A SNP MACE model for international genomic evaluation: technical challenges and possible solutions

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Summary

Since the routine implementation of genomic selection in dairy cattle, breeding bulls have being genomically pre-selected with increasing selection intensity in Holsteins. Conventional evaluation of those highly pre-selected bulls would be biased without proper consideration of genomic information. Consequently, using those biased conventional evaluation of the bulls as reference animals would lead to biased genomic prediction. Meanwhile, more and more female animals are being genotyped. The genotyped female animals or cows are likely recorded for novel traits, such as claw health traits or feed efficiency. To optimally use phenotypic information of foreign genotyped cows, a multiple country BLUP model was developed to improve the accuracy of SNP effect estimates. In contrast to the current MACE bull evaluation, input data from participating countries are national SNP effect estimates instead of bull conventional EBV. The multi-country BLUP model is referred to as a SNP MACE model. Prediction error (co)variances of the national SNP effect estimates or original least-squares part of national mixed model equations are used to set up mixed model equations for the SNP MACE model. Equal country correlations are assumed across all the SNP markers for a given country pair. When the national SNP effects were estimated without using phenotype information from foreign countries, no residual covariance needs to be accounted for between the SNP effect estimates of a country pair. Countries using a genomic model other than the SNP BLUP model in national genomic evaluation need to convert GEBV of reference animals, e.g. from a GBLUP model, to SNP effects prior to data submission to the SNP MACE evaluation. The mixed model equations of the SNP MACE model are dense and must be solved using different computing algorithms than for sparse equations of the current conventional MACE bull evaluation. As long as the number of SNP markers and the number of participating countries do not increase significantly over time, solving algorithms including matrix inversion and parallel computing seem to be a promising alternative for the dense equations. Variances of the national SNP effects as well as country correlations of SNP effects may be estimated with REML. Using a unique set of SNP markers across all the countries makes the SNP MACE evaluation easier than direct modelling heterogeneous SNP marker sets among the countries. However, national SNP effect estimates need to be converted between the common and national set of SNP markers before and after the SNP MACE evaluation. Direct modelling the heterogeneous SNP marker sets across countries is more technically challenging but minimises the workload for national genetic evaluation centres, because countries no longer need to convert the national SNP effects to a common set of SNP markers. The SNP MACE model provides an efficient tool to optimally utilise phenotypic information of foreign genotyped cows, in particular for novel traits.

Neither an international cow evaluation nor an exchange of genotypes of likely millions of reference cows is needed. Compared to other international genomic evaluation, the SNP MACE evaluation does not require access to foreign genotypes or raw phenotypes of individual animals, thus this model allows keeping the current infra-structure of national genetic and genomic evaluations. The SNP MACE model enables fast increasing accuracy of genomic prediction for new traits.

Keywords: SNP, MACE, genomic model, international evaluation

Introduction

Since the routine implementation of genomic evaluation in major dairy countries, bulls used for breeding the next generations have being genomically pre-selected with increasing selection intensity like in the Holstein breed. Conventional evaluation of those highly pre-selected bulls would be biased if the genomic information from genomic selection was not properly accounted for. Conversely, using those biased conventional evaluations of bulls as reference animals may lead to biased genomic prediction. In last years more and more cows have been added to national genomic reference populations. Because it is technically difficult to conduct international evaluation of all cows worldwide, phenotype and genotype data of cows from foreign countries cannot be utilized for own national genomic evaluation by now. Goddard (2011) and Schaeffer (2014) recommended an international evaluation based on national SNP effect estimates similar current multiple across country evaluation (MACE) based on national bull EBV.

The purposes of this study were to describe a BLUP model for international evaluation of country estimated SNP effects and to develop statistical methods and computing algorithms for estimating international SNP effects.

Material and methods

An international SNP model

A BLUP model (Liu et al., 2016) is applied to national SNP effect estimates from multiple countries by assuming the national SNP effects are genetically correlated between countries. The multi-country BLUP model for the SNP effects is referred to hereafter as a SNP MACE model:

$$\mathbf{g}_i^N = \mathbf{g}_i + \boldsymbol{\varepsilon}_i \qquad [1]$$

where $\mathbf{g}_i^N$ is a vector of estimated national SNP effects of country i (i=1, …, c); $\mathbf{g}_i$ is a vector of international MACE SNP effects for country i; and $\boldsymbol{\varepsilon}_i$ is a vector of residual effects for country i.

For the sake of simplicity, we assume that the input national SNP effect estimates for country i are estimated with a SNP BLUP model (Liu et al., 2016) that would be equivalent to:

$$\mathbf{y}_i = \mu_i \mathbf{1} + \mathbf{Z}_i \mathbf{g}_i^N + \mathbf{e}_i \qquad [2]$$

where $\mathbf{y}_i$ is a vector of phenotypes of reference animals corrected for all but additive genetic effects of an original genomic model, a residual polygenic effect (RPG) is assumed to have

been adjusted as well; μ_i is a general mean of country *i*; $\mathbf{1}$ is a vector of 1s; $\mathbf{Z}_i$ represents the design matrix for genotypes of reference animals. Genotypic values of reference animals take 3 possible values (VanRaden, 2008): $2-2p_{ij}$, $1-2p_{ij}$ and $0-2p_{ij}$ for genotypes AA, AB or BB, respectively, p_{ij} represents allele frequency of SNP marker *j* (*j*=1, …, *m*) of the country *i*; $\mathbf{e}_i$ is a vector of residual effects for the reference animals with a (co)variance matrix:

$$\left[\text{var}(\mathbf{e}_i)\right]^{-1} = \mathbf{R}_i^{-1} = diag\{n_{ik}\sigma_{e_i}^{-2}\} \quad [3]$$

with $\sigma_{e_i}^2$ representing error variance of country *i* and n_{ik} effective daughter/data contribution (EDC) of reference animal *k* in country *i*.

Under the SNP BLUP model (Liu et al., 2016) SNP effects are distributed as:

$$\text{var}(\mathbf{g}_i) = \mathbf{B}_i\sigma_i^2 \quad [4]$$

where $\mathbf{B}_i = \dfrac{1}{\sum_j 2p_{ij}(1-p_{ij})}\mathbf{I} = \theta_i\mathbf{I}$ (VanRaden, 2008) [5]

σ_i^2 represents variance of direct genomic values (DGV) of country *i*.

Please note that DGV represents the sum of all SNP effects:

$$\text{DGV}_{ik} = \mathbf{z}_{ik}\mathbf{g}_i^N \quad [6]$$

where DGV_{ik} is direct genomic value for animal *k*; $\mathbf{z}_{ik}$ is a row in the design matrix $\mathbf{Z}_i$ corresponding to the animal *k*.

Mixed model equations (MME) can be set up equivalently as if the SNP effects of the country were estimated with:

$$\begin{bmatrix} \mathbf{1}'\mathbf{R}_i^{-1}\mathbf{1} & \mathbf{1}'\mathbf{R}_i^{-1}\mathbf{Z}_i \\ \mathbf{Z}_i'\mathbf{R}_i^{-1}\mathbf{1} & \mathbf{Z}_i'\mathbf{R}_i^{-1}\mathbf{Z}_i + \sigma_i^{-2}\mathbf{B}_i^{-1} \end{bmatrix} \begin{bmatrix} \hat{\mu}_i \\ \hat{\mathbf{g}}_i^N \end{bmatrix} = \begin{bmatrix} \mathbf{1}'\mathbf{R}_i^{-1}\mathbf{y}_i \\ \mathbf{Z}_i'\mathbf{R}_i^{-1}\mathbf{y}_i \end{bmatrix}. \quad [7]$$

Note that the general mean μ_i is expressed on the DGV, whereas it is usually expressed in national genomic evaluation on genomic breeding values (GEBV) which is the sum of DGV and RPG.

For the SNP MACE model [1], SNP effects from different countries have the following (co)variance matrix:

$$\text{var}\begin{bmatrix} \mathbf{g}_1 \\ \mathbf{g}_2 \\ \text{M} \\ \mathbf{g}_c \end{bmatrix} = \begin{bmatrix} \sigma_1^2\mathbf{B}_1 & \sigma_{12}\mathbf{B}_{12} & \Lambda & \sigma_{1c}\mathbf{B}_{1c} \\ & \sigma_2^2\mathbf{B}_2 & \Lambda & \sigma_{2c}\mathbf{B}_{2c} \\ & & \text{O} & \text{M} \\ \textit{symm.} & & & \sigma_c^2\mathbf{B}_c \end{bmatrix} = \mathbf{G} \quad [8]$$

and its inverse matrix is:

$$\mathbf{G}^{-1} = \begin{bmatrix} \mathbf{G}^{11} & \mathbf{G}^{12} & \Lambda & \mathbf{G}^{1c} \\ & \mathbf{G}^{22} & \Lambda & \mathbf{G}^{2c} \\ & & \text{O} & \text{M} \\ \textit{symm.} & & & \mathbf{G}^{cc} \end{bmatrix} \quad [9]$$

where σ_{i,i^+}^2 is DGV covariance between countries *i* and i^+. In order to guarantee sum of the SNP genetic covariances equal the total additive genetic covariance between the two countries, all the involving countries must code the three possible SNP genotypes in the same way, e.g. AA=2, AB=1 and BB=0.

Similar to the definition of matrix $\mathbf{B}_i$ for country *i*, matrix $\mathbf{B}_{i,i^+}$ for the two countries relies on the assumption that the same set of SNP markers are used in the two countries:

$$\mathbf{B}_{i,i^+} = \frac{1}{\sqrt{\sum_j 2p_{ij}(1-p_{ij})}\sqrt{\sum_j 2p_{i^+j}(1-p_{i^+j})}}\mathbf{I} = \sqrt{\theta_i\theta_{i^+}}\mathbf{I} \qquad [10]$$

It can be seen that matrix $\mathbf{B}_{i,i^+}$ between the two countries is an identity matrix multiplied with a scalar as long as the two countries submit SNP effect estimates derived from the same set of SNP markers. Under the assumption of using the same set of SNP markers by all the *c* countries, the (co)variance matrix of the country SNP effects, Equation [8], becomes:

$$\mathbf{G} = \mathrm{var}\begin{bmatrix}\mathbf{g}_1\\ \mathbf{g}_2\\ \mathrm{M}\\ \mathbf{g}_c\end{bmatrix} = \begin{bmatrix}\sigma_1^2\theta_1\mathbf{I} & \sigma_{12}\sqrt{\theta_1\theta_2}\mathbf{I} & \Lambda & \sigma_{1c}\sqrt{\theta_1\theta_c}\mathbf{I}\\ & \sigma_2^2\theta_2\mathbf{I} & \Lambda & \sigma_{2c}\sqrt{\theta_2\theta_c}\mathbf{I}\\ & & \mathrm{O} & \mathrm{M}\\ \textit{symm.} & & & \sigma_c\theta_c\mathbf{I}\end{bmatrix}. \qquad [11]$$

Estimation of SNP effects of the SNP MACE model

The effects of the SNP MACE model [1] are estimated using mixed model equations:

$$\begin{bmatrix}\mathrm{O} & & \Lambda & & \Lambda & & \Lambda\\ & \begin{bmatrix}\mathbf{1}'\mathbf{R}_i^{-1}\mathbf{1} & \mathbf{1}'\mathbf{R}_i^{-1}\mathbf{Z}_i\\ \mathbf{Z}_i'\mathbf{R}_i^{-1}\mathbf{1} & \mathbf{Z}_i'\mathbf{R}_i^{-1}\mathbf{Z}_i\end{bmatrix} + \begin{bmatrix}\mathbf{0} & \mathbf{0}\\ \mathbf{0} & \mathbf{G}^{ii}\end{bmatrix} & \Lambda & \begin{bmatrix}\mathbf{0} & \mathbf{0}\\ \mathbf{0} & \mathbf{\Psi}_{ii^+}\end{bmatrix} + \begin{bmatrix}\mathbf{0} & \mathbf{0}\\ \mathbf{0} & \mathbf{G}^{ii^+}\end{bmatrix} & & \mathrm{M}\\ & & \mathrm{O} & & \mathrm{M} & & \mathrm{M}\\ & & & \begin{bmatrix}\mathbf{1}'\mathbf{R}_{i^+}^{-1}\mathbf{1} & \mathbf{1}'\mathbf{R}_{i^+}^{-1}\mathbf{Z}_{i^+}\\ \mathbf{Z}_{i^+}'\mathbf{R}_{i^+}^{-1}\mathbf{1} & \mathbf{Z}_{i^+}'\mathbf{R}_{i^+}^{-1}\mathbf{Z}_{i^+}\end{bmatrix} + \begin{bmatrix}\mathbf{0} & \mathbf{0}\\ \mathbf{0} & \mathbf{G}^{i^+i^+}\end{bmatrix} & \mathrm{M}\\ & & & & & & \mathrm{O}\end{bmatrix}$$

$$\mathrm{X}\begin{bmatrix}\Lambda\\ \begin{bmatrix}\hat{\mu}_i\\ \hat{\mathbf{g}}_i\end{bmatrix}\\ \mathrm{M}\\ \begin{bmatrix}\hat{\mu}_{i^+}\\ \hat{\mathbf{g}}_{i^+}\end{bmatrix}\\ \Lambda\end{bmatrix} = \begin{bmatrix}\Lambda\\ \begin{bmatrix}\mathbf{1}'\mathbf{R}_i^{-1}\mathbf{y}_i\\ \mathbf{Z}_i'\mathbf{R}_i^{-1}\mathbf{y}_i\end{bmatrix}\\ \mathrm{M}\\ \begin{bmatrix}\mathbf{1}'\mathbf{R}_{i^+}^{-1}\mathbf{y}_{i^+}\\ \mathbf{Z}_{i^+}'\mathbf{R}_{i^+}^{-1}\mathbf{y}_{i^+}\end{bmatrix}\\ \Lambda\end{bmatrix} \qquad [12]$$

The residual (co)variances between countries *i* and i^+, $\mathbf{\Psi}_{ii^+}$, depends on the fact if the two countries use bull MACE phenotypes containing common daughter information in their national genomic evaluations. If the MACE EBV of reference bulls are used in national SNP effect estimation in countries i and i^+, the residual covariance can be defined as:

$$\mathbf{\Psi}_{ii^+} = (\mathbf{Z}_i'\mathbf{R}_i^{-\frac{1}{2}})(\mathbf{R}_{i^+}^{-\frac{1}{2}}\mathbf{Z}_{i^+}) \qquad [13]$$

If the two countries use only national phenotypes for their SNP effect estimation, then

$$\mathbf{\Psi}_{ii^+} = 0 \qquad [14]$$

The residual covariance between the SNP effects of the two countries, $\mathbf{\Psi}_{ii^+}$, depends on the number of common reference bulls used in the two national reference populations and EDC of those common reference bulls. Procedures for approximating the residual covariance for

GEBV (Sullivan, 2016) may be used here for the residual covariance between the country SNP effect estimates.

National data for the SNP MACE evaluation

Countries need to submit national SNP effect estimates: $\mathbf{g}_i^N$, $\mathbf{Z}_i'\mathbf{R}_i^{-1}\mathbf{y}_i$ and $\mathbf{Z}_i'\mathbf{R}_i^{-1}\mathbf{Z}_i$ for a measure of prediction error (co)variances of the SNP effect estimates. All the participating countries must code two SNP alleles A and B in the same way. Marker allele frequencies of a reference SNP allele, like allele A, must be provided by the countries for the international SNP effect estimation. Because different genomic models may be used in national genomic evaluations, like the genomic BLUP model (GBLUP) or Bayesian genomic models (Meuwissen et al., 2001), we show below how the countries obtain national SNP effects for the SNP MACE evaluation from a genomic model other than the SNP BLUP model.

Converting GEBV of the GBLUP model to SNP effects

Countries may use a GBLUP model, either single-step or multi-step ones, for genomic evaluation. GEBV of the GBLUP model can be converted directly to SNP effects following Liu et al. (2016):

$$\mathbf{g}_i = (1-k)\mathbf{B}_i\mathbf{Z}_i'\mathbf{G}_{rel}^{-1}\mathbf{u}_i^* \qquad [15]$$

where k is proportion of residual polygenic variance in total additive genetic variance, $\mathbf{u}_i^*$ is a vector of GEBV of reference animals, and a genomic relationship matrix:

$$\mathbf{G}_{rel} = (1-k)\mathbf{Z}_i\mathbf{B}_i\mathbf{Z}_i' + k\mathbf{A}_i \qquad [16]$$

with $\mathbf{A}_i$ representing pedigree relationship matrix of the reference animals.

SNP effects from the Bayesian genomic models

The SNP MACE model [1] makes the same assumption on SNP variances as the SNP BLUP model. Additionally, the SNP MACE model assumes the SNP markers explain equal genetic covariance among the SNP markers. The assumption of equal SNP genetic variances may be relaxed by allowing heterogeneous SNP genetic variances, like the Bayesian genomic models (Meuwissen et al., 2001). Likewise, we could also relax the assumption on each SNP contributing equally to the total genetic covariance between any country pair.

Alternative methods for handling different sets of SNP markers between countries

International SNP effect estimation is complicated by the fact that the participating countries use different sets of SNP markers in their own national genomic evaluation. Depending what data the countries are willing to share, there are several alternatives to handle the heterogeneity in SNP marker sets across countries.

Method 1: Conversion of country SNP effects to a common set of SNP markers

A country *i* has own national SNP effects, $\mathbf{g}_i^N$, for its own set of SNP markers. We would like to express its SNP effects to a common set of SNP markers, $\mathbf{g}_c^N$, under the assumption that

DGV of all reference animals are equal for the two sets of SNP markers. Let denote DGV of the reference animals with its own SNP markers as:

$$\mathbf{u}_i = \mathbf{Z}_i \mathbf{g}_i^N . \quad [17]$$

A SNP BLUP model can be applied to the DGV of the reference animals with the common set of SNP markers as:

$$\mathbf{u}_i = \mathbf{Z}_i^c \mathbf{g}_c^N + \xi \quad [18]$$

where ξ is a vector of residuals that are expected to be small, and $\mathbf{Z}_i^c$ is a design matrix using the common set of SNP markers. MME of the above model [18] is:

$$(\mathbf{Z}_i^{c\prime}\mathbf{R}_i^{-1}\mathbf{Z}_i^c + \sigma_i^{-2}\mathbf{B}_c^{-1})\mathbf{g}_c^N = \mathbf{Z}_i^{c\prime}\mathbf{R}_i^{-1}\mathbf{u}_i \quad [19]$$

where $\mathbf{B}_c$ is matrix $\mathbf{B}$ of Equation [5] for the common set of SNP markers.

From the above Equation [19] we can convert the SNP effects from the country own set to the common set of SNP markers:

$$\mathbf{g}_c^N = (\mathbf{Z}_i^{c\prime}\mathbf{R}_i^{-1}\mathbf{Z}_i^c + \sigma_i^{-2}\mathbf{B}_c^{-1})^{-1}\mathbf{Z}_i^{c\prime}\mathbf{R}_i^{-1}(\mathbf{Z}_i\mathbf{g}_i^N). \quad [20]$$

At the end of the SNP MACE evaluation, MACE SNP effects for this country, $\mathbf{g}_i^c$, can be converted back to its original set of SNP markers based on DGV of the reference animals:

$$\mathbf{g}_i = (\mathbf{Z}_i'\mathbf{R}_i^{-1}\mathbf{Z}_i + \sigma_i^{-2}\mathbf{B}_i^{-1})^{-1}\mathbf{Z}_i'\mathbf{R}_i^{-1}(\mathbf{Z}_i^c\mathbf{g}_i^c). \quad [21]$$

As input data, the country *i* would be required to submit $\mathbf{Z}_i^{c\prime}\mathbf{R}_i^{-1}\mathbf{Z}_i$ in addition to $\mathbf{Z}_i^{c\prime}\mathbf{R}_i^{-1}\mathbf{Z}_i^c$ and $\mathbf{g}_i^N$. If the back conversion is done by an international organization like Interbull, the country needs also to submit $\mathbf{Z}_i'\mathbf{R}_i^{-1}\mathbf{Z}_i$ for the original set of SNP markers for the SNP MACE evaluation.

The common set of SNP markers may include all SNP markers used in all the participating countries. If there is a set of reference animals with genotypes for the common set of SNP markers, we could impute genotypes of all reference animals from a country, based on own SNP marker set, to genotypes for the common set of SNP markers.

Method 2: Conversion of SNP effects using the genomic relationship matrix

When a country applies the GBLUP model to routinely estimate GEBV of genotyped animals, a genomic relationship matrix ($\mathbf{G}_{\text{rel}}$) can be used for converting its SNP effects between any two sets of SNP markers. GEBV of the reference animals based on own set of SNP markers, $\mathbf{u}_i^*$, are converted to SNP effects of the common set SNP markers like using the formula 16 in Liu et al. (2016):

$$\mathbf{g}_i^c = (1-k)\mathbf{B}_c\mathbf{Z}_i^{c\prime}\mathbf{G}_{rel}^{-1}\mathbf{u}_i^* \quad [22]$$

where the inverse of genomic relationship matrix is calculated as (Liu et al., 2016):

$$\mathbf{G}_{rel}^{-1} = [(1-k)\mathbf{Z}_i^c\mathbf{B}_c\mathbf{Z}_i^{c\prime} + k\mathbf{A}_i]^{-1} \quad [23]$$

An assumption has been made in deriving Equation [22] between the two sets of SNP markers:

$$(1-k)\mathbf{Z}_i^c\mathbf{B}_c\mathbf{Z}_i^{c\prime} + k\mathbf{A}_i = (1-k)\mathbf{Z}_i\mathbf{B}_i\mathbf{Z}_i' + k\mathbf{A}_i . \quad [24]$$

From Equation [24] we can see that we have assumed additionally equal proportion of residual polygenic variances, *k*, with the two sets of SNP markers. In comparison to the Method 1, the conversion of GEBV to SNP effects requires that the inverse of genomic

relationship matrix exists and can be readily obtained like using the Algorithm for Proven and Young animals by Misztal et al. (2014).

Estimation of country DGV variances

Countries may supply their own estimates of DGV variance, σ_i^2 for the SNP MACE evaluation. Alternatively, the country DGV variances may be estimated using REML based on the national MME [7]. In the current MACE evaluation Interbull estimates country genetic variance with REML during the deregression process of country bull EBV. Because no deregression of the national SNP effect estimates is needed for the SNP MACE evaluation, the country DGV variances must be estimated separately.

Approximating reliabilities of the international SNP effect estimates

Similar to the reliability calculation procedure for national SNP effect estimates (Liu et al., 2017), we can approximate reliabilities of the international SNP effect estimates based on the MME [12]. SNP information from other countries may be absorbed to obtain the prediction error covariance matrix without inverting left-hand-sides of the whole MME [12]. Because the SNP effect estimates are highly correlated, a prediction error covariance matrix is needed by the countries to calculate reliabilities of DGV.

Discussion

For Holsteins many countries routinely exchange genotypes of male breeding animals. Thanks to Interbull's MACE bull evaluation, genotyped foreign daughter-proven bulls can be included in national genomic reference population to increase the accuracy of genomic prediction. Conventional evaluation of genomically pre-selected bulls is being biased with increasing selection intensity. Although more and more cows are genotyped in many countries, foreign genotyped cows cannot be used directly as own national reference animals, because there is no international cow evaluation. Additionally, exchanging genotypes of up to millions of cows is technically difficult between countries. Furthermore, newly genotyped cows tend to be recorded for novel traits for which no international conventional evaluation is available yet.

The proposed SNP MACE model evaluates national effects of SNP markers containing genotype and phenotype information from different countries. Therefore, the SNP MACE model can increase the accuracy of SNP effect estimates and thus national genomic prediction. Our SNP MACE model does not require an access to genotypes and raw phenotypes from the participating countries. Thus, the SNP MACE evaluation would keep the current infra-structure of national genetic evaluation intact. For the participating countries, the SNP MACE model may be, for the countries, the only acceptable model that allows utilizing phenotype information of foreign reference cows for own national genomic evaluation. This is particularly important for new traits with many genotyped cows.

Estimation of SNP effects using the SNP MACE model requires new solving algorithms, as the mixed model equations are dense, contrasting the sparse MME of conventional evaluation. Parallel computing can help solve the SNP effects more efficiently. Alternative procedures were developed to account for the heterogeneous sets of SNP markers between countries. For different national genomic models, we proposed several methods to

prepare the required submission data. Country correlations for SNP effects between countries may be estimated using genomic information more accurately than the current country correlations based on conventional evaluation. Integration of the international SNP evaluation results to national publication has to deal with aspects such as: accounting for RPG effect, combination with parental information, and approximation of reliabilities for GEBV.

We have developed the SNP MACE model for a more accurate international evaluation. We have shown several technical challenges and provided possible solutions. Proper validation and verification of the SNP MACE model need to be done before a routine implementation of the SNP MACE model.

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