Multiple-trait multiple country genetic evaluation of fertility traits in dairy cattle

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Abstract

Female fertility is one of the most economically important traits for the dairy cattle industry. Because of a few decades of selection mainly for higher milk production, many dairy farms around the world suffer from the consequences of female fertility loss. The aims of this thesis were to study the international genetic evaluation of female fertility traits, to quantify the bias of analyzing multiple female fertility traits per country with the current method in use for international genetic evaluations (MACE), to study the implementation of a new method (MT-MACE) for the analysis of multiple traits per country, and also to study the effect of across country selection for milk yield on the international genetic evaluation of female fertility traits, when MT-MACE is applied.

Female fertility traits are low heritable, each describing a part of the female fertility complex. International genetic evaluation is useful for improving the accuracy of female fertility evaluations and making the across country comparisons of bulls possible. Despite the low heritability values of female fertility traits, the estimated across country genetic correlations were moderate to high, making the international genetic evaluations feasible for female fertility traits.

Results for female fertility traits showed that including multiple traits per country in a MACE analysis would lead to considerable bias. This bias is due to ignoring covariances from multiple-trait national models. Avoiding bias by performing several unbiased MACE analyses, each including one trait per country is not advantageous, because it is computationally prohibitive and it does not make an optimal use of the available data.

MT-MACE was applied to female fertility data, which led to higher reliabilities compared to the (unbiased) MACE evaluations. The reliability gains were larger for foreign bulls and the Top 100 bulls in each country-trait. The results showed that when the within country selection for milk yield is already taken care of by the multiple-trait national models, the across country selection for milk yield did not make significant bias in the international evaluation of female fertility traits.

Keywords: MACE, multiple-trait, Interbull, female fertility, milk yield, bias, genetic correlation, reliability, genetic trend

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Avelsvärdering av fruktsamhetsegenskaper hos mjölkkor med “Multiple-trait multiple country” metoden

Sammanfattning

Honlig fruktsamhet är en av de viktigaste egenskaperna för mjölkbranschen. Några få decenniers urval som huvudsakligen baserats på högre mjölkproduktion har gjort att många mjölkbönder runt om i världen drabbats av försämrad fruktsamhet hos sina mjölkkor. Syftet med avhandlingen var att studera den internationella avelsvärderingen för honliga fruktsamhetsegenskaper, att kvantifiera det skattningsfel (bias) man får genom att analysera flera honliga fruktsamhetsegenskaper per land samtidigt då man använder sig av den nuvarande metoden för internationell avelsvärdering (MACE), att studera implementeringen av en ny metod (MT-MACE) vid analys av flera delegenskaper per land samtidigt, samt att studera om avelsurvalet för mjölkavkastning i de olika länderna påverkar den internationella avelsvärderingen för honliga fruktsamhetsegenskaper när man använder sig av MT-MACE.

Honliga fruktsamhetsegenskaper har låg arvbarhet och de beskriver olika delar av fruktsamhetskomplexet. Internationell avelsvärdering är användbar för att förbättra säkerheten vid urvalet för honlig fruktsamhet och möjliggör jämförelser av tjurar mellan länder. Trots de låga arvbarheterna för fruktsamhetsegenskaperna, så var de skattade genetiska korrelationerna mellan länder medelhöga till höga vilket möjliggör en internationell avelsvärdering för egenskaperna.

Resultaten visade att om man inkluderar flera fruktsamhetsegenskaper per land i en MACE analys kommer detta att leda till betydande skattningsfel. Att försöka undvika skattningsfel genom att utföra ett flertal MACE-analyser, var och en innehållande en egenskap, är inte att rekommendera då det dels är beräkningsmässigt mycket krävande och dessutom inte använder sig av alla data på ett optimalt sätt.

Då MT-MACE applicerades på fruktsamhetsdata ökade säkerheten (reliability) för de analyser där en egenskap åt gången analyserades med MACE. Den största ökningen i säkerhet erhölls för utländska tjurar samt för de 100 högst rankade tjurarna i varje land-egenskap. Resultaten visade vidare att när urvalet inom länderna redan beaktat korrelerade effekter av urvalet för mjölkproduktion på fruktsamhetsegenskaperna i en fleregenskapsmodell, så medför inte urval mellan länderna något signifikant skattningsfel i de internationella avelsvärderingarna för fruktsamhet.

Sökord: MACE, Multiple trait, Interbull, honlig fruktsamhet, mjölkavkastning, skattningsfel, säkerhet, genetisk trend

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Dedication

To my all: My martyred father & my beloved mother

Contents

List of Publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

I Loberg, A., Nilforooshan, M.A., Philipsson, J. & Jorjani, H. (2011) An overview of national and international genetic evaluation of female fertility traits (manuscript).

II Nilforooshan, M.A., Fikse, W.F., Berglund, B., Jakobsen, J.H. & Jorjani, H. (2011) Quantifying bias in a single-trait international model ignoring covariances from multiple-trait national models. *Journal of Dairy Science*, 94 (5), 2631-2636.

III Nilforooshan, M.A., Jakobsen, J.H., Fikse, W.F., Berglund, B. & Jorjani, H. (2010) Application of a multiple-trait, multiple-country genetic evaluation model for female fertility traits. *Journal of Dairy Science*, 93 (12), 5977-5986.

IV Nilforooshan, M.A., Jakobsen, J.H., Fikse, W.F., Berglund, B. & Jorjani, H. (2011) Multiple-trait multiple country genetic evaluation of Holstein bulls for female fertility traits and milk yield (submitted manuscript).

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Abbreviations

BLUP	Best linear unbiased prediction
BSW	Brown Swiss
CE	Conversion equation
CF	Calving to first insemination
CI	Calving interval
DBV	De-regressed national breeding value
DO	Days open
DP	Daughter pregnancy rate
DYD	Daughter yield deviation
EBV	Estimated breeding value
EDC	Effective daughter contribution
EM-REML	Expectation-maximization residual maximum likelihood
FC	First insemination to calving
FL	First to last insemination
GUE	Guernsey
HOL	Holstein
JER	Jersey
MACE	Multiple across country evaluation
MCE	Multiple country evaluation
MT-MACE	Multiple-trait multiple across country evaluation
MY	Milk yield
NR	Non-return rate at 56 days after calving
PEV	Prediction error variance
RDC	Red dairy breed
SIM	Simmental

1 Background

1.1 Genetic evaluation of female fertility

Female fertility is one of the most economically important traits for the dairy cattle industry. Consequences of reduced fertility include prolonged lactations, additional AI and veterinary costs, and increased involuntary culling and replacement costs (Boichard, 1990). Decreasing national genetic trends for female fertility have been shown in different countries (Berglund, 2008; Liu et al., 2008). Even though Nordic countries have selected for fertility for a few decades, fertility problems are the most common culling reasons, accounting for 23.6% and 25.9% of the culls in the Swedish organic and conventional production systems, respectively (Ahlman et al., 2011). The problem seems to be more severe for Holstein than for the other breeds like Jersey and Red Dairy Cattle (Philipsson et al., 2009).

Compared to many other traits, the history of national genetic evaluations for female fertility traits is rather short. Also, international genetic evaluation of female fertility has started as late as February 2007.

Genetic evaluation of female fertility has not been an easy task, mainly due to different management practices that either directly or indirectly affects the female fertility. For example, some cows may be inseminated by the first oestrus, but the first insemination of some cows may be deliberately delayed. More examples are provided by Kadarmideen et al. (2003). Even though there is genetic variation in female fertility, it is hard to make progress by selecting bulls on their female fertility EBV (de Jong, 2005). Because of the low heritability of female fertility traits, larger daughter groups are needed to obtain the similar reliabilities as for traits with higher heritability.

Selection on any single female fertility measurement alone does not optimally improve the female fertility performance, because no single female fertility measurement can describe the whole female fertility complexity (Jorjani, 2006). The genetic and residual correlations between female fertility measurements are low to medium (Roxström et al., 2001b), even the same measurement in different lactations are genetically different traits (Roxström et al., 2001a), i.e., genetic correlations are less than unity.

Multiple-trait genetic evaluation of these measurements can be helpful to complement the genetic evaluation of one measurement for the other measurements. Extension of these multiple-trait national models to multiple-trait international models can improve the accuracy of female fertility genetic evaluations, as well as the effectiveness of breeding programs to improve female fertility.

In the presence of selection, for BLUP to be unbiased, the data upon which selection decisions have been made should be included in the analysis (Henderson, 1975; Schaeffer et al., 1998; Mrode, 2005). Female fertility genetic evaluations are good examples of the evaluations that are subjected to bias due to selection on milk production traits, especially milk yield. This bias has previously been addressed (Kadarmideen et al., 2003; Mrode & Coffey, 2009; Sewalem & Kistemaker, 2008; Sun et al., 2010). Multiple-trait genetic evaluation of female fertility traits with other traits like milk yield is a solution for this possible source of bias.

1.2 International genetic evaluations

The tremendous increase of international genetic exchange in the last decades has resulted in many bulls having progeny in several countries. The increased genetic links among countries makes the international genetic evaluations possible. Without international genetic evaluations, the genetic evaluations made by the exporter country may not be a good criterion for the importing country. This is because the selection criteria and the genetic levels are different in different countries, and genetic materials may perform differently in different environments as a result of genotype by environment interaction.

Across country selection of bulls can accelerate genetic progress, especially when countries have close breeding objectives (Banos & Smith, 1991). International genetic evaluations provide a large multinational reference population, which permits greater genetic response, as a larger number of bulls are being tested.

International genetic evaluations of dairy bulls are performed three times a year under the auspices of Interbull (Interbull Centre, Uppsala, Sweden). Methods for international genetic evaluations have been under continuous development. A brief historical review of the methods used for the international genetic evaluations of dairy sires is presented.

1.2.1 Conversion equations (CE)

International genetic evaluation of dairy bulls started with pairwise country comparisons, using conversion equations between the two countries. Using the estimated regression parameters (a and b) based on the bulls that are evaluated in both countries, the EBV of the bull in the importing country (EBV_{IMP}) could be predicted from the available EBV in the exporting country (EBV_{EXP}) (IDF, 1981):

$$\text{EBV}_{\text{IMP}} = a + b \times \text{EBV}_{\text{EXP}} + e \qquad (1)$$

This method was further developed, including improvement of the regression approach and accounting for the reliability of the EBV in each country (Goddard, 1985; Wilmink et al., 1986). The reliability of conversion equations heavily depends on the number of bulls progeny tested in the two countries, and how representative those bulls are for the exchange bulls between the two countries.

Conversion equations are still estimated and reported based on international genetic evaluations rather than national genetic evaluations. Those conversion equations are very helpful for the evaluation of bulls that are not included in the international genetic evaluation, and for the bull dams.

1.2.2 Multiple-country evaluation (MCE)

This method was the first BLUP based method proposed for international genetic evaluation of sires (Schaeffer, 1985). The mixed model equations of MCE are as follow:

$$\begin{bmatrix} X'D^{-1}X & X'D^{-1}ZQ & X'D^{-1}Z \\ Q'Z'D^{-1}X & Q'Z'D^{-1}ZQ & Q'Z'D^{-1}Z \\ Z'D^{-1}X & Z'D^{-1}ZQ & Z'D^{-1}Z + A^{-1}\lambda \end{bmatrix} \begin{bmatrix} \hat{c} \\ \hat{g} \\ \hat{s} \end{bmatrix} = \begin{bmatrix} X'D^{-1}y \\ Q'Z'D^{-1}y \\ Z'D^{-1}y \end{bmatrix} \qquad (2)$$

where,

$\mathbf{y}$ = vector of observations, calculated from the EBV of bulls, the reliability of the EBV, and λ (the variance ratio)

$\hat{\mathbf{c}}$ = vector of fixed country (of evaluation) genetic averages

$\hat{\mathbf{g}}$ = vector of fixed effects for genetic groups (country and year of birth of each bull)

$\hat{\mathbf{s}}$ = vector of random sire genetic effects (ND ~ 0, $\mathbf{A}\sigma^2_s$), where **A** is the relationship matrix and σ^2_s is the sire genetic variance

D = diagonal matrix with elements equal to the error variance divided by the number of daughters in different countries of evaluation.

X = design matrix, relating observations to country means

Z = design matrix, relating sires to observations

Q = design matrix, relating sires to genetic groups

There were several benefits for this method compared to conversion equations. Whereas conversion equations were based on a small number of common bulls between the two countries, the use of a pedigree relationship matrix could increase the connectedness between the countries. Therefore, comparisons might be less subjected to bias than comparisons based on some popular bulls that have daughters in the two countries (Schaeffer, 1985). Also, using MCE, more than a country pair could be evaluated simultaneously and comparisons were based on a considerably larger number of daughters per bull in multiple countries. Considering genetic groups in the MCE model was another advantage. After solving the mixed model equations, the solutions of genetic groups ($\hat{g}$) should be added to the solutions of genetic merits ($\hat{s}$).

1.2.3 Multiple-trait across country evaluation (MACE)

MCE was a single-trait model and it had some unrealistic assumptions like the same heritability for all countries and also, the model did not allow for any genotype by environment interactions (i.e., genetic correlations set to one). Schaeffer (1994) extended his MCE model to MACE (also called ST-MACE), which is a multiple-trait model for international genetic evaluation. In this model, similar traits in different countries are considered as different traits. Therefore, it was possible to consider different heritabilities for each country and genetic correlations less than one. As a result of the considering genotype by environment interaction, bulls could rank differently in different countries. Nowadays, MACE is in use for the international genetic evaluation of six breeds and 39 traits in seven trait groups. The results are widely in use by the global dairy cattle breeding industry and scientists.

MACE is similar to MCE in design, but as different as a multiple-trait model compared to a single-trait model. As a result of a multiple-trait analysis, all bulls receive an evaluation in each country included in the analysis, whether they have any daughters in that country or not (Schaeffer, 1994).

1.2.4 Multiple-trait multiple across country evaluation (MT-MACE)

One of the assumptions of MACE is that traits from different countries are measured on different sets of daughter groups (daughters are recorded in only one country) that are genetically correlated, but not residually. As a result, only one trait per country could be included in an analysis. However, the need for an international genetic evaluation model which could consider multiple traits per country in the analysis became more pronounced as more and more countries changed from single-trait to multiple-trait national models. For example, countries were more interested to have international EBV of bulls for different lactations rather than a single EBV for a lactation or an index of several lactations. With MACE, countries are limited to combine different lactations into an index and submit that index for international genetic evaluations. Separate EBVs for different lactations are more informative than a single EBV for the dairy industry, because production patterns of the bull daughters tend to be different across lactations (Schaeffer, 2001).

Schaeffer (2001) extended MACE to MT-MACE, which was able to handle multiple traits per country in the analysis. Up to now, this method has not been used for routine international genetic evaluation, perhaps because of two main reasons. First, multi-trait de-regression of national EBVs was not easy, especially because of different number of traits per country, and the required number of daughters for each bull in each trait and trait combination to weight the residual variance-covariances. The number of daughters might not be available for all bulls and all the trait combinations. Second, there was a possible risk of a lack of harmonization in the method of calculating multi-trait de-regression, if this was to be done by the participating countries (Schaeffer, 2001). By the development of techniques to estimate effective daughter contributions (EDC) to be used in MACE (Fikse & Banos, 2001), there was no longer interest in using the number of daughters for international genetic evaluations. There was a lack of a method for estimating block EDC matrices to be used in MT-MACE. Later, Liu et al. (2004) developed a method for the computation of multiple-trait EDC for multiple-trait national models and the approximation of reliabilities from those EDC matrices. This method was tested and validated on simulated data (Tarrés et al., 2007), as well as on real production data (Liu et al., 2004), and real female fertility data (Liu et al., 2008) from Germany, Austria and Luxemburg.

To simplify the difficulties of MT-MACE, Sullivan & Wilton (2001) suggested modifications to MACE to make it applicable for the analysis of multiple traits per country. To provide this ability, there were two obstacles to overcome: conversion of EDC from effective dependent scalars (dependent on the other traits in the multiple-trait national model) to effective independent scalars, and multi-trait de-regression of the national EBVs. Overcoming these two obstacles could make the MACE analysis of multiple traits per country possible.

2 Aim of the Thesis

The general aim of the thesis was to study the international genetic evaluation of female fertility traits (Paper I), the current methodology in use (Papers II & III), and to investigate and apply another method for the international genetic evaluation of female fertility, where several traits per country can be analyzed simultaneously (Papers III & IV). In more details, the aims were:

- To study the international genetic evaluations of female fertility traits, considering the six breeds included in the international genetic evaluations (Paper I);
- To quantify the effect of bias resulting from including traits from the same multiple-trait national model in MACE as if those were from different national genetic evaluations (Paper II);
- To study the implementation of the MT-MACE method with scalar residual matrices in the international genetic evaluation of female fertility traits (Paper III);
- To study the possible effect of bias from across country selection for milk yield on the estimated international breeding values, reliabilities and genetic trends for female fertility traits (Paper IV).

3 Summary of the Investigations

3.1 Materials

Data on female fertility traits and milk yield from different countries and years were used. Since Paper I aimed to study the current situation of international genetic evaluations for female fertility trait, data on six breeds from the latest Interbull routine evaluation (April, 2011) was used. Table 1 gives the information about the number of bulls from each country and the breeds involved in the international genetic evaluations for female fertility. For Papers II-IV, only data of the Holstein breed was included (Table 2).

In Papers II and III, data from September 2007 on female fertility were used. There were four traits from four countries with single-trait national genetic evaluation models, and six traits from three countries (two traits each) with multiple-trait national genetic evaluation models. The countries contributing with two traits were chosen because they had multiple-trait national models including only female fertility traits.

In paper IV, data from May 2009 on two female fertility traits as well as milk yield from three countries and milk yield data from USA were used. The countries contributing with three traits were chosen because they had multiple-trait national genetic evaluation models including both female fertility traits and milk yield. Milk yield from USA was chosen as it was assumed to have a large influence on the correlated responses in the other countries and traits.

For the estimation of parameters, data included bulls born since 1970, and for the EBV prediction, data included bulls born since 1986. Bulls had to have at least 10 daughters in at least 10 herds. These were in accordance with Interbull's rules for the incoming data (Interbull, 2008).

Table 1. *Summary of the data structure in Paper I, including the number of bulls from each country and breed*[1] *considered in the international genetic evaluations*

Country	BSW	GUE	JER	HOL	RDC	SIM
Canada	90	32	215	5,040	314	
Deutschland[2]	4,117			18,604	266	
The Nordic[3]			1,959	10,149	7,157	
France				12,261		
Italy				6,963		
The Netherlands	92		88	11,418		41
USA	791	648	2,937	27,415	453	
Switzerland	2,391			965		
Switzerland(R&W)[4]				1,283		
Great Britain	46	163	358	4,451	218	
New Zealand	67	58	3,202	5,386	944	
Belgium				752		
Ireland				1,641		
Spain				1,773		
Czech Republic				2,375		1,530
Israel				943		
Poland				3,567		
South Africa			502	954	141	
Norway					2,984	
SUM	7,594	901	9,261	115,940	12,477	1,571

[1] See the abbreviation list for the breed abbreviations; [2] Germany-Austria-Luxemburg; [3] Denmark-Finland-Sweden; [4] Red & White Holstein

Table 2. *Summary of the data structure in Papers II, III and IV*

Country	Trait[1]	no. bulls	h^2	Paper
Belgium	DO	1,542	0.040	II, III
Canada	CF	4,108	0.072	II, III
Canada	FC	3,597	0.077	II, III
Switzerland	CF	1,135	0.059	II, III
Deutschland[2]	CF	16,764	0.039	II, III
Deutschland	FL	15,166	0.010	II, III
The Nordic[3]	CF	12,312	0.040	II, III
The Nordic	FL	12,325	0.020	II, III
Spain	DO	3,614	0.045	II, III
USA	DP	35,125	0.040	II, III
Great Britain	NR	5,395	0.019	IV
Great Britain	CI	4,981	0.033	IV
Great Britain	MY	9,942	0.548	IV
Italy	CF	7,218	0.057	IV
Italy	CI	6,706	0.038	IV
Italy	MY	7,994	0.309	IV
The Netherlands	CF	12,486	0.222	IV
The Netherlands	CI	12,499	0.145	IV
The Netherlands	MY	13,314	0.570	IV
USA	MY	37,763	0.300	IV

[1] See the abbreviation list for the breed abbreviations; [2] Germany-Austria-Luxemburg; [3] Denmark-Finland-Sweden

3.2 Methods

All the international genetic evaluations were performed using MACE (Schaeffer, 1994) or its extension to MT-MACE (Sullivan & Wilton, 2001). MACE was used in the first three papers and MT-MACE was used in the last two papers. Genetic correlations were estimated using an EM-REML algorithm (Klei & Weigel, 1998) and sire genetic variances were estimated within country and trait, using an EM-REML algorithm (Sullivan, 1999). The estimated genetic correlations and the sire genetic variances were used in the mixed model equations of MACE/MT-MACE.

The country reported EDC values were directly used in MACE. Those EDC values were converted to multi-trait EDC scalars using an iterative procedure (Sullivan & Wilton, 2001) for MT-MACE. National EBVs were de-regressed for each country separately, using the corresponding EDC values. The de-regression procedure of Jairath et al. (1998) was used for MACE and the de-regression procedure of Schaeffer (2001) was used for MT-MACE. Detailed differences between the MACE and MT-MACE methodologies and the methods for EDC conversion and de-regression of national EBVs are discussed in General Discussion.

In Papers II, in an attempt to quantify the bias of analyzing multiple traits per country that should be taken care by MT-MACE in the future, two sets of biased and unbiased MACE analyses were compared. The bias was quantified in the framework of MACE, which was already in place and known to be a robust method. The biased MACE analysis was including all the 10 traits. The only way to avoid this bias was to divide the data into several subsets, each including only one trait per country. Hence, the unbiased MACE scenario was a set of eight 7-trait analyses, each including only one trait per country.

In Paper III, the advantage of MT-MACE over MACE was studied by comparing the results of a 10-trait MT-MACE analysis with the results of the set of the unbiased MACE analyses. This advantage was from the benefit of analyzing traits from the same country together and considering the relationships among them, which potentially could also benefit the other traits in the analysis. The bias of ignoring covariances from multiple-trait national models by MACE was studied by comparing the results of the biased MACE analysis with the MT-MACE analysis. The comparisons were made for the difference between the biased and the unbiased EBVs, regression parameters of the regressed biased EBVs to the unbiased EBVs, and re-ranking of bulls between the biased and the unbiased analyses.

In Paper IV, a possible bias of across country selection for milk yield in an MT-MACE genetic evaluation of female fertility traits was investigated.

A 6-trait MT-MACE analysis including two female fertility traits per three countries was compared with a 10-trait MT-MACE analysis, also including milk yield data from the same countries and USA.

The methods and the analyses were compared by considering the changes in the estimated genetic correlations, international EBVs, rankings of bulls in the scale of each country-trait, reliabilities, and the number of predicted bull-EBVs.

3.3 Main findings

3.3.1 International genetic evaluation of female fertility traits

An increasing number of countries include female fertility traits in the national genetic evaluations. Currently 19 genetic evaluation systems, comprising 23 countries, contribute data to the international genetic evaluations. More than half of these countries perform genetic evaluations for more than one breed. The majority of genetic evaluation systems include more than one female fertility traits in the evaluations. Female fertility traits have generally low heritability value, but the range of the reported heritability values is almost 4 times larger than the mean of heritability values. Number of bulls evaluated for female fertility traits is also large. Number of bulls with daughters in more than one country (the so-called common bulls) is at such high levels that make it possible to estimate across country genetic correlations. Genetic correlations between similarly defined traits (e.g., interval traits) are quite high, around 0.90. However, if trait definitions are very different, genetic correlations can be as low as 0.25.

In international genetic evaluation of the other traits, for example milk production, almost all bulls from all countries have evaluations for all the traits evaluated in that trait group. As an example, all bulls from Great Britain have evaluations for milk, fat and protein yield. The same is true for bull from Canada. Therefore, direct comparison of all bulls for all the traits and on all the country scales is possible. However, this is not the case for female fertility traits. The data for female fertility traits is very unbalanced in the sense that all bulls of a country do not have evaluation for all the female fertility traits, and all the countries do not have evaluations for all the female fertility traits. As an example, only a proportion of USA bulls with evaluation for daughter pregnancy rate (DP) have evaluation for heifer conception rate. In Spain, the only fertility trait under evaluation is days open (DO), while in France there is no evaluation for DO. The consequence of the unbalanced data is that with the classification of female fertility traits into 5 different groups and separate international genetic evaluations for these 5 different trait groups, direct comparison of all bulls for all the traits and on all the country scales is not possible.

3.3.2 MACE and multiple traits per country

Analyzing multiple traits per country in the framework of MACE would lead to bias, because any trait is assumed to be from a different country and residual correlations between traits are zero. This assumption is not true when several traits from the same country are considered.

The bias was the highest for the genetic correlations among 2-trait countries (0.11) and the lowest for the genetic correlations among 1-trait countries (0.03). Whereas, the bias was low for EBVs in the whole data, it was larger for Top 100 and Bottom 100 bulls, resulting in changes of ranks for Top 100 bulls. Using incorrect parameters is expected to decrease reliabilities. However, the reliabilities by the biased analysis were on average higher. This can be attributed to the larger number of traits included in the biased analysis.

The results of the study proved that even with a few traits from a few countries, the effect of bias resulting from ignoring covariances from multiple-trait national models was considerable on the genetic correlations, the estimated breeding values and rankings of Top 100 bulls in each country-trait. Performing several unbiased MACE analyses is practically prohibitive because of the high computational demand for repeatedly estimating the same parameters and evaluations across the analyses. Moreover, it does not make an optimal use of the available data. Therefore, a new method such as MT-MACE should be adopted for international genetic evaluations of multiple traits per country.

3.3.3 Implementation of MT-MACE for female fertility

MT-MACE (Sullivan et al., 2005) was applied to female fertility traits and the results were compared to the results of the two biased and unbiased MACE evaluations. The estimated genetic correlations by MT-MACE are shown in Table 3.

Correlations obtained from the biased and the unbiased MACE analyses were almost equally (± 0.065) deviated from the correlations obtained from the MT-MACE analysis. On average, the genetic correlations from the biased MACE were 0.053 lower and the genetic correlations from the unbiased MACE were 0.059 higher than the genetic correlations from the MT-MACE analysis. Reliabilities from the biased MACE were larger than those from MT-MACE and also the average reliabilities from the biased MACE. This was assumed to be a result of upward bias in the estimated genetic correlations and the EDC values for the biased MACE analysis. The upward bias was more obvious for 2-trait countries and foreign bulls. As a result of making use of information from multiple traits per country, the estimated reliabilities by the MT-MACE analysis were higher than the averages and also the top reliabilities in the set of unbiased MACE analyses, especially for foreign bulls. Compared to the whole data, reliability gains were larger for Top 100 bulls.

The rank correlations were high between the MT-MACE analysis, the biased MACE and the unbiased MACE analyses (0.98 ± 0.01). However, there were not many bulls in common between each three pairs of Top 100 bulls (50-90). This indicated that the bias in the single MACE analysis or making no use of the correlated information of traits from the same country in the multiple MACE analyses can considerably influence the rankings for the top animals.

As a result of simultaneous analysis of traits from the same country, 1,660 additional international EBVs were obtained by the MT-MACE analysis for the bulls that had been evaluated for one trait in the countries that were contributed with two traits. Overall, the study showed that MT-MACE is a feasible method to handle female fertility data from multiple countries with more than one trait per country.

Table 3. *The estimated genetic correlations by the MT-MACE analysis*

Country	Trait[1]	DO	CF	FC	CF	CF	FL	CF	FL	DO
Belgium	DO									
Canada	CF	0.736								
Canada	FC	0.670	0.323							
Switzerland	CF	0.776	0.916	0.257						
Deutschland[2]	CF	0.855	0.877	0.443	0.913					
Deutschland	FL	0.889	0.690	0.728	0.710	0.809				
The Nordic[3]	CF	0.716	0.944	0.255	0.942	0.879	0.681			
The Nordic	FL	0.782	0.542	0.806	0.539	0.628	0.880	0.557		
Spain	DO	0.952	0.768	0.665	0.784	0.844	0.920	0.723	0.801	
USA	DP	0.881	0.728	0.726	0.728	0.812	0.945	0.712	0.877	0.944

[1] See the abbreviation list for the breed abbreviations; [2] Germany-Austria-Luxemburg; [3] Denmark-Finland-Sweden

3.3.4 Female fertility and across country selection for milk yield

The results of a joint international genetic evaluation of female fertility traits and milk yield were compared with the results of separate international genetic evaluations of female fertility traits and milk yield.

Changes in the genetic correlations among female fertility traits due to inclusion of milk yield data in the analysis were in a range of -0.08 to 0.08. Reliabilities increased from national to international genetic evaluations, whether analyzing female fertility and milk yield traits together or separately. The gain was higher for country-traits with low heritability or low reliability. The simultaneous analysis of female fertility and milk yield traits increased the reliability of international genetic evaluations for the traits that showed higher increase in the genetic correlations. For the traits with high national reliability, the inclusion of more traits to the analysis had small effects. Analyzing female fertility and milk yield traits together or separately, rankings of bulls in different country-trait scales were relatively similar (> 0.96). However, these rank changes should be taken seriously, because as it was found in Paper III, the bias was unequally distributed through the data, which led to higher re-ranking for Top 100 bulls compared to the whole data.

For milk yield traits, reliabilities did not increase by the inclusion of female fertility traits in the analysis, as a result of reduction (-0.004) in genetic correlations among milk yield traits. While milk yield is a good indicator for female fertility traits, female fertility traits are not good indicators for milk yield. Compared to milk yield, female fertility traits have considerably less number of observations, they have low heritabilities and their EBVs have low reliability.

The genetic trends for milk yield in different countries were very similar to each other and all continuously progressive. The genetic trends for all female fertility traits were undesirable. However, improvements could be seen since 2000. Including milk yield traits in the MT-MACE analysis of female fertility traits slightly changed the international genetic trends for different traits and different countries. The deviations were more visible for older bulls. The bias of selection for milk yield did not change the genetic averages, neither the genetic trends for female fertility significantly. However, the way the bias influenced the traits was different from a female fertility trait to another.

4 General Discussion

4.1 MACE and MT-MACE methodologies

In our studies, the two methodologies of MACE and MT-MACE were used to analyze the data. The three sub-sections below provide a methodological overview about the way these methods work and the differences between them.

4.1.1 Mixed model equations

The mixed model equations of MACE are as follow:

$$\begin{bmatrix} X'D^{-1}X & 0 & X'D^{-1}Z \\ 0 & Q'A^{-1}Q\otimes G^{-1} & -Q'A^{-1}\otimes G^{-1} \\ Z'D^{-1}X & -A^{-1}Q\otimes G^{-1} & Z'D^{-1}Z+A^{-1}\otimes G^{-1} \end{bmatrix} \begin{bmatrix} \hat{c} \\ \hat{g} \\ Q\hat{g}+\hat{s} \end{bmatrix} = \begin{bmatrix} X'D^{-1}y \\ 0 \\ Z'D^{-1}y \end{bmatrix} \tag{3}$$

where,

y = vector of DBV or DYD for a particular trait from a country

G = matrix of sire variance-covariances

$\otimes$ = Kronecker product, and the rest as in Equation 2

Unlike MCE, heritabilities and variances are different for the same trait in different countries, and the **Q** matrix is also connected to $\mathbf{A}^{-1}$. As a result of the multiple-trait international genetic evaluation, all bulls receive different EBVs and rankings in all the country scales.

The mixed model equations of MT-MACE, are as follow:

$$\begin{bmatrix} X'D^{-1}X & X'D^{-1} & 0 & 0 \\ D^{-1}X & D^{-1}+A^{ss}\otimes G^{-1} & A^{sp}\otimes G^{-1} & A^{sg}\otimes G^{-1} \\ 0 & A^{ps}\otimes G^{-1} & A^{pp}\otimes G^{-1} & A^{pg}\otimes G^{-1} \\ 0 & A^{gs}\otimes G^{-1} & A^{gp}\otimes G^{-1} & A^{gg}\otimes G^{-1} \end{bmatrix} \begin{bmatrix} \hat{\mu} \\ \hat{u}_s \\ \hat{u}_p \\ \hat{g} \end{bmatrix} = \begin{bmatrix} X'\left(D^{-1}y\right) \\ \left(D^{-1}y\right) \\ 0 \\ 0 \end{bmatrix} \tag{4}$$

where, s, p and g correspond to the sires with observations (DBV or DYD), sires without observations, and unknown phantom parents, respectively; $\mathbf{A}^{**}$ are the blocks of the inverse of the pedigree relationship matrix corresponding to different parts of the data (s, p and g); $\hat{\mathbf{u}} = \mathbf{Q}\hat{\mathbf{g}} + \hat{\mathbf{s}}$; and for country i:

$$X_i = \sum_{j=1}^{t_i} \oplus 1 \tag{5}$$

$$D_i^{-1} = \sum_{k=1}^{b} \oplus B_{ik} \tag{6}$$

where, t_i is the number of traits from country i, b is the number of bulls with EBVs, and $\oplus$ is the direct sum operator. In an example of a model with three lactations:

$$B_{ik} = n_{1,0,0}R^{-}_{1,0,0} + n_{1,1,0}R^{-}_{1,1,0} + n_{1,1,1}R^{-}_{1,1,1} \tag{7}$$

where, $n_{1,0,0}$, $n_{1,1,0}$, $n_{1,1,1}$ are the number of recorded daughters for the first lactation only, recorded for the first and the second lactations but not for the third lactation, and recorded for all the lactations; and

$$R_{1,0,0} = \begin{bmatrix} r_{11} & 0 & 0 \\ 0 & 0 & 0 \\ 0 & 0 & 0 \end{bmatrix}, R_{1,1,0} = \begin{bmatrix} r_{11} & r_{12} & 0 \\ r_{21} & r_{22} & 0 \\ 0 & 0 & 0 \end{bmatrix}, R_{1,1,1} = \begin{bmatrix} r_{11} & r_{12} & r_{13} \\ r_{21} & r_{22} & r_{23} \\ r_{31} & r_{32} & r_{33} \end{bmatrix} \tag{8}$$

where: r_{**} = residual variance-covariance

However, it may not always be the case that daughters recorded for the second lactation are recorded for the first lactation, and daughters recorded for the third lactation are recorded for the first and the second lactations. It is especially the case for analysis of three biologically distinct traits rather than three lactations of a trait. In such situations, the derivation of B_{ik} can be modified as:

$$B_{ik} = n_{1,0,0}R^{-}_{1,0,0} + n_{1,1,0}R^{-}_{1,1,0} + n_{1,1,1}R^{-}_{1,1,1} + n_{0,1,0}R^{-}_{0,1,0} + n_{0,1,1}R^{-}_{0,1,1} + n_{0,0,1}R^{-}_{0,0,1} + n_{1,0,1}R^{-}_{1,0,1} \tag{9}$$

As a result of a multiple trait per country international genetic evaluation, all bulls receive different EBVs and rankings for all the traits in all the country-trait scales.

4.1.2 Derivation of effective daughter contributions

The idea behind using effective daughter contributions (EDC) rather than the number of daughters is that the content of daughter information contributed to national genetic evaluations varies for each bull, both within and across countries (Fikse & Banos, 2001), even different for different traits. Therefore, the inverse of the number of daughters to weight the residual variances are not optimal weights to consider different residual variances on the country-bull scale. The number of daughters is not the only information that contributes to the precision of bull's evaluation. Other sources of information such as the number of lactations per daughter, whether the lactations were completed, in progress or early terminated, daughter dam information, and contemporary group structure are also contributing factors (Fikse & Banos, 2001). Therefore, there was a need for methods to describe the effectiveness of daughter information based on different sources of information. Fikse & Banos (2001) suggested a method for the calculation of EDC for each bull in each country. The equation is as follows:

$$w_i = \sum_k \frac{\lambda R_k(o)}{4 - R_k(o) \cdot (1 + R_{dam}(o))} \tag{10}$$

where w_i is the EDC (single-trait effective independent EDC) value for bull i as the summation of all its daughters' information, $R_{dam(o)}$ is the reliability of the dam's own record (see Fikse & Banos (2001) for the way of calculation), λ is the variance ratio, and $R_{k(o)}$ is the reliability of the kth animal's own record, estimated as:

$$R_{k(o)} = z.h^2, \tag{11}$$

where,

$$z = m/(1+(m-1)r) \tag{12}$$

and r is the repeatability of the trait in the national genetic evaluation. See Interbull Code of Practice (Interbull, 2004) for the calculation of m value.

Using the same equation, this method was then extended for the calculation of EDC (effective dependent EDC ($\mathbf{n}$)) values for multiple-trait national genetic evaluation models (Interbull, 2004), in which:

$$R_{k(o)} = \mathbf{k}'\mathbf{G}'(\mathbf{z}^{-1}\bullet\mathbf{P})^{-1}\mathbf{Gk}(\mathbf{k}'\mathbf{Gk})^{-1} \tag{13}$$

where, $\mathbf{k}$ is the vector of weights given to each lactation/trait, $\mathbf{G}$ is the genetic variance-covariance matrix, $\mathbf{z}$ is a diagonal matrix with elements equal to z_j as defined for the single-trait national model (Equation 12) for trait *j*, • is the Hadamard function, and **P** is the phenotypic variance-covariance matrix. These EDC values are estimated at the national level and routinely reported to Interbull for international genetic evaluations.

With the introduction of MT-MACE (Schaeffer, 2001), again the estimation of EDC values was a challenge. This time, it was even more challenging, since for the residually correlated traits, block EDC matrices were required. Sullivan & Wilton (2001) introduced a method for the conversion of **n**, which are weighted by the within country genetic and residual correlations, to multi-trait effective independent EDC scalars ($\boldsymbol{\eta}$), using known residual and genetic variance-covariances. This conversion is independent from the information on the population structure in the country. The iterative method for this conversion is illustrated in Figure 1. The aim of this conversion is that the derived $\boldsymbol{\eta}$ together with **G** should produce similar PEV as the reported **n** produces with diag(**G**). According to Figure 1, while the $\boldsymbol{\eta}$ is changing from iteration to the next, the matrix containing its associated PEV (**b**) should create a scalar EDC as close as possible to **n**.

Assuming a 3-lactation model, at convergence:

$$PEV_i \simeq diag\left[\begin{bmatrix}\eta_{11} & 0 & 0\\ 0 & \eta_{22} & 0\\ 0 & 0 & \eta_{33}\end{bmatrix}\left[diag(R)\right]^{-1} + G^{-1}\right]_i^{-1} = \left[\begin{bmatrix}n_{11} & 0 & 0\\ 0 & n_{22} & 0\\ 0 & 0 & n_{33}\end{bmatrix}\left[diag(R)\right]^{-1} + \left[diag(G)\right]^{-1}\right]_i^{-1} \quad (14)$$

This conversion takes away the influence of the genetic correlations from **n** to avoid extra weighting of national EBVs for the genetic correlations. Because in this implementation of MT-MACE it is not possible to re-regress DBVs to international EBVs for residual correlations, the weight from residual correlations is kept in $\boldsymbol{\eta}$.

Also, Liu et al. (2004) introduced a procedure for the accumulation of multiple-trait progeny information into multi-trait block EDC matrices with the available data at the national genetic evaluation center. More research is in progress on the implementation and the harmonization of this method for different national models (e.g., Sullivan et al., 2006).

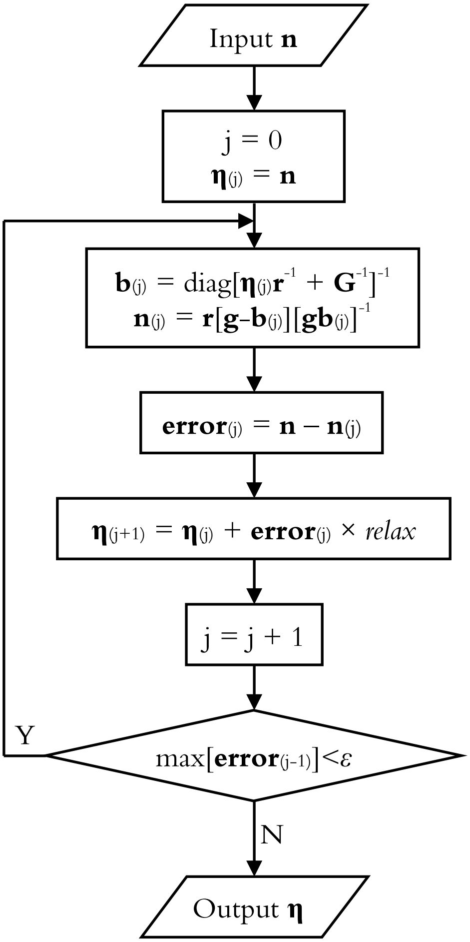

Figure 1. Flowchart of the derivation of multi-trait effective independent EDC ($\boldsymbol{\eta}$) from known single-trait effective dependent EDC ($\mathbf{n}$) for each bull; $\mathbf{r}$ = diag[$\mathbf{R}$]; $\mathbf{g}$ = diag[$\mathbf{G}$]; $\mathbf{R}$ = residual variance-covariance matrix; $\mathbf{G}$ = genetic variance-covariance matrix; *relax* = relaxation factor; ε = convergence criteria; j = iteration number

4.1.3 De-regression of national genetic evaluations

National EBVs should go through a country-wise de-regression procedure before being used in the international genetic evaluations. The aim of the de-regression procedure is to avoid double-counting of national genetic evaluation information in the international genetic evaluation. Generally, the information that has to be considered in the de-regression procedure is the national pedigree (**A**), the heritability by which the genetic connections through the pedigree are weighted, and the national residual information matrix (**D**). However, the sources of information to be considered in the de-regression procedure are different depending on whether the national genetic evaluation model is single- or multiple-trait, and whether the international genetic evaluation model is MACE or MT-MACE (even different between MT-MACE implementation of Schaeffer (2001) and MT-MACE implementation of Sullivan et al. (2005).

Using MACE for single trait per country international genetic evaluations, whether the national genetic evaluations are single- or multiple-trait, a single-trait de-regression procedure (Jairath et al., 1998) is used. This procedure is illustrated in Figure 2. In this procedure the reported EDC (w or $\mathbf{n}$) are used to shape the diagonal **D**. If the national genetic evaluation model is multiple-trait, the reported **n** can be used directly with no double-counting problem for the national information. In this situation, the trait in the international genetic evaluation will carry information from the traits in the multiple-trait national model, which do not exist in the international genetic evaluation.

In order to estimate the DBVs ($\hat{\mathbf{y}}$: Figure 2), first the solution for the bull with EBV ($\mathbf{Qg} + \mathbf{s}$) is set to the country mean (μ: set to zero in the first iteration) subtracted from the national EBV (**a**). In the next step, the solutions for the identified parents without EBV (**p**) and the genetic groups (**g**) are predicted from the predicted solutions of their progeny and the blocks of the inverse of the pedigree relationship matrix that connect them to the solutions of those progeny. The unknown ($\mathbf{D}^{-1}\mathbf{y}$) is predicted from $\mathbf{D}^{-1}$ and the elements that build the true DBV (**y**), which are already known or predicted previously. Afterwards, the country mean (μ) is predicted. The five predictions of ($\mathbf{Qg} + \mathbf{s}$), **p**, **g**, ($\mathbf{D}^{-1}\mathbf{y}$), and μ are estimated repeatedly until reaching the convergence. The ($\mathbf{D}^{-1}\mathbf{y}$) at the convergence is used to estimate DBV ($\hat{\mathbf{y}} = \mathbf{D}(\mathbf{D}^{-1}\mathbf{y})$).

When MT-MACE is used for international genetic evaluation and national genetic evaluations are multiple-trait, the multi-trait de-regression procedure (Schaeffer, 2001) is applied. Multi-trait de-regression aims to avoid double-counting national information including the pedigree, the genetic correlations, and the residual correlations through block residual information matrices (Schaeffer, 2001). Because in the MT-MACE implementation of Sullivan et al. (2005), MACE mixed model equations are used, DBVs will not be re-regressed for residual correlations. Therefore, residual correlations can be omitted in the de-regression. The $\boldsymbol{\eta}$ will then carry the information on residual correlations (Figure 1). With no de-regression and no re-regression for residual correlations, it can be supposed that the studied MT-MACE method assumes equal residual correlations for de-regression of national EBV and re-regression of DBV. This assumption can be true, because unlike genetic correlations, residual correlations are internationally and also pedigree independent.

The multi-trait de-regression procedure (Schaeffer, 2001) is very similar to the single-trait one (Jairath et al., 1998). In multi-trait de-regression, multiple traits from a country are processed rather than one trait. The differences between the multi-trait and the single-trait de-regression procedures are: the vectors and matrices include information on multiple traits rather than information on a single trait. The constant μ becomes the vector of $\boldsymbol{\mu}$, the vector of ones ($\mathbf{1}$) becomes the matrix of $\mathbf{X}$, and instead of using the constant of genetic variance (in the constant of λ), the genetic variance-covariance matrix of $\mathbf{G}$ is used (Figure 3).

A situation can be imagined, where, the international genetic evaluation is MT-MACE and some traits from a country are from single-trait national models or separate multiple-trait models. For this type of traits, if they are from single-trait models, then their reported w can be used directly. This may not be an optimal EDC for the multi-trait de-regression, but it does not cause double-counting of national information. The w values will then be used in a single-trait de-regression procedure. If the traits are from separate multiple-trait models, then their $\mathbf{n}$ can be converted to $\boldsymbol{\eta}$ with genetic covariances equal to zero between the traits from separate national models. The $\boldsymbol{\eta}$ with those zero genetic covariances will then be used in the multi-trait de-regression procedure. A problem that seems to happen in this situation is that in MT-MACE, DBVs should be re-regressed for the within country residual correlations. MACE, in its extension to the MT-MACE (Sullivan & Wilton, 2001), does not provide this possibility and even the MT-MACE as Schaeffer (2001) needs different block EDC matrices for de-regression and re-regression for such traits, which makes things more complex. This situation was not considered in our studies.

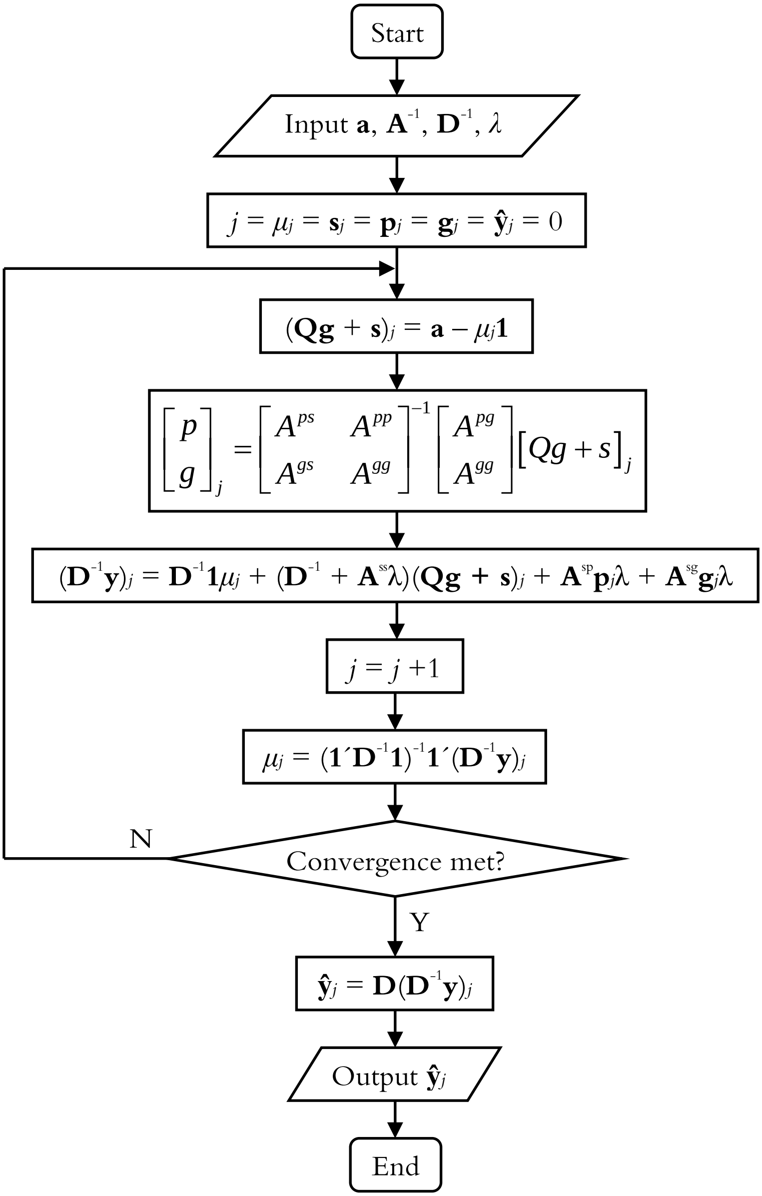

Figure 2. Flowchart of the single-trait de-regression procedure; **a** is the vector of national EBV; **1** is the vector of ones; **A** is the pedigree relationship matrix; **D** is the residual information matrix; λ is the variance ratio; μ is the country mean; **s** is the vector of solutions for bulls with EBV; **p** is the vector of solutions for bulls without EBV; **g** is the vector of solutions for genetic groups; $\hat{\mathbf{y}}$ is the vector of DBV; **Q** is the design matrix relating bulls to genetic groups; *j* corresponds to iteration number

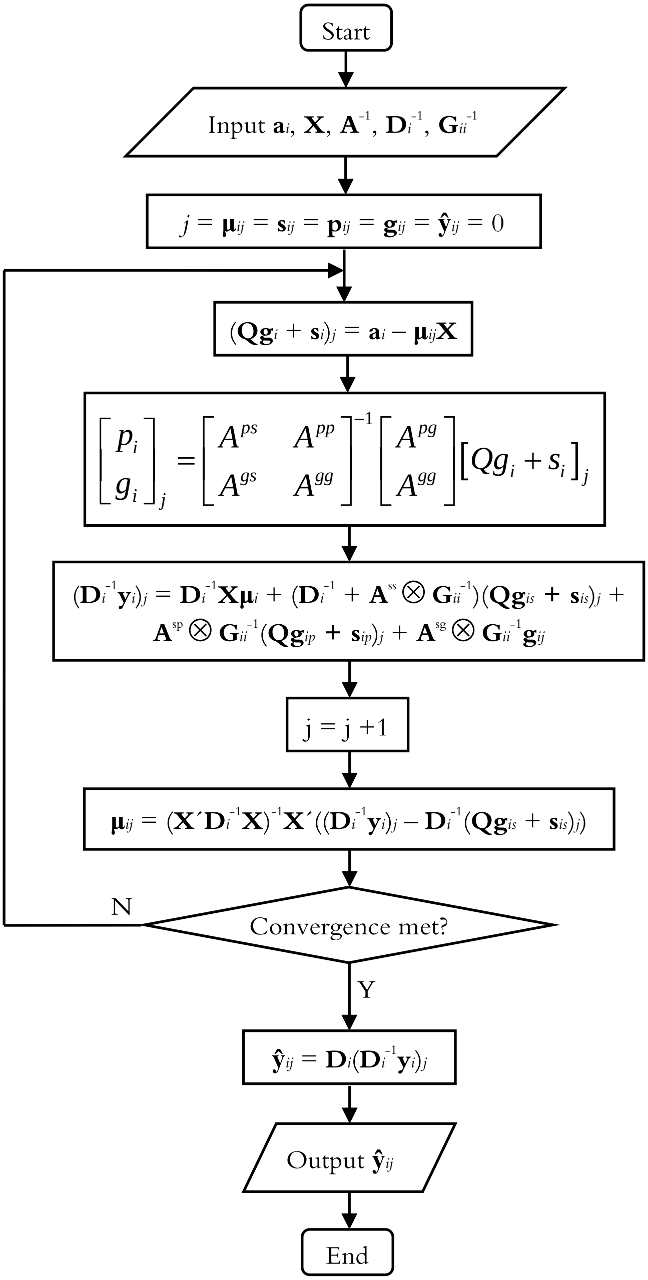

Figure 3. Flowchart of the multi-trait de-regression procedure; $\mathbf{X}$ is the matrix of ones and zeros corresponding to traits within a country; $\mathbf{G}$ is the genetic variance-covariance matrix; $\boldsymbol{\mu}$ is the vector of trait means; i corresponds to the trait and j corresponds to the iteration number; the other elements are as defined in Figure 2.

4.2 International genetic evaluations for female fertility

For the first Interbull pilot study (Jorjani, 2005), 11 genetic evaluation systems contributed with Holstein data. In the latest Interbull routine evaluation in April 2011 the number of such populations increased to 18. Two conclusions can be drawn from this simple count. The first obvious conclusion is that genetic evaluation of female fertility traits is still in its infancy. What might happen in the future is accumulation of more data, improvement of genetic evaluation models and higher stability of genetic parameters and reported EBVs. The second conclusion is that there are still many countries that might join the international genetic evaluations of female fertility.

Diversity of trait definition in different countries can contribute to the reduction of estimated genetic correlations. For example, non-return rate (NR) after a certain number of days post-insemination may be highly correlated across different countries. However, if number of days used in different countries is not the same (i.e., 28, 56 or 90 days) the genetic correlations may decrease. Further, if the trait of evaluation is very differently defined, there is no obvious way of forming a biological interpretation of results. An example of such a situation could be the use of heat detection / heat strength as an indicator of the onset of maturity in one country, and the use of body weight at the first insemination as an indicator of the same trait in another country. The results show clearly that the genetic correlations among interval traits, such as CF in different countries, are quite high. The same level of high genetic correlations can be seen for rate traits, such as NR. In contrast, genetic correlations between interval traits from one country and rate traits from another country are usually low.

There is also a trend toward an increasing use of multiple-trait evaluations. For female fertility traits with their general low heritability value, it is important to use as much as extra information as possible. For traits of high heritability value it may suffice to use the information on the same trait measured on different relatives. However, for female fertility traits the extra information should preferably include other traits measured on the individual itself and its relatives. Inclusion of several female fertility traits in one single national genetic evaluation would provide enough information to estimate a bull's EBVs for all traits as soon as the data for any of the traits is collected for that bull. In this respect it is also important to keep in mind that inclusion of milk production traits in the evaluation of female fertility traits has an added value. First, early production records can be used as a correlated trait for those traits that take longer time to record. An example of a late recorded trait could be calving interval, which becomes available not sooner than 350-400 days after the start of lactation. The second reason is the possible effect of selection bias as milk production traits have been the main target of selection decisions in dairy cattle for many generations.

4.3 MT-MACE applied to female fertility

Multiple-trait models are of special benefit for traits like female fertility, where heritabilities are low. There are complexities for female fertility traits, some due to management practices that cannot be explained well by the model of evaluation for a single female fertility measurement. International genetic evaluations of female fertility traits whether as a form of single trait or multiple traits per country is a good complement for multiple-trait national genetic evaluations to account for across country genetic correlations and pedigree relationships.

The 3% reliability gain by MT-MACE was in accordance with the results of the previous study on udder health (Mark & Sullivan, 2006), where they found an average of 1.58% reliability gain for an analysis with two traits from a multiple-trait national model among nine other traits from single-trait national models. Also, using a simulated dataset, (Sullivan & Wilton, 2001) reported improvements in the accuracy and the predictive ability of international genetic evaluations. Mark & Sullivan (2006) reported that the reliability gain by MT-MACE over MACE depends on the trait and the group of bulls in question (more reliability gain for young bulls). In our study, the reliability gain was different from one trait to another and from one bull to another within a trait.

The variance of sire EBVs obtained from the biased MACE analysis were on average 10% higher than the variances obtained from the multiple unbiased MACE analyses. This led to a larger amount of bias for the bulls with the lowest and the highest EBV in each country-trait.

While using incorrect genetic and residual (equal to zero in our study) correlations for the same combination of traits increase PEV and consequently decrease reliabilities (Schaeffer, 1984), there were several reasons for higher reliabilities obtained by the biased analysis. The first and the most important reason was that, there was larger number of traits involved in the single 10-trait MACE analysis. There were double-counting for within country genetic correlations, because of single-trait de-regression of national EBVs. Analyzing multiple traits per country requires proper $\boldsymbol{\eta}$; using $\mathbf{n}$ that tend to have numerically larger elements than $\boldsymbol{\eta}$ (Liu et al., 2004) increases the reliabilities. The methods that are based on single-trait absorption equations (i.e., Interbull, 2004; Sullivan et al., 2004) accumulate multiple-trait progeny information into EDC values for each trait (Sullivan et al., 2006). The absolute difference between genetic and residual correlations is another factor influencing PEV and reliabilities: higher absolute deviations, higher reliabilities (Schaeffer, 1984).

There is a possibility for practical/computational challenges for simultaneous analysis of all the female fertility traits, due to the large number of traits and countries. A strategy of sub-setting female fertility traits, such as rate-interval traits or cow-heifer traits may be unavoidable in the future due to the large number of genetic correlations to estimate. Those estimated genetic correlations may be in need of bending for making a single matrix. However, bending such a matrix is not as easy as it seems in the first look. To avoid extra unnecessary analyses, some correlations (across subsets) remain not estimated. Such correlations should be kept fixed to an expected value in the bending procedure. A bending procedure that can keep some elements of the matrix as fixed does not currently exist.

4.3.1 Including milk yield in the evaluation

In the presence of selection for a correlated trait, a multiple-trait model including the selection information on the correlated trait can correct for the selection bias. Reliability of female fertility traits increased as a result of analyzing them with milk yield traits. Female fertility traits on the other hand, were not good indicators for milk yield. Milk yield reliabilities did not increase by the inclusion of female fertility traits in the analysis, as a response to the reduced genetic correlations among milk yield traits. Assuming an MT-MACE international genetic analysis for female fertility and milk yield traits, the slight reduction in milk yield reliabilities was not of such a magnitude to necessitate a separate analysis only for milk yield traits.

Selection bias did not significantly change the genetic trends and bull rankings for female fertility traits. This indicated that the MT-MACE analysis of female fertility traits without milk yield traits was unbiased. This may be explained by the fact that the significant bias of selection for milk yield is mainly due to within country selection, and the across country selection bias for milk yield is marginal. The within country selection bias was already corrected by the multiple-trait national genetic evaluation models. Because the multiple-trait national models for female fertility traits were including milk yield, the bias of selection for milk yield on female fertility traits was only due to ignoring across (excluding within) country selection decisions.

A great benefit from analyzing female fertility and milk yield traits together was obtaining 260,063 extra EBVs over 17,989 EBVs for each female fertility trait (six traits), and obtaining 260 extra EBVs over 43,792 EBVs for each milk yield trait (four traits). These benefits were obtained for the bulls with no national EBV for any of the female fertility traits, but with national EBV for milk yield in at least one of the countries, and *vice versa*.

The increasing importance of female fertility or associated traits like longevity in different countries' breeding programs in the last two decades has resulted in improvements in all the studied genetic trends for female fertility since 2000. These improvements occurred in the presence of genetic improvements for milk yield. This shows that despite unfavorable genetic correlations between female fertility and milk yield traits, genetic improvements of both can be possible.

It seems that the MT-MACE analysis of traits that belong to the same trait group should receive a higher priority than the MT-MACE analysis of traits from different trait groups. With faster computational resources becoming available, the MT-MACE analysis of traits from different groups should be considered if one trait is a good indicator for the other, relatively high genetic correlations between the traits from different groups, and if one has been under strong selection. Within and across country genetic correlations among traits from different groups can only become available from such joint international genetic evaluations, which can be helpful for national breeding organizations. The joint international genetic evaluation of female fertility and milk production traits is the only way of correcting bias due to selection for production traits, internationally.

5 Conclusions

Correspondence to the aims of the thesis, the main conclusions were:

- An increasing number of countries include female fertility traits in their national genetic evaluations. These countries would also like to have access to the results of international genetic evaluations for these traits. Existence of enough bulls with daughters, and consequently EBV, in more than one country for similarly defined traits warrants the feasibility of international genetic evaluations. Estimated across country genetic correlations show high values for a large number of country trait combinations.
- Ignoring covariances from multiple-trait national models created considerable amount of bias in the results of international genetic evaluations for female fertility. Therefore, analyzing multiple traits per country, a new method such as MT-MACE should be adopted.
- Application of MT-MACE method with scalar EDC matrices ($\boldsymbol{\eta}$) works efficiently for the analysis of data from multiple traits per country. It handles the covariances from multiple-trait national models, and it makes a better use of the available data, time and computational resources compared to a set of unbiased MACE analyses.
- In a situation, where the within country selection bias for milk yield on female fertility traits has already been taken care of by the multiple-trait national models, the across country selection for milk yield did not make a significant bias in the international genetic evaluation of female fertility traits. Considering computational limitations, the MT-MACE analysis of traits that belong to the same group receives a higher priority.

6 Future Research

The studied MT-MACE method has many strong features and it is built upon correct principles. However, like any other method, it has its own assumptions and shortcomings, which stimulate future studies and developments.

The implementation of the studied MT-MACE assumes the same contribution of within country correlations to the national single-trait effective dependent EDC scalars ($\boldsymbol{\eta}$) for all bulls. However, information from recorded daughters can be genetically and/or residually correlated to a higher or lower extend, both within and across contemporary groups. The reason is that the daughters of each bull are differently distributed across contemporary groups, the strength of pedigree relationships, and the number of lactations, whether completed, in progress or early terminated are different within and across contemporary groups. Considering these differences is out of the hand of Interbull and is better to be handled at the national level.

With the studied MT-MACE methodology, there are complexities to handle multiple traits per country, when the traits from the same country are analyzed by single-trait models or separate multiple-trait models. At the de-regression level, this problem can be solved by using zero within country correlations between the traits from different national genetic evaluation models. However, solving mixed model equations, it seems necessary to consider the residual covariances via block EDC matrices. This is out of the scope of the studied version of MT-MACE. Therefore, two options are available; either, only traits from the same multiple-trait national genetic evaluation model should be analyzed simultaneously using this version of MT-MACE (Sullivan et al., 2005), or another version of MT-MACE (Schaeffer, 2001) that can handle block EDC matrices should be adopted in the future.

The estimation of sire variances is still based on a single-trait EM-REML algorithm (Sullivan, 1999), using the multi-trait effective independent EDC scalars ($\boldsymbol{\eta}$) and DBVs. This may be in need of more future development.

Another important issue is that the estimated genetic correlations are not close to the true genetic correlations within and across countries. This is because those carry information about residual correlations included via multi-trait effective independent EDC scalars ($\boldsymbol{\eta}$), which are also used in the de-regression procedure, and DBVs not de-regressed for residual correlations. These estimated genetic correlations are expected to produce unbiased international genetic evaluations. With the knowledge and the usage of the true genetic correlations, international genetic evaluations using this MT-MACE method would be biased. It is evident that predicting unbiased international genetic evaluations are more important than estimating genetic correlations close to the true values. Perhaps a main question is to what extent the true genetic correlations are needed by the dairy industry.

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