation; DFS_{CF} = calving to first insemination from the joint Nordic (Denmark-Sweden-Finland) evaluation; DFS_{FL} = first to last insemination from the joint Nordic evaluation; ESP_{DO} = days open from Spain; and USA_{DP} = daughter pregnancy rate from the United States.

²Standardized to the country-trait standard deviation of $\hat{\mathbf{a}}$.

Table 5. Rank correlations between the biased and the unbiased analyses for the top 100 bulls, and average deviations of predicted genetic merits ($\hat{a}$) and reliabilities (REL) of the biased analysis from the unbiased analyses for top 100 and bottom 100 bulls in each country trait

Trait ¹	Rank _{Top100} ²	$\hat{a}$ ³		REL	
		Top 100	Bottom 100	Top 100	Bottom 100
BEL _{DO}	0.69	0.11	−0.09	11.86	5.58
CAN _{CF}	0.78	0.01	−0.08	0.96	1.50
CAN _{FC}	0.73	−0.26	−0.05	−3.82	−0.16
CHE _{CF}	0.79	−0.04	−0.12	0.65	0.55
DEU _{CF}	0.78	0.09	−0.13	2.98	3.53
DEU _{FL}	0.76	−0.07	−0.06	12.65	6.14
DFS _{CF}	0.79	0.06	−0.14	3.45	2.61
DFS _{FL}	0.69	−0.02	−0.06	11.15	5.38
ESP _{DO}	0.69	0.05	−0.10	11.27	4.09
USA _{DP}	0.70	0.04	−0.02	9.49	3.87

¹BEL_{DO} = days open from Belgium; CAN_{CF} = calving to first insemination from Canada; CAN_{FC} = first insemination to conception from Canada; CHE_{CF} = calving to first insemination from Switzerland; DEU_{CF} = calving to first insemination from the joint Germany-Austria evaluation; DEU_{FL} = first to last insemination from the joint Germany-Austria evaluation; DFS_{CF} = calving to first insemination from the joint Nordic (Denmark-Sweden-Finland) evaluation; DFS_{FL} = first to last insemination from the joint Nordic evaluation; ESP_{DO} = days open from Spain; and USA_{DP} = daughter pregnancy rate from the United States.

²Top 100 based on the unbiased evaluations.

³Standardized to the country trait standard deviation of $\hat{a}$.

and using information from a larger number of records and parameters (45 genetic correlations instead of 21). Second, single-trait EDC values tend to be larger than multiple-trait EDC values (Liu et al., 2004; Nilforooshan et al., 2010). Therefore, using higher single-trait EDC values instead of multiple-trait EDC values can increase reliabilities. Third, considering traits as residually independent during the estimation of genetic correlations led to the estimation of higher genetic correlations and, consequently, higher reliabilities. The bias resulting from ignoring residual covariances in a multiple-trait analysis will depend on the number of residually correlated traits, number of observations per trait, and the size of the residual covariances.

There were bulls for which $\hat{a}_{ij}$ had a higher reliability than did $\hat{a}_{ij}^*$. This situation was more obvious for CAN_{FC} top100 and bottom100 bulls (Table 5). Although, $\hat{a}_{ij}^*$ was predicted from an analysis with more traits involved, $\hat{a}_{ij}$ was chosen, based on the maximum reliability from 8 distinct 7-variate analyses with different reliability distributions, estimated based on different genetic correlations, some of which were higher compared with the 10-variate analysis.

In conclusion, results of this study showed that even with the addition of 3 traits to a set of 7 independent country traits (ignoring covariances from multiple-trait national models) the effect of bias on the genetic correlation among 2-trait countries and on reliabilities was considerable. The effect of bias on $\hat{a}$ was not equally distributed in the entire data set; it was, on average,

low for the whole data but high for the top/bottom 100 bulls. Rankings were considerably affected by bias. The substantial effect of bias on genetic correlations among 2-trait countries and its consequence on the reliability of evaluations rule out the use of a single ST-MACE method for analyzing traits from multiple-trait national models. Even though results of multiple ST-MACE analyses, each including only 1 trait per country, seem to be unaffected by bias, performing all of these analyses would require more time and computational resources than a single MT-MACE analysis. In addition, these ST-MACE analyses would not make optimal use of the data, because not all of the data are analyzed simultaneously. Therefore, a new method, such as MT-MACE, should be adopted for international genetic evaluations of these traits.

ACKNOWLEDGMENTS

Mohammad A. Nilforooshan greatly acknowledges the Swedish Institute (Stockholm, Sweden) for the scholarship award for a part of his PhD program.

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