MULTIBREED SIRE EVALUATION PROCEDURES ACROSS COUNTRIES

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Summary

Multiple trait sire evaluation procedures that use information from several countries were developed and are presented. These procedures account for direct and maternal, additive and nonadditive effects and unequal genetic and environmental covariances as well as genotype × environment interaction effects. Intra- and inter-country additive genetic covariances must be estimated before these procedures can be used. Because data will come from different countries, international cooperation will be necessary to carry out the evaluations described. These procedures could be used to obtain more accurate exotic, hybrid and native sire evaluations in native environments. Also, they could be used to obtain preliminary sire proofs and sire proofs for sires used in several countries.
(Key Words: Across-Country Sire Evaluation, Multiple Trait Sire Evaluation, Multibreed Sire Evaluation, Crossbreeding Evaluation.)

Introduction

The discovery of the deep freezing method of cattle semen preservation by Polge and Rowson in 1952 (Nishikawa, 1964) allowed for a world-wide exchange of genetic material. Thus, the need arose for comparing the genetic potential of daughters of sires from exotic (semen exporting) countries with those of sires [straightbred and(or) crossbred] from native (semen importing) countries, in native environments.

Elzo and Famula (1985) presented intra-country procedures to evaluate exotic, hybrid and native sires. These methods accounted for additive and nonadditive direct and maternal effects using data from a native country only. In some cases, however, native country data may be insufficient to yield accurate sire proofs. Also, it may be desirable to preselect a sample of exotic sires before testing them in a native country. A solution to both problems is to use information from all countries involved. Because environmental conditions in these countries may differ substantially from each other, genotype × country interaction should be included in the analysis. Hence, the objective of this research is to present procedures to evaluate exotic, crossbred and native sires using data from several countries. These procedures will take into account unequal genetic variances and genotype × country interactions.

Development of Maternal Multibreed Sire-Maternal Grand Sire Evaluation Models Using Data From Several Countries

Best linear unbiased prediction (BLUP) procedures to evaluate exotic, native and crossbred sires using only records, only sire proofs or both records and sire proofs in the data vector will be presented. Data are assumed to come from several countries. A character measured in several countries (i.e., several environments) is treated as a set of different traits (Falconer, 1952). Additive and nonadditive genetic covariances as well as environmental covariances are allowed to differ among breed groups and also among countries. Thus, these procedures will account for genotype × environment (country interactions of the type that cause changes in genetic and(or) environmental variances and those that alter the

ranking of genotypes among countries. Evidence has been found for changes in ranking among sires for milk production in cattle in different countries (Katpatal, 1977; Buvanendran and Petersen, 1980; Parekh and Pande, 1982) and also for changes in variances (Buvanendran and Petersen, 1980). However, more field data studies are needed in both aspects of genotype × country interaction in order to have a better understanding of these effects in a wide variety of countries.

The procedures to be developed will assume that genetic and environmental covariances within countries and genetic covariances across countries are known. While the latter estimates are generally not available now, use of semen from proven exotic sires in several countries, for example as is occurring with U.S. Holstein bulls in Europe and elsewhere, should provide good data for such estimates. Comparable data from temperate-tropical country combinations are not yet available but could be obtained in future. Such across-country data have the additional advantage that intra- and inter-country methods can be compared. The methodology proposed provides a basis for efficiency collection and use of data for across-country genetic evaluations.

The methods that use sire proofs, alone or in combination with records, contain nonzero covariances between random predictors in the model and the error term. Because several component matrices of these nonzero covariances will probably be unavailable, approximate BLUP methods, which assume these covariances to be zero, will be proposed. The approximate sire proofs will be unbiased, but their error variances of prediction may not be minimum. However, if exotic semen comes from well-proven sires, whose proofs have small error variances of prediction, then the covariances between their proofs and the error variance of prediction vector should approach zero. Hence, the approximate sire BLUP should approach the BLUP of the models in question.

The description, discussion and practical applications of the proposed multi-country evaluation procedures are presented in the main text, and an illustration of them, using a small numerical example, is given in the Appendix.

Multibreed Sire-Maternal Grandsire Evaluation Procedures Using Records From Several Countries in the Data Vector

These procedures are a multiple trait version

of intra-country models 1 and 2 (Elzo and Famula, 1985), which treat the expression of a character in different countries as different traits. Because sire proofs from model 2 are at least as good as those from model 1, only the multiple trait expression corresponding to model 2 will be given here. In matrix notation, multiple trait model 1 (MT1) can be represented as:

$$y = X\alpha + Z_1 Q_1 P b + Z_2 Q_2 \delta_1 + Z_3 a^S + Z_2 \delta_2 + e \qquad (1)$$

$$E(y) = X\alpha + Z_1 Q_1 P_1 b + Z_2 Q_2 \delta_1$$

$$var(y) = var(Z_3 a^S + Z_2 \delta_2 + e),$$

where y is the vector of observations, ordered by country within sires; α is a vector of environmental fixed effects, a^S is a vector of direct and maternal sire additive effects over all countries, ordered within sire and country within sire, b is a vector of direct and maternal sire group effects and maternal grand dam group effects, δ_2 is a vector of alternating random intra-locus and inter-locus (at two loci) direct and maternal interaction effects, associated with sires, δ_1 is a vector of alternating fixed intra-locus and inter-locus (at two loci) direct and maternal interaction effects, associated with sire time groups, and e is a vector of residual effects. For a more detailed explanation of δ_1 and δ_2 see Elzo and Famula (1985).

The X, Z_1, Z_2, Z_3 are known incidence matrices relating observations to environmental fixed effects, direct and maternal sire effects and maternal granddam effects, direct and maternal interactions in δ_2, and direct and maternal sire effects, respectively. The Q_1 and Q_2 are known incidence matrices relating sires, maternal grandsires and maternal granddams to time × breed group genetic groups, and sire subclass interactions in δ_2 to sire group subclass interactions in δ_1, respectively. The P is a known incidence matrix relating time × breed group genetic groups to time × breed genetic groups (Elzo and Famula, 1985).

The covariance matrix of the random effects in MT1 (1) is:

$$var \begin{bmatrix} a^S \\ \delta_2 \\ e \end{bmatrix} = \begin{bmatrix} G & 0 & 0 \\ 0 & D_2 & 0 \\ 0 & 0 & R \end{bmatrix},$$

where G is a multiple trait covariance matrix

that accounts for unequal direct and maternal additive genetic covariances across breed groups and across countries (see Appendix for an explicit expression of G), D_2 is a multiple trait diagonal covariance matrix of nonadditive direct and maternal effects and R is a multiple trait diagonal covariance matrix of residual effects. The R is diagonal because a trait measured in different countries is measured in separate individuals. Hence no environmental covariance exists among these measurements.

The mixed model equations (MME) for MT1 can be written in the same fashion as in model 2 (Elzo and Famula, 1985), using appropriate coefficients for each country. Again, the inverses of D_2 and R are the reciprocal of their diagonal elements, and the inverse of G is obtained using the modified Henderson procedure for multiple traits with heterogeneous additive genetic covariance matrices across breed groups (Elzo, 1983).

The multiple trait vector of sire proofs for direct and maternal effects is:

$$\hat{s}_1 = L \hat{d}_1, \qquad (2)$$

where

$$L = [Q^S P^S : T^S Q_2 : I : T^S],$$

$$\hat{d}_1 = [\hat{b}_1^{S'} : \hat{\delta}_{11}' : \hat{a}_1^{S'} : \hat{\delta}_{21}']'$$

and Q^S, P^S, b^S are similar to Q_1, P, b, but contain information for sires and maternal grandsires only, T^S is a known matrix relating direct and maternal sire × group of dam interaction effects to elements of $\hat{\delta}_2$ through the probabilities of occurrence of these effects (see Elzo, 1983; Elzo and Famula, 1985 for details on these probabilities); $\hat{d}_1$ contains generalized least-squares (GLS) solutions and BLUP of parameters in d_1 obtained by solving the MME for MT1 (1).

The error variance of prediction (EVP) of the vector of sire proofs, $\hat{s}_1$, is $L (LHS)^- L'$, where $(LHS)^-$ is a generalized inverse of the left-hand side of the MME for MT1 (1). The EVP of sire proofs from MT1 will be at least as small as that of the intra-country sire proofs because more information is used to obtain BLUP of s in MT1 than in the intra-country methods.

Model 1 accounts for additive and non-additive, intra- and inter-locus direct and maternal genetic effects in a multibreed,

multicountry data set, where subsets from different countries are connected by sires. Thus, model 1 will be useful to improve sire selection in countries where open crossbreeding systems (Elzo and Famula, 1985) are being carried out and insufficient intra-country data exist to evaluate native, hybrid and exotic sires. Also, MT1 has all the advantages of the intra-country model 2, i.e., its flexibility to be adapted to data sets of different sizes, its efficiency to extract information from the data and its ability to handle flexible crossbred mating designs (Elzo and Famula, 1985). However, MT1 also shares the disadvantages of intra-country model 2, i.e., its requirement of a minimum number and type of matings to permit comparison between any pair of sires and its need to reach a compromise between computational costs and accuracy of prediction if these costs were too high. Also, there might be difficulties in obtaining data across countries to carry out sire evaluations using MT1. However, as long as data sets from different countries are connected by some sires, and some additive covariances across countries are available, MT1 can be used. By design, MT1 can evaluate sires for different numbers of traits. Good international cooperation will be necessary to evaluate sires using MT1. The number of additive genetic covariances to be estimated will depend on the number of countries and the number of traits per country, e.g., a within-breed sire evaluation for direct and maternal effects in two countries will require ten covariances: six intra-country covariances (three for each country) and four across-country covariances. The number of additive genetic covariances needed also depends on the number of breeds involved. It can be shown (Elzo, 1983) that, under the assumptions of no linkage and constant covariances over time, the number of additive genetic covariances needed to be known in crossbred populations is equal to the number of within-breed additive genetic covariances. This is so because, under these conditions, crossbred additive genetic covariances can be expressed as weighted means of within breed covariances, the weights being the expected allelic fractions of particular breeds. Thus, the problem of accounting for unequal additive genetic covariances across genetic groups becomes more manageable. The number and type of nonadditive genetic covariances needed will depend on the number of breeds present and the assumptions about

nonaddittive genetic effects made for each country. So, their number can be as small as two per country (one for direct and one for maternal intra-locus interbreed interaction effects) if all inter-locus interactions are assumed to be negligible, all intra-locus intrabreed interactions are assumed to be the same and all intra-locus interbreed interactions are assumed to be the same. Several nonadditive strategies are presented and discussed in more detail in Elzo (1983).

Maternal Multibreed Sire-Maternal Grandsire Evaluation Procedure Using Sire Proofs From Several Countries in the Data Vector

Sire proofs for direct and maternal effects within countries using BLUP, BLP (best linear prediction) or other procedures will be used as data for the multiple trait BLUP procedure proposed in this section. In other words, linear combinations of records within countries instead of the records themselves are used to obtain sire BLUP in several countries.

The multiple trait model using sire proofs in the data vector (MT2) can be represented as:

$$\hat{s} = Q^S P^S b^S + T^S Q_2 \delta_1 + a^S + T^S \delta_2 + \overset{*}{e} \quad (3)$$

$$E(\hat{s}) = Q^S P^S b^S + T^S Q_2 \delta_1$$

$$\text{var}(\hat{s}) = \text{var}(a^S + T^S \delta_2 + \overset{*}{e}),$$

where $\hat{s}$ is an intra-country sire proof, $\overset{*}{e} = \hat{s} - s$, i.e., the prediction error of s and all other terms are as previously defined.

The covariance matrix of the random effects in MT2 (3) is:

$$\text{var} \begin{bmatrix} a^S \\ \delta_2 \\ \overset{*}{e} \end{bmatrix} = \begin{bmatrix} G & 0 & M \\ 0 & D_2 & N \\ M' & N' & \overset{*}{R} \end{bmatrix}, \quad (4)$$

where G and D_2 are as defined earlier; $\overset{*}{R}$ is a multiple trait covariance matrix of the prediction errors of sire proofs over all countries; M is a multiple trait covariance matrix between direct and maternal additive effects; N is a multiple trait covariance matrix between direct and maternal nonadditive effects and the prediction error of sire proofs over all countries. Explicit expressions for $\overset{*}{R}$, M and N for the case when intra-country sire proofs come from model 2 are given in the Appendix.

The vector of sire BLUP for direct and maternal effects using MT2 is:

$$\hat{s}_2 = Q^S P^S \hat{b}_2^S + T^S Q_2 \hat{\delta}_{12} + WV^{-1}(\hat{s} - Q^S P^S \hat{b}_2^S - T^S Q_2 \hat{\delta}_{12}), \quad (5)$$

where W is the covariance matrix between the predictand (s) and the data vector ($\hat{s}$), V^{-1} is the inverse of the covariance matrix vector $\hat{s}$, $\hat{b}_2^S$ and $\hat{\delta}_{12}$ are GLS estimators of b_2^S and $\hat{\delta}_{12}$, obtained by the usual GLS equations. Explicit formulae for W and V^{-1}, assuming $\hat{s} = $ intra-country BLUP of s, and an expression for EVP of $\hat{s}_2$ are given in the Appendix.

The BLUP of s using MT2, i.e., $\hat{s}_2$, will have an error variance of prediction less than or equal to the one from the intra-country BLUP, i.e., $\hat{s}$, because of the additional information (i.e., sire proofs from several countries) used in MT2.

The computations involved in obtaining $\hat{s}_2$ and its EVP may be very large. Also, some intra-country error variance of prediction submatrices necessary to build N, M and $\overset{*}{R}$ (see Appendix) may be unavailable. These facts suggest the use of approximate procedures that ignore some covariances in such a way that a computationally feasible set of MME can be written. Hence, it will be assumed that N, M and all off diagonal elements of $\overset{*}{R}$ are zero. Thus, the approximate covariance matrix of the random effects becomes diagonal, where G and D_2 are as in (4) and $\overset{*}{R}$ is substituted for $\overset{*}{R}$, a diagonal matrix containing the EVP of the intra-country sire proofs.

The MME for the approximate MT2 procedure, i.e., $\widetilde{MT2}$, can be written using a method similar to that given for MT1. The $\overset{*}{R}^{-1}$, D_2^{-1} and G^{-1} are also obtained as for MT1. The vector of approximate direct and maternal BLUP from $\widetilde{MT2}$ is $\tilde{\hat{s}}_2 = L \tilde{\hat{d}}_2$. The EVP of $\tilde{\hat{s}}_2$ (see Appendix) is a complex expression involving elements of the inverse of the left hand side of the MME for $\widetilde{MT2}$, $\overset{*}{R}^{-1}$, inverses of the left hand sides of intra-country BLUP and the covariance of y, a^S and δ_2, hence unlikely to be obtained given the reasons for using $\widetilde{MT2}$ stated above.

The predictors obtained from $\widetilde{MT2}$ are unbiased, but not of minimum EVP. Hence, their EVP will be at least as large as those of MT2. Whether their EVP will be smaller or larger than the intra-country proofs will depend on the intra-country methods used, on the amount and accuracy of the intra-country information (data, covariance estimates, known

relationships, et cetera) and on the value of the genetic correlation among measurements of a trait in the countries considered. The usefulness of $\widetilde{MT2}$ will probably be greater when exotic sires are precisely proven in their country of origin and the information for them, hybrid and native sires is scant and(or) inaccurate in the native countries.

Maternal Multibreed Sire-Maternal Grandsire Evaluation Procedure Using Records and Sire Proofs From Several Countries in the Data Vector

This procedure (MT3) is a combination of the previous two multiple trait methods, i.e., MT1 and MT2. Covariance matrices N, M and $\overset{*}{R}$ in MT3 are more sparse, but the data vector is larger than in MT2. Thus, computational difficulties to obtain BLUP of s using MT3 may be even greater than for MT2. Also, the problem of possible unavailability of some matrices necessary to build N, M and $\overset{*}{R}$ remains. Hence, an approximate MT3, i.e., $\widetilde{MT3}$, with the same assumptions as MT2 (for relevant covariances only) will be proposed.

The multiple trait model using records and sire proofs in the data vector (i.e., MT3) can be represented as:

$$\overset{*}{y} = \overset{*}{X}\alpha + \overset{*}{Z}_1 \overset{*}{Q}_1 \overset{*}{P} b + \overset{*}{Z}_2 \overset{*}{Q}_2 \delta_1 +$$
$$\overset{*}{Z}_3 a^2 + \overset{*}{Z}_2 \delta_2 + e_3 \qquad (6)$$
$$E(\overset{*}{y}) = \overset{*}{X}\alpha + \overset{*}{Z}_1 \overset{*}{Q}_1 \overset{*}{P} b + \overset{*}{Z}_2 \overset{*}{Q}_2 \delta_1$$
$$var\,(y) = var\,(\overset{*}{Z}_3 a^S + \overset{*}{Z}_2 \delta_2 + e_3),$$

where $\overset{*}{y}$ is a vector containing records and sire proofs, ordered by country within sire; α, b, δ_1, a^S, δ_2, Q_1, Q_2 are defined in (1); $\overset{*}{X}$, $\overset{*}{Z}_1$, $\overset{*}{Z}_2$, $\overset{*}{Z}_3$ are known matrices relating records and sire proofs to effects indicated in (1) and e_3 is a vector of residual effects and prediction errors of intra-country sire proofs.

The covariance matrix of the random effects of MT3 (6) has a form similar to (4), but it has zero for all covariances between random parameters in the model and residual effects from records. The vector of sire BLUP for MT3, and its corresponding EVP, also have similar representation to those for MT2. The EVP of the BLUP of S from MT3 will be at least as small as that for the intra-country BLUP of s, due to the larger amount of information

[records and(or) sire proofs from several countries] used in MT3.

The approximate covariance of the random effects for MT3 is a diagonal matrix, where G and D_2 are as in (4) and $\overset{*}{\tilde{R}}$ is substituted for $\widetilde{R}_3$, a multiple trait diagonal matrix of direct and maternal residual variances and EVP of sire proofs.

The MME for $\widetilde{MT3}$ are written in similar fashion to those for MT1 and MT2. The vector of approximate sire BLUP from $\widetilde{MT3}$ is $\overset{\sim}{\hat{s}}_3 = L\overset{\sim}{\hat{d}}_3$; and its EVP has the same general expression as the one for $\widetilde{MT2}$.

The predictors from $\widetilde{MT3}$ are unbiased, but not minimum variance, as those from $\widetilde{MT2}$. However, their EVP should be at least as small as those from $\widetilde{MT2}$, because $\widetilde{MT3}$ requires fewer covariances to be assumed equal to zero. Like $\widetilde{MT2}$, the EVP of MT3 sire proofs may be smaller or larger than the intra-country sire proofs depending on the amount and accuracy of the intra-country data and genetic parameters, on the value of the additive genetic covariances across countries and on the intra-country sire evaluation method used. Also, $\widetilde{MT3}$ will be more useful when sires have little information in native countries and exotic sires have accurate proofs in their own countries.

Applications and Discussion

Applications of the across-country sire evaluation methods include: (i) obtaining more precise sire proofs for exotic, hybrid and native sires in a native country, (ii) obtaining preliminary sire proofs for sires of potential interest in a native country, as a means of preselecting them for testing or for limited use in native environments and (iii) obtaining multiple trait sire proofs for sires whose semen is widely used in various native countries.

The multibreed sire evaluations described here will be particularly useful in the early stages of open crossbreeding systems (Elzo and Famula, 1985), when little information on native, hybrid and exotic sires in a semen importing country is available. For instance, in the grading-up system to form the Simmental breed in the United States, across-country procedures could have been used to evaluate exotic Simmental bulls and(or) to help evaluate local hybrid sires. Across-country procedures will continue to be of use in countries with open crossbreeding systems based on recurrent rounds of semen importation or stratified

crossbreeding schemes (Elzo and Famula, 1985) whose top stratum of breeders is small and that depend (at least partially) on exotic semen for their program. For instance, they could be used to aid in the selection of exotic, hybrid and native dairy and beef cattle in various Latin American and European countries, whose breeding practices, described by Madalena (1977) and Leroy (1977), respectively, can be considered cases of recurrent rounds of importation of exotic genetic material. These procedures could also be used for similar selection purposes in the stratified cattle crossbreeding programs suggested for Ethiopia by Schaar et al. (1981) and for the Sudan by Osman and Russell (1974).

The method of choice will depend on the particular situation. If records from exotic and native countries are available, then MT1 would be used. However, in some cases, records may be unavailable from some countries, but some kind of sire proof can be obtained. Then, either $\widetilde{MT2}$ or $\widetilde{MT3}$ could be used to meet one or more of the objectives above. It should be stressed that the EVP of $\widetilde{MT2}$ or $\widetilde{MT3}$ might be larger than the intra-country BLUP. Hence, it would be safer to use them when intra-country sire proofs are poor or nonexistent, and when exotic sire proofs have small EVP. In other cases, sire proofs may be available, but only approximate EVP. In such cases, the EVP of $\widetilde{MT2}$ and $\widetilde{MT3}$ are likely to be larger than when the actual EVP are used in their respective MME. In general, caution should be exercised when interpreting multiple trait sire proofs based on $\widetilde{MT2}$ and $\widetilde{MT3}$.

The formation of an international data bank (IDB), as suggested by Heiman (1980), would be a very useful source of information to evaluate sires in different countries. Records of different traits of interest measured in the various contributing countries would be used to predict the genetic value of widely used sires in different environmental regions of the world. The multiple trait method used could be MT1 (1). The definition of environmental region of the world could involve climatic, management, nutrition, disease, educational level and socio-economical factors. From a practical point of view, a classification based on production level might suffice, at least as a first approach. An international sire evaluation program would be a long-term project. Hence, it might be helpful to describe an alternative improvement strategy

from the point of view of a native country. This general plan could be the following:

(i) Introduction of semen from one or several breed groups of sires into the native country. Use this semen to obtain F_1, F_2 and backcrosses to native and exotic breeds.

(ii) Estimate genetic covariances for native and exotic breeds using hybrid and straightbred progeny from the first two generations.

(iii) Pick out the simplest model that describes a record with reasonable accuracy under the conditions of the design matrix.

(iv) Evaluate sires within groups and across groups as soon as possible using intra-country sire evaluation procedures.

(v) If data from exotic sires in their countries of origin are available, estimate genetic covariances across countries.

(vi) Preselect exotic, hybrid and native sires using intra- or inter-country sire evaluation procedures.

(vii) Continue to import semen from the best proven sires under native conditions for wide use in the native population, together with the best hybrid and native sires, to obtain more crossbred groups.

(viii) Continue the preselection of sires to be tested under native conditions.

(ix) Re-estimate genetic covariances when more information becomes available.

(x) Test more complete models when more diversity of matings is available.

(xi) Carry out flexible mating plans, e.g., plan matings depending on production predictions and economic conditions of a region in a country.

This scheme has as its objective the prediction of additive and nonadditive performance of future progeny of specific sires and breed groups of dams. Subsequently, matings can be planned to emphasize additive genetic effects, nonadditive genetic effects or both.

Admittedly, the above outline is very general, but a specific strategy for a particular country would require an accurate assessment of that country's goals and production conditions. However, it points out the need for an organized evaluation of exotic, hybrid and

native genotypes in a native environment to allow breeders to decide on future mating plans on an objective basis. The procedures described in this paper and those presented in Elzo and Famula (1985) could be used to carry out such evaluations.

Appendix

Explicit Expressions for N, M, $\overset{*}{R}$, W, V, EVP of $MT2$ and EVP of $\widetilde{MT2}$. Formulae are given below for the case when the intra-country sire proofs are BLUP of s, where $s = L\,d$. Thus,

(i) $N = \text{diag}\,\{N_{ii}\}$, $1 \leqslant i \leqslant I$, $I = $ number of countries, where $N_{ii} = B_{3i}\,[C^i_{41}\,B'_{1i} - C^i_{42}\,B'_{2i} - C^i_{43} - C^i_{44}\,B'_{3i}]$, where $\{C^i_{kk'}\}$, $1 \leqslant k$, $k' \leqslant 4$ is the EVP of $[\hat{b}^{S'}_i : \hat{\delta}'_{1i} : \hat{a}^{S'}_i : \hat{\delta}'_{2i}]$ for the ith country, and $B_{1i} = Q^S_i P^S_i$, $B_{2i} = T^S_i Q_{2i}$, $B_{3i} = T^S_i$;

(ii) $M = \{M_{ii'}\}$, $1 \leqslant i, i' \leqslant I$, where
$$M_{ii'} = -G_{ii}\,G^{-1}_{i'i'}[C^{i'}_{31}\,B'_{1i'} + C^{i'}_{32}\,B'_{2i'} + C^{i'}_{33} + C^{i'}_{34}\,B'_{3i'}]\,;$$

(iii) $\overset{*}{R} = \{\overset{*}{R}_{ii'}\}$, $1 \leqslant i, i' \leqslant I$, where
$R_{ii} = B_i\,C^i\,B'_i$, where
$$B_i = [B_{1i} : B_{2i} : I_i : B_{3i}]\,,$$
$R_{ii'} = B_{1i}C^i_{13}G^{-1}_{ii}\,G_{ii'}G^{-1}_{i'i'}C^{i'}_{31}\,B'_{1i'} +$
$\qquad B_{2i}C^i_{23}G^{-1}_{ii}\,G_{ii'}G^{-1}_{i'i'}C^{i'}_{32}\,B'_{2i'} +$
$\qquad C^i_{33}G^{-1}_{ii}\,G_{ii'}G^{-1}_{i'i'}C^{i'}_{33} +$
$\qquad B_{3i}C^i_{43}G^{-1}_{ii}\,G_{ii'}G^{-1}_{i'i'}C^{i'}_{34}\,B'_{3i'} +$
$\qquad B_{1i}C^i_{13}G^{-1}_{ii}\,G_{ii'} + B_{2i}C^i_{23}G^{-1}_{ii}\,G_{ii'} +$
$\qquad B_{3i}C^i_{43}G^{-1}_{ii}\,G_{ii'} +$
$\qquad G_{ii'}G^{-1}_{i'i'}C^{i'}_{31}\,B'_{1i'} +$
$\qquad G_{ii'}G^{-1}_{i'i'}C^{i'}_{32}\,B'_{2i'} +$
$\qquad G_{ii'}G^{-1}_{i'i'}C^{i'}_{34}\,B'_{3i'}\,;$

(iv) $W = \{W_{ii'}\}$, $1 \leqslant i, i' \leqslant I$, where
$W_{ii} = -C^i_{31}\,B'_{1i} - C^i_{32}\,B'_{2i} + (G_{ii} - C^i_{33}) - C^i_{34}\,B'_{3i} - B_{3i}C^i_{41}\,B'_{1i} -$

$\qquad B_{3i}C^i_{42}\,B'_{2i} - B_{3i}C^i_{43} + B_{3i}(D_{2i} - C^i_{44})B'_{3i}\,,$
$W_{ii'} = -G_{ii'}G^{-1}_{i'i'}C^{i'}_{31}\,B'_{1i'} -$
$\qquad G_{ii'}G^{-1}_{i'i'}C^{i'}_{32}\,B'_{2i'} + G_{ii'} -$
$\qquad G_{ii'}G^{-1}_{i'i'}C^{i'}_{33} - G_{ii'}G^{-1}_{i'i'}C^{i'}_{34}\,B'_{3i'}\,;$

(v) $V = \{V_{ii'}\}$, $1 \leqslant i, i' \leqslant I$, where
$V_{ii} = G_{ii} + D_{2i} + \overset{*}{R}_{ii} + M_{ii} + M'_{ii} + N_{ii} + N'_{ii}\,,$
$V_{ii'} = G_{ii'} + \overset{*}{R}_{ii'} + M_{ii'} + M_{i'i}\,;$

(vi) EVP of $\hat{s}_2$

$E(\hat{s}_2 - s)^2 = (I - WV^{-1})B[B'V^{-1}B]^{-1}B'(I - WV^{-1})' +$
$\qquad WV^{-1}W' + WV^{-1}UV^{-1}W' +$
$\qquad WV^{-1}B[B'V^{-1}B]^{-1}B'(I - WV^{-1})' +$
$\qquad (I - WV^{-1})B[B'V^{-1}B]^{-1}B'V^{-1}W' -$
$\qquad (I - WV^{-1})B[B'V^{-1}B]^{-1}B'V^{-1}W'V^{-1}W -$
$\qquad W'V^{-1}WV^{-1}B[B'V^{-1}B]^{-1}B'(I - WV^{-1})' -$
$\qquad WV^{-1}W'V^{-1}W' - WV^{-1}WV^{-1}W'\,,$

where

$B = [Q^S P^S : T^S Q_2]\,,$
$V = \text{var}\,[a^S + T^S \delta_2]\,;$

(vii) EVP of $\widetilde{\hat{s}}_2$

$E(\widetilde{\hat{s}}_2 - s)^2 = \overset{*}{C}_{33}\,\dot{R}^{-1}\,K'\overset{*}{V}K\dot{R}^{-1}\,\overset{*}{C}_{33}\,,$

where

$\overset{*}{C}_{33} = $ submatrix of the inverse of the left hand side of the rearranged MME corresponding to $\widetilde{\hat{s}}_2$,

$K' = [\text{diag}\,\{B_i C^i N_i\} : -I : -B_{3i}]\,,$

$V = \text{var} \begin{bmatrix} \{y_i\} \\ \{a^S_i\} \\ \{\delta_{2i}\} \end{bmatrix}$, $1 \leqslant i \leqslant I$.

To obtain the above formulae, an identity similar to the one presented in Appendix A, Henderson (1975) was used.

Explicit Expression for G. Using Quaas' (1975) notation, G can be explicitly written as follows:

$$G = (I = .5P)^{-1} \, H \, (I - .5P')^{-1},$$

where

     I = identity matrix,

     P = lower triangular incidence matrix relating sires and maternal grandsires to progeny within traits. The only nonzero elements of a row of P are a 1 for a progeny's sire, if identified, and a .5 for a progeny's maternal grandsire, if identified,

     H = block diagonal matrix. The ith block of H is a $k_i \times k_i$ matrix of covariances among the residual additive effects after fitting a model, for the k_i traits the ith individual is evaluated for.

For a complete description of G and of recursive methods to compute G and its inverse, see Elzo (1983).

Numerical Example for MT1, $\widetilde{MT2}$ and $\widetilde{\widetilde{MT3}}$. Consider the case of two countries (i.e., two traits) and the evaluation of two unrelated sires belonging to the same breed and genetic group. For simplicity, assume that only direct additive effects are important for the trait being analyzed. Let the number of progeny of sires 1 and 2 be 20 and 30 in country 1 and 70 and 80 in country 2, respectively. Let the trait means for these progeny groups be 2,000, 3,000, 2,500 and 1,500 respectively. Let the two trait additive covariance matrix, G, be:

$$G = \begin{bmatrix} 18{,}750 & 0 & 12{,}837.2 & 0 \\ 0 & 18{,}750 & 0 & 12{,}837.2 \\ 12{,}837.2 & 0 & 15{,}625 & 0 \\ 0 & 12{,}837.2 & 0 & 15{,}625 \end{bmatrix},$$

i.e., the additive correlation between the trait measured in countries 1 and 2 is .5. Let the environmental variance in both countries be equal to 250,000. Thus, the residual variance for progeny record in country 1 is 231,250 (i.e., 250,000 − 18,750) and for progeny in country 2 is 234,375 (i.e., 250,000 − 15,625). Mixed model equations for the intra-country sire evaluations and across-country sire evaluation (MT1, $\widetilde{MT2}$ and $\widetilde{\widetilde{MT3}}$) will be set according to the modified MME of Quaas and Pollak (1981). So, the effects being evaluated by the

TABLE 1. MIXED MODEL EQUATIONS FOR MT1 (EXAMPLE CASE)

$$
\begin{bmatrix}
.000142^a & -.000078 & -.000071 & -.000071 & .000039 & .000039 \\
-.000078 & .000171 & .000039 & .000039 & -.000085 & -.000085 \\
-.000071 & .000039 & .000156 & 0 & -.000039 & 0 \\
-.000071 & .000039 & 0 & .000201 & 0 & -.000039 \\
.000039 & -.000085 & -.000039 & 0 & .000384 & 0 \\
.000039 & -.000085 & 0 & -.000039 & 0 & .000427
\end{bmatrix}
\begin{bmatrix}
\hat{g}_{11}{}^{,b} \\
\hat{g}_{12} \\
\hat{s}_{111} \\
\hat{s}_{112} \\
\hat{s}_{121} \\
\hat{s}_{122}
\end{bmatrix}
=
\begin{bmatrix}
0 \\
0 \\
.172979 \\
.324324 \\
.896000 \\
.512000
\end{bmatrix}
$$

[a] All numbers were approximated to six digits.

[b] The first subscript of the $\hat{g}$ and $\hat{s}$ refers to MT1, the second one to country (i.e., trait) number and the third one of the $\hat{s}$ to sire number.

intra- and inter-country MME of this example are sire group effects (g) and sire proofs (s = Qg + a^s), for additive effects. Because intra-country sire proofs will be used in $\widetilde{\widetilde{MT2}}$ and $\widetilde{\widetilde{MT3}}$, they will be evaluated first. The MME used to evaluate sires 1 and 2 in country 1 are:

$$\begin{bmatrix} .000107 & -.000053 & -.000053 \\ -.000053 & .000140 & 0 \\ -.000053 & 0 & .000183 \end{bmatrix} \begin{bmatrix} \hat{g}_1 \\ \hat{s}_{11} \\ \hat{s}_{12} \end{bmatrix} = \begin{bmatrix} 0 \\ .171979 \\ .324324 \end{bmatrix},$$

where the subscript of $\hat{g}$ and the first subscript of $\hat{s}$ denote country number, and the second subscript of $\hat{s}$, sire number. Country 1 sire proofs and their EVP are $\hat{s}_{11}$ = 2,092, EVP ($\hat{s}_{11}$) = 9,207 and s_{12} = 2,430, EVP ($\hat{s}_{12}$) = 6,662. Intra-country EVP are taken from the diagonal elements of the inverse of the LHS of the MME above. Sire proofs and their EVP in country 2 are calculated in similar fashion. Their values are: $\hat{s}_{21}$ = 2,866, EVP ($\hat{s}_{21}$) = 3,050 for sire 1 and $\hat{s}_{22}$ = 1,617, EVP ($\hat{s}_{22}$) = 2,701 for sire 2.

Sire evaluations for sires 1 and 2 in countries 1 and 2 will now be predicted, first by using records from both countires (MT1), second by using sire proofs from both countries ($\widetilde{MT2}$) and third by using records from country 1 and intra-country sire proofs from country 2 ($\widetilde{MT3}$).

The MME for MT1 are presented in table 1. The sire proofs and their EVP for MT1 are:

$$\begin{bmatrix} \hat{s}_{111} \\ \hat{s}_{112} \\ \hat{s}_{121} \\ \hat{s}_{122} \end{bmatrix} = \begin{bmatrix} 2,280 \\ 2,314 \\ 2,829 \\ 1,649 \end{bmatrix} \text{ and } \begin{bmatrix} EVP\,(\hat{s}_{111}) \\ EVP\,(\hat{s}_{112}) \\ EVP\,(\hat{s}_{121}) \\ EVP\,(\hat{s}_{122}) \end{bmatrix} = \begin{bmatrix} 8,832 \\ 6,495 \\ 3,002 \\ 2,665 \end{bmatrix}.$$

The EVP for MT1 sire proofs were taken from the diagonal elements of the inverse of the LHS of the MME in table 1.

The MME for $\widetilde{MT2}$ are shown in table 2. Notice that the diagonal matrix of residual effects for $\widetilde{MT2}$ is formed by the EVP of the intra-country sire proofs, i.e., $\hat{R}$ = diag [9,207, 6,662, 3,050, 2,701]. The sire proofs and their EVP for $\widetilde{MT2}$ are:

$$\begin{bmatrix} \tilde{\tilde{s}}_{211} \\ \tilde{\tilde{s}}_{212} \\ \tilde{\tilde{s}}_{221} \\ \tilde{\tilde{s}}_{222} \end{bmatrix} = \begin{bmatrix} 2,278 \\ 2,296 \\ 2,735 \\ 1,733 \end{bmatrix} \text{ and } \begin{bmatrix} EVP\,(\tilde{\tilde{s}}_{211}) \\ EVP\,(\tilde{\tilde{s}}_{212}) \\ EVP\,(\tilde{\tilde{s}}_{221}) \\ EVP\,(\tilde{\tilde{s}}_{222}) \end{bmatrix} = \begin{bmatrix} 9,551 \\ 6,864 \\ 3,198 \\ 2,819 \end{bmatrix}.$$

The EVP for $\widetilde{\widetilde{MT2}}$ sire proofs were calculated using the expression given in (vii) above.

TABLE 2. MIXED MODEL EQUATIONS FOR $\widetilde{\widetilde{MT2}}$ (EXAMPLE CASE)

$$\begin{bmatrix} .000142^a & -.000078 & -.000071 & -.000071 & .000039 & .000039 \\ -.000078 & .000171 & .000039 & .000039 & -.000085 & -.000085 \\ -.000071 & .000039 & .000180 & 0 & -.000039 & 0 \\ -.000071 & .000039 & 0 & .000221 & 0 & -.000039 \\ .000039 & -.000085 & -.000039 & 0 & .000413 & 0 \\ .000039 & -.000085 & 0 & -.000039 & 0 & .000456 \end{bmatrix} \begin{bmatrix} \tilde{\tilde{g}}_{21}{}^b \\ \tilde{\tilde{g}}_{22} \\ \tilde{\tilde{s}}_{211} \\ \tilde{\tilde{s}}_{212} \\ \tilde{\tilde{s}}_{221} \\ \tilde{\tilde{s}}_{222} \end{bmatrix} = \begin{bmatrix} 0 \\ 0 \\ .227270 \\ .364847 \\ .939886 \\ .598709 \end{bmatrix}$$

[a] All numbers were approximated to six digits.
[b] The first subscript of the $\tilde{\tilde{g}}$ and $\hat{\tilde{s}}$ refers to $\widetilde{\widetilde{MT2}}$, the second one to country (i.e., trait) number and the third one of the $\hat{\tilde{s}}$ to sire number.

The MME for $\widetilde{MT3}$ are shown in table 3. The elements of the matrix of residual effects for $\widetilde{MT3}$, i.e., $\tilde{R}_3$, for the records from country 1 are equal to the corresponding ones for the matrix of residual effects for MT1, and those for the proofs from country 2 are the same as the corresponding ones for matrix $\tilde{R}$ from $\widetilde{MT2}$. The sire proofs and their EVP for $\widetilde{MT3}$ are:

$$\begin{bmatrix} \tilde{\hat{s}}_{311} \\ \tilde{\hat{s}}_{312} \\ \tilde{\hat{s}}_{321} \\ \tilde{\hat{s}}_{322} \end{bmatrix} = \begin{bmatrix} 2,255 \\ 2,330 \\ 2,732 \\ 1,736 \end{bmatrix} \quad \text{and} \quad \begin{bmatrix} EVP\,(\tilde{\hat{s}}_{311}) \\ EVP\,(\tilde{\hat{s}}_{312}) \\ EVP\,(\tilde{\hat{s}}_{321}) \\ EVP\,(\tilde{\hat{s}}_{322}) \end{bmatrix} = \begin{bmatrix} 8,843 \\ 6,500 \\ 3,168 \\ 2,795 \end{bmatrix} .$$

The EVP for $\widetilde{MT3}$ sire proofs were also calculated using expression (vii) above. As expected, MT1 sire proofs have the smallest EVP, followed by $\widetilde{MT3}$ sire proofs and $\widetilde{MT2}$ sire proofs. Notice that the EVP of $\widetilde{MT3}$ sire proofs are smaller than the intra-country sire proofs for country 1 (small number of progeny per sire), but slightly larger than intra-country 2 sire proofs (fairly large number of progeny per sire). The EVP of $\widetilde{MT3}$ sire proofs is larger than the EVP of sire proofs within countries 1 and 2, which, in turn, are larger than the EVP of MT1 sire proofs. The results of this example support the statements made in the main text that MT1 should be preferred to $\widetilde{MT3}$ and $\widetilde{MT2}$, and that the EVP of $\widetilde{MT2}$ and $\widetilde{MT3}$ may, in some cases, be larger than the intra-country sire proofs' EVP but smaller in others.

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TABLE 3. MIXED MODEL EQUATIONS FOR $\widetilde{MT3}$ (EXAMPLE CASE)

.000142[a]	−.000078	−.000071	−.000071	.000039		$\tilde{\hat{g}}_{31}$ [b]		0
	.000177	.000039	.000039	−.000085		$\tilde{\hat{g}}_{32}$		0
		.000156	0	0		$\tilde{\hat{s}}_{311}$	=	.172979
			.000201	−.000039		$\tilde{\hat{s}}_{312}$		.324324
Symmetric				.000413		$\tilde{\hat{s}}_{321}$		.939886
				.000456		$\tilde{\hat{s}}_{322}$		.598709

[a] All numbers were approximated to six digits.
[b] The first subscript of the $\tilde{\hat{g}}$ and $\tilde{\hat{s}}$ refers to $\widetilde{MT3}$, the second one to country (i.e., trait) number and the third one of the $\tilde{\hat{s}}$ to sire number.

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