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Methods to Combine Estimated Breeding Values Obtained from Separate Sources

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ABSTRACT

Separate estimates of breeding value can be combined using meta-analysis if a combined analysis of all data is not possible or efficient. Computation is fast but not exact if the reliabilities of the separate estimates are approximate, if the extent of overlap of the datasets is unknown, or if selection has occurred across the datasets. Selection index methods were used to combine single-trait evaluations into approximate multitrait evaluations for productive life and to combine single-country rankings into multicountry rankings for yield traits. The same methods are used for males and females. To avoid iteration, parent evaluations were included in the data and combined before progeny evaluations. A little information is lost because foreign progeny contribute to domestic parents but not to domestic grandparents. Exchange of sire and dam evaluations provides a closer connection between national and international evaluations and may be more accurate than the current sire-maternal grandsire model used internationally. Correlations of the two evaluation methods were about 0.99 for 35,414 bulls from eight countries. The estimated breeding value of each bull was adjusted separately for information from foreign parents and foreign progeny. Reliabilities of the animal, its sire, and its dam were used to determine how much information came from the parents of the animal versus from its progeny and records. Multitrait reliabilities for productive life were higher than single-trait reliabilities by a mean of 7% for recent bulls and 3% for recent cows. Selection index methods may allow current multitrait across-country evaluations for bulls to be improved and to be extended to cows.
(**Key words:** breeding values, multitrait, meta-analysis, selection index)

Abbreviation key: **AIPL** = Animal Improvement Programs Laboratory, **DE** = daughter equivalent, $\mathbf{h^2}$ = heritability, **MACE** = multitrait, across-country evaluation, **MGS** = maternal grandsire, **MS** = Mendelian sampling, **PA** = mean of genetic merit of parents, **PEV** = prediction error variance, **PL** = productive life, **REL** = reliability, **SI** = selection index.

INTRODUCTION

Statistical methods such as selection indexes (**SI**), BLUP, and Bayes' theorem allow animal breeders to get the most accuracy from their available data. The use of more data can provide even higher accuracy, but data from all traits, all places, and all times may not be available in the same database. Exact statistical methods that work well for smaller data subsets may not work at all with a large, combined dataset. Approximate combination of estimates from separate datasets can be achieved through an SI (Hazel, 1943; Smith, 1936). Better models might be applied to each dataset and then evaluations combined to include information from all sources.

Multitrait models can increase accuracy by adding correlated data from other traits. Although more accurate, multitrait equations are harder to set up and to solve when different traits have different models and different patterns of missing data. Approximate multitrait evaluations might result from first computing single-trait evaluations and then combining those evaluations through an SI. This approach reduces computation because only covariances among EBV are required instead of covariances among all data points.

"It seems inevitable that, as solutions to existing problems are sought, the methodology will become more complex, both in the statistical solutions and in the computations needed to obtain numerical answers. Ideally, however, simple methods of estimation are needed. Understanding of statistical methods is improving. Larger and faster computers are becoming more common, and the work that can be accomplished relative to costs is increasing. As solutions to problems are found and computing algorithms developed, perhaps the goal of simplifying estimation can be achieved." Those conclusions were presented by A. E. Freeman at the 1979 conference to honor his major professor, C. R. Henderson (Freeman, 1979).

Henderson's mixed model methods and BLUP are now used so much by animal breeders that all of his excellent papers no longer need to be cited in research reports. The statistical methods of Henderson (e.g., 1973) give accurate predictions and are easy to follow for those with training in matrix algebra. Traits such as longevity or performance in another environment may be difficult to observe directly or early in life, but correlated traits of relatives may aid in predictions. Because relatives share different fractions of the same genes, statistical models that include data from related animals more accurately predict the merit of each by accounting for their shared genes.

Henderson and Quaas (1976) concluded that accuracy and cost must be balanced when dealing with multiple traits. Thompson and Meyer (1986) discussed the similarity of SI methods and multitrait BLUP. Weigel et al. (1996, 1998) developed SI methods to obtain approximate multitrait EBV for productive life (**PL**) from direct longevity and earlier correlated traits of daughters.

A goal of statistics is to predict the future by using past data to estimate real causes and effects in systems that are not 100% repeatable because some random chance (error) occurs.

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Because of this error, predictions are not exact, and, therefore, statisticians provide confidence intervals or reliabilities (**REL**) to measure the expected error. Bayes (1763) realized that posterior confidence is a function of prior confidence. His methods were not accepted for most statistical analyses because statisticians could not agree on a prior confidence. Bayes' theorem is ideally suited to the analysis of quantitative traits, however, because Wright's (1922) relationship matrix provides an ideal informative prior for genetic merit. For traits that are affected by many genes, Wright's informative prior may be the easiest part of the analysis on which to agree.

Prior information refers to the mean and variance assumed for the unknowns. Estimates that include prior information are computed as weighted means of the prior mean and the data mean (Gianola and Fernando, 1986). Programs that compute estimates using weighted least squares can be manipulated to include prior information by adding prior observations to the dataset (Harville, 1986). An observed value of 0 is added for each random effect and weighted by the ratio of error to random effect variance; i.e., each random effect belongs to some population of random effects with a mean of 0 and known variance, and this approach converts the fixed model into a mixed model. For related animals, differences between progeny and parent breeding values have an expectation of 0 and known variance. The prior distribution may be viewed as a separate source of information to be combined.

To include information from all data, researchers could use approximate methods instead of exchanging their separate datasets and computing an exact analysis. Each could treat the separate EBV and REL as the data to analyze and determine how much weight each EBV should receive in the combined EBV by calculating expected variances and covariances from the separate REL. The combined EBV would have higher REL than the separate EBV depending on how many observations were included in each dataset.

Experimental design is perhaps more important than statistical analysis, and sophisticated equations cannot compensate for a lack of good data. Freeman (1983) reviewed experiments designed to rank cattle globally and reported, "Application of science to cattle breeding was confined initially to improvement of breeds within countries ... Then, to make accurate choices of which cattle to import from different countries, it is necessary to know the mean merit of cattle in the different countries. If this is known, ... the question still remains of how well imported cattle can adjust to the environment in the importing country." He concluded, "The best determination for potentially importing cattle into any country is to compare imported cattle within the importing country in unbiased comparisons and in large enough numbers to be able to draw valid conclusions."

This global approach to animal breeding that was suggested by Freeman (1983) is now routine. Table 1 lists the countries that submitted data for February 2000 evaluations that were calculated by the Interbull Centre (Uppsala, Sweden), the number of Holstein bulls that were evaluated in each country, and the percentages of those bulls with foreign parents or foreign daughters. A parent was considered to be foreign if the country code in its preferred Interbull identification differed from the code of the country that had submitted the bull evaluation. Daughters were considered to be foreign if any other country reported an evaluation for the same bull. Many (28) of the best bulls from previous years now have daughter evaluations in at least half of the 26 national datasets. Two dams (Conant-Acres JY Sweetnes-ET and Eric-Dew Mars Marcy) had the most sons (42), and those sons were progeny tested in eight and nine different countries, respectively. The same genes are now evaluated separately in many countries.

Table 1. Percentages of bulls with foreign relatives and numbers of Holstein and Red and White bulls that were born from 1990 to 1995 for countries that submitted data to the Interbull Centre (Uppsala, Sweden) for February 2000 evaluations.

		Bulls with foreign relatives		
Country	Bulls	Sires	Dams	Daughters
	(no.)	------------------(%)------------------		
Australia	1365	97	61	24
Austria	52	100	69	67
Belgium[1]	355	100	84	68
Canada[1]	2297	52	33	21
Czech Republic	368	87	80	35
Denmark[1]	1964	99	37	2
Estonia[1]	110	91	32	17
Finland	214	66	3	0
France[1]	3085	96	58	13
France (Red)	29	100	97	21
Germany	4493	90	24	9
Hungary	217	93	27	2
Ireland	209	>99	100	1
Israel	228	54	1	1
Italy	1546	93	16	7
New Zealand	1249	78	36	22
Poland	1218	74	10	<1
Slovenia	21	100	33	0
South Africa	133	94	56	3
Spain	209	100	94	17
Sweden	465	97	34	13
Switzerland	146	100	12	12
Switzerland (Red)[1]	221	86	22	21
The Netherlands[1]	2377	69	41	17
United Kingdom	995	99	86	25
United States[1]	7943	9	2	8

[1] Participant in test of selection index approach.

The objectives of this study were 1) to derive improved methods to combine separate evaluations of the same genetic effect or of correlated effects, 2) to apply the methods to combine genetic evaluations of yield traits from separate nations, 3) to combine evaluations of several correlated traits into a multitrait evaluation of longevity, and 4) to unite some of the statistical terms and concepts that in the past were stated separately.

METHODS

Suppose that two estimates ($\hat{u}_1$ and $\hat{u}_2$) of one unknown (u) are available. Further suppose that the two estimates were obtained by applying BLUP or Bayes' theorem separately to data vectors $\mathbf{y}_1$ and $\mathbf{y}_2$ such that $\hat{u}_1$ and $\hat{u}_2$ are the expected values of u given the data:

$$\hat{u}_1 = \mathrm{E}(u\,|\,\mathbf{y}_1), \text{ and}$$

$$\hat{u}_2 = \mathrm{E}(u\,|\,\mathbf{y}_2).$$

The two datasets could be from different traits or different nations, e.g., and could have some correlated errors or be completely independent. In either case, the two datasets could be merged, and then a combined estimate ($\hat{u}_{1,2}$) would be obtained as

$$\hat{u}_{1,2} = \mathrm{E}(u|\boldsymbol{y}_1,\boldsymbol{y}_2).$$

An SI method (Hazel, 1943) also can be used to combine information from separate sources (Hanson and Johnson, 1957). Let the covariances of $\hat{u}_1$ and $\hat{u}_2$ with u be in vector $\boldsymbol{c}$, the variance matrix for $\hat{u}_1$ and $\hat{u}_2$ be $\boldsymbol{V}$, and the expected value of u be 0. The combined SI estimate ($\tilde{u}_{1,2}$) is then

$$\tilde{u}_{1,2} = \boldsymbol{c}'\boldsymbol{V}^{-1}[\hat{u}_1 \quad \hat{u}_2]'.$$

In this case, the two evaluations are combined instead of combining the original data. The SI, BLUP, and Bayesian methods can be applied to three or more datasets simply by increasing the number or size of the arrays above.

Statistical methods that combine estimates instead of combining data often are referred to as meta-analysis (Abrams and Sansó, 1998; Normand, 1999). Meta-analysis has three main advantages: 1) original data files are not required, 2) time required to compute $\tilde{u}_{1,2}$ is often much less than time required to compute $\hat{u}_{1,2}$, and 3) different datasets may require different models and different statistical methods.

With normally distributed data and priors, only the mean and $\mathrm{Var}(u|\boldsymbol{y}_1,\boldsymbol{y}_2)$ are needed to describe completely the posterior distribution, which is also normal. Thus, the SI, BLUP, and Bayesian estimates may be identical in theory. Henderson (1963) showed that BLUP and SI formulas are equivalent if fixed effects are known or if BLUP estimates of the fixed effects are used to adjust data. An SI is a useful tool for combining solutions for random effects because the fixed environmental factors already are removed by single-trait BLUP. Multitrait estimates of fixed effects may be nearly identical or may not be needed. Formulas from BLUP and SI methods will differ in practice because elements of $\boldsymbol{c}$ and $\boldsymbol{V}$ often are not computed exactly.

Reliabilities

Animal breeders use REL as a measure of confidence. For $\hat{u}_1$ and $\hat{u}_2$, REL are defined as

$$REL_1 = 1 - \mathrm{Var}(u|\boldsymbol{y}_1)/\mathrm{Var}(u), \text{ and}$$

$$REL_2 = 1 - \mathrm{Var}(u|\boldsymbol{y}_2)/\mathrm{Var}(u).$$

Exact REL often cannot be computed, but Misztal and Wiggans (1988) showed that REL within 1% often can be obtained. Diagonals of $\boldsymbol{V}$ equal $\mathrm{Var}(u)$ multiplied by REL. Off-diagonals of $\boldsymbol{V}$ are more difficult to obtain, especially if $\boldsymbol{y}_1$ and $\boldsymbol{y}_2$ are not independent. Elements of c equal diagonals of $\boldsymbol{V}$ because covariance of the estimate with the true effect equals variance of the estimate (see Van Vleck, 1993).

Henderson (1973) showed that variance of solutions for random effects equals variance of the prior minus variance of prediction error variance (**PEV**). In his notation, the subtraction was given as $\boldsymbol{G} - \boldsymbol{C}_{22}$. Thus, prior variance is partitioned into variance of the predictions and the prediction errors (estimated effects minus true effects). To obtain either PEV or REL requires the inverse of the mixed model matrix. Misztal and Wiggans (1988) used a series of 3 × 3 approximate inverse elements with much less computation.

Let $\boldsymbol{A}$ be the 3 × 3 relationship matrix for an animal, its sire, and its dam. Let $\boldsymbol{D}$ be a diagonal matrix with diagonal elements D_a, D_s, and D_d that correspond to the same three animals. Those diagonals measure the amount of information for progeny excluding that received from its parents and information for parents excluding that received from this progeny. Amount of information was expressed as record equivalents in Misztal and Wiggans (1988), but daughter equivalents (**DE**) (VanRaden and Wiggans, 1991) also can be used. The ratio of error to genetic variance was denoted as k for an animal model and k_s for a sire model. Values of k_s were calculated from heritability ($\mathbf{h}^2$) as $[4 - h^2]/h^2$ by VanRaden and Wiggans (1991), but higher or lower k_s that match assumptions used in computing $\boldsymbol{D}$ can provide equivalent REL.

Let $\boldsymbol{C}$ be the mixed model coefficient matrix for those three animals after absorbing all other effects and all other animals. Matrix $\boldsymbol{C}$ can be approximated as

$$\boldsymbol{C} = \boldsymbol{D} + \boldsymbol{A}^{-1}k.$$

The formula is approximate because off-diagonals of $\boldsymbol{D}$ are assumed to be 0, but information may not really be completely independent if, e.g., the dam and progeny both had records in the same management group. Let $\hat{a}$, $\hat{s}$, and $\hat{d}$ be BLUP solutions for the three animals. Variance of those three solutions is obtained as

$$\mathrm{Var}([\hat{a} \quad \hat{s} \quad \hat{d}]') = \boldsymbol{A}\mathrm{Var}(u) - \boldsymbol{C}^{-1}\mathrm{Var}(e).$$

Diagonals of $\boldsymbol{A}$ equal 1 plus the inbreeding coefficient of each animal. Let $\boldsymbol{F}$ be a diagonal matrix with diagonals equal to the square roots of the reciprocals of the diagonals of $\boldsymbol{A}$. Pre- and postmultiplication of $\boldsymbol{A}$ by $\boldsymbol{F}$ converts the numerator relationship covariance matrix of Henderson (1973) to the relationship correlation matrix of Wright (1922). Similarly, an REL matrix ($\boldsymbol{R}$) for the three animals is obtained by

$$\boldsymbol{R} = \boldsymbol{F}(\boldsymbol{A} - \boldsymbol{C}^{-1}k)\boldsymbol{F}.$$

Diagonals of $\boldsymbol{R}$ contain REL for each animal. If none of the three animals is inbred, the matrix simplifies to the more familiar $\boldsymbol{A} - \boldsymbol{C}^{-1}k$. Those formulas can be used to compute REL and also to backsolve for $\boldsymbol{D}$ from released REL for an animal, its sire, and its dam. Specific formulas in the case of no inbreeding are presented in the section “Updated Parent Information.”

Off-diagonals of $\boldsymbol{C}^{-1}$ were ignored by Misztal and Wiggans (1988) and by VanRaden and Wiggans (1991), but those off-diagonals actually are very useful. Because the mean of genetic merit of parents (**PA**) equals $0.5(\hat{s} + \hat{d})$, the REL of PA (REL_{PA}) should include the covariance of the solutions for sire and dam (R_{sd}):

$$REL_{PA} = 0.25(REL_s + REL_d + 2\,R_{sd}).$$

In the past, R_{sd} was not available and was assumed to equal 0. If the REL of either or both parents is large, R_{sd} tends to be small by comparison.

Mendelian sampling (**MS**) is estimated as the difference between $\hat{a}$ and the mean of $\hat{s}$ and $\hat{d}$. Thus, the variance of predicted MS ($\hat{m}$) can be obtained as

$$\mathrm{Var}(\hat{m}) = [1 \quad -0.5 \quad -0.5]\mathrm{Var}([\hat{a} \quad \hat{s} \quad \hat{d}]')[1 \quad -0.5 \quad -0.5]'.$$

Matrix $\boldsymbol{C}$ also can be used to deregress breeding values or to backsolve for independent right-hand-sides ($\boldsymbol{r}$). Elements of $\boldsymbol{r}$ divided by diagonals of $\boldsymbol{D}$ may be better suited to later statistical analysis than daughter yield deviations because of the explicit attempt to provide independent information:

$$[\hat{a} \quad \hat{s} \quad \hat{d}]' = \boldsymbol{C}^{-1}\boldsymbol{r}.$$

Also, this simple formula can be used to split apart and to recombine information from parents and progeny when improved evaluations of either become available.

Finally, matrix $\boldsymbol{C}$ could be useful in variance estimation. The EBV and prediction errors for an animal, its sire, and dam may be correlated if estimated from the same dataset, but the Mendelian sampling effects for each animal in the population are uncorrelated. Because the variance of true MS is diagonal, simplified variance estimation may be possible by equating the sum of squared MS with its expectation, which involves the sum of Var($\hat{m}$) given previously.

Selection

Mixed model equations from a model that ignores selection may fully account for selection based only on linear functions of the data. Proof was given by Henderson (1973) at the symposium in honor of his major professor, J. L. Lush. The proof was later translated into Bayesian terms by Gianola and Fernando (1986). They also suggested that posterior estimates from one dataset could be used as priors when evaluating the next dataset but did not address the problem of separate datasets that were previously evaluated independently.

Actual selection may be based on combined information from both datasets. Then, separate analysis of the two datasets followed by an approximate multitrait evaluation may not fully account for the selection. For example, if the breeders in each country selected their animals based on domestic information and ignored foreign data, then a combination of separate analyses within country would not be biased. If breeding stock were selected based on foreign evaluations, the domestic evaluations might not account properly for this selection.

Formally, separate selection on linear functions $\boldsymbol{L}_1\boldsymbol{y}_1$ and $\boldsymbol{L}_2\boldsymbol{y}_2$ might not cause any problems in separate evaluations, but joint selection on the linear function $\boldsymbol{L}_{1,2}[\boldsymbol{y}_1' \quad \boldsymbol{y}_2']'$ may require a joint evaluation. Many national evaluations already are, in fact, joint evaluations because foreign or international information for parents or relatives is included in released national estimates. To combine national evaluations properly, researchers need to know which data were included. Foreign pedigree and foreign EBV may both be needed to account properly for foreign selection.

International Evaluation

Multicountry evaluations are now computed routinely for bulls using the multitrait, across-country evaluation method (**MACE**) (Schaeffer, 1994). National evaluations are combined into Interbull evaluations by BLUP, but the REL of the Interbull evaluations are computed through an SI (Harris and Johnson, 1998). Separate progeny from each country provide for uncorrelated errors across countries. Colleau et al. (2000) presented an approximate BLUP method to combine single-trait evaluations that also can account for residual covariances.

Mixed model equations and BLUP can be avoided if each country supplies parent evaluations along with the national evaluation of each bull. Estimates of MS from each country can be combined through an SI and then added to PA on the scale of that country (VanRaden et al., 2000). This approach can provide MACE evaluations for cows as easily as for bulls.

Domestic evaluations are not available for many foreign parents. If foreign evaluations are converted or combined through an SI into MACE evaluations in age order, parent information always precedes progeny information. Because MS has an expected value of 0 regardless of scale, only the regression (or slope) of the conversion formula is needed to combine MS estimates. The intercept is needed only for the earliest animals with parents that are not included. With this approach, no iteration is needed.

An international relationship matrix is not needed for the SI method because domestic evaluations already include information from all relatives within that country. Information from foreign parents and descendants (if any) is added for each animal and the animal's improved evaluation is incorporated into the evaluations of its domestic descendants. A little information is lost because data from descendants in other countries do not contribute back to the parents of the animal as a result of the order in which the international evaluations are computed.

For each bull or cow, a matrix must be inverted with dimensions equal to the number of countries with progeny records. For 95% of the bulls and perhaps 99% of the cows, only a 1 × 1 inversion is needed. To obtain estimates of MS on 26 national scales, this inverse is premultiplied by a vector of 26 genetic covariances and postmultiplied by the difference between the evaluation of the animal and its PA. National PA from an animal model could be superior to those from the sire-maternal grandsire (**MGS**) model used by the Interbull Centre. A closer connection between national and international evaluations could result from exchange of either PA or the individual evaluations of both sire and dam when the parents are from different foreign countries.

Information Sources

The PTA from an animal model are weighted means of PA for the animal, half of its yield deviation (YD) if present, and progeny contribution (PC) (VanRaden and Wiggans, 1991). Thus,

$$PTA = w_1PA + w_2(YD/2) + w_3PC$$

where w_1, w_2, and w_3 are weights that sum to 1. The variables YD and PC and the exact weights w_1, w_2, and w_3 often are not provided with an evaluation. If only PTA and REL of the animal, its sire, and its dam are provided, the two variables YD and PC, which cannot be obtained directly, can be combined into an estimate of the merit of the animal that is independent of its PA. Similarly, the total DE of the animal (DE_a) can be obtained and then split into DE from PA (DE_{PA}) and DE from progeny and records (D_a as defined earlier as a diagonal element of $\boldsymbol{D}$) so that

$$DE_a = DE_{PA} + D_a.$$

The PTA can be split apart and recombined when new information becomes available for the parents by using methods presented in the section "Updated Parent Information."

Unknown Parents

Information for some sires and dams must be missing in every population because pedigrees do not go back forever. For the earliest ancestors, PA is computed from solutions for unknown-parent groups for the sire (UNK_s) and dam (UNK_d). Estimates of UNK_s and UNK_d are assumed to be expressed as transmitting ability rather than breeding value. If information from either parent is missing, progeny MS is confounded with parent deviation from group mean and is not estimated cleanly in the animal model. A sire or dam may have been treated as known in one dataset and unknown in another but can always be treated as known using the phantom parent idea introduced by Westell et al. (1988).

If both parents are unknown but assumed to be noninbred, only half the variance of the reported MS is the result of true MS, and the other half is the result of parent deviations from group mean. If one parent is unknown, two-thirds of the variance of reported MS is true MS. Estimates of MS that are free of missing parent deviations can be obtained by predicting and removing actual merits of each missing parent. Let PTA_s and PTA_d be sire and dam PTA, respectively. If PTA_s is missing and UNK_s is reported instead,

$$PTA_s = UNK_s + 0.67(PTA - 0.5UNK_s - 0.5PTA_d).$$

If PTA_d is missing and UNK_d is reported instead,

$$PTA_d = UNK_d + 0.67(PTA - 0.5PTA_s - 0.5UNK_d).$$

If PTA_s and PTA_d are both missing,

$$PTA_s = UNK_s + 0.5(PTA - 0.5UNK_s - 0.5UNK_d), \text{ and}$$

$$PTA_d = UNK_d + 0.5(PTA - 0.5UNK_s - 0.5UNK_d).$$

An unknown parent contributes no information to its known progeny, but REL for an unknown parent is greater than 0 because the known progeny contributes information about the parent. Formulas to obtain REL for unknown parents are presented in the section “Updated Parent Information.”

Updated Parent Information

The PTA of an animal and its REL (REL_a) may change if new information is received for the sire or dam. Suppose that updated and previous REL are available for the sire (REL_s), dam (REL_d) and, consequently, REL_{PA}. Although DE_a, DE_{PA}, and D_a usually are not reported, those variables can be backsolved from REL_a and REL_{PA} by algebra similar to that of Misztal and Wiggans (1988) and VanRaden and Wiggans (1991). Reduced REL that exclude the contribution of the animal also are needed for the sire (REL_{s-a}) and dam (REL_{d-a}), but to begin iteration, REL_{s-a} can be set equal to REL_s, and REL_{d-a} can be set equal to REL_d.

The following steps can be used to iterate for DE beginning with either single- or multitrait REL. First, the REL contributed by this animal to its sire (REL_{s_a}) and dam (REL_{d_a}) are used to compute the analogous DE contributed by the animal to its sire (DE_{s_a}) and dam (DE_{d_a}):

$$REL_{s_a} = REL_a/(4 - REL_a\,REL_{d-a}),$$

$$REL_{d_a} = REL_a/(4 - REL_a\,REL_{s-a}),$$

$$DE_{s_a} = k_s REL_{s_a}/(1 - REL_{s_a}), \text{ and}$$

$$DE_{d_a} = k_s REL_{d_a}/(1 - REL_{d_a}).$$

New estimates of DE of parents that exclude DE contributed by the animal are obtained for the sire (DE_{s-a}) and dam (DE_{d-a}) by subtracting DE_{s_a} and DE_{d_a} from the known total DE of sire (DE_s) and dam (DE_d):

$$DE_{s-a} = DE_s - DE_{s_a}, \text{ and}$$

$$DE_{d-a} = DE_d - DE_{d_a}.$$

The DE_{s-a} and DE_{d-a} are used to compute REL_{s-a} and REL_{d-a}:

$$REL_{s-a} = DE_{s-a}/(DE_{s-a} + k_s), \text{ and}$$

$$REL_{d-a} = DE_{d-a}/(DE_{d-a} + k_s).$$

From those REL, the REL and DE for PA are computed with contributions of the animal to its parents excluded: REL_{PA-a} and DE_{PA-a}. Then D_a is obtained by subtracting DE_{PA-a} from DE_a:

$$REL_{PA-a} = (REL_{s-a} + REL_{d-a})/4,$$

$$DE_{PA-a} = k_s REL_{PA-a}/(1 - REL_{PA-a}), \text{ and}$$

$$D_a = DE_a - DE_{PA-a}.$$

When new information becomes available for one or both parents, updated DE_a (DE_a^+) and updated REL_a (REL_a^+) may not be available but must be computed instead. Changes in parent REL have no effect on D_a. Thus, the previous equation can be rearranged to obtain DE_a^+ instead by summing the updated DE_{PA} (DE_{PA}^+) and a converged estimate of D_a obtained from REL_a, REL_s, and REL_d:

$$DE_a^+ = DE_{PA}^+ + D_a, \text{ and}$$

$$REL_a^+ = DE_a^+/(DE_a^+ + k_s).$$

If the REL of either parent is 0, the parent evaluation is assumed to be the solution for an unknown-parent group instead of a PTA. If either the sire or dam is unknown, their total DE are not available. Instead, the reported REL of 0 for unknown parents indicates that the parent DE with the contribution of the animal excluded is 0. True REL for an unknown parent is >0 because data are available for one of its descendants. For unknown parents, REL with the contribution of the animal excluded are 0 because such parents contribute no new information back to the animal. Thus, DE_s is set equal to DE_{s_a}, and DE_d is set equal to DE_{d_a} if the reported REL of the parent is 0.

After the DE and REL equations converge, an updated PTA (PTA^+) can be obtained from the original PTA of the animal and the difference between its updated PA (PA^+) and original PA. If neither the animal, its sire, nor its dam is inbred, this adjustment is

$$PTA^{+} = PTA + (PA^{+} - PA)[2k_s/(2k_s + D_a)].$$

This formula is obtained from the first row of matrix ***C***. The right-hand-side vector ***r*** for the animal is free of parent contributions and is not affected by new information on the merit of parents. Because the first element of ***r*** is a constant, the first row of ***C*** multiplied by the original evaluations of the animal, its sire, and its dam must equal the first row of ***C*** multiplied by their updated evaluations.

Updated Progeny Information

The PTA and REL of an animal also change as more progeny information becomes available. This new information also could cause small changes to the evaluations of the parents of the animal (grandparents of the progeny) or more distant ancestors. Often, REL of sire and MGS are already 99% when grandprogeny data arrive, which leaves little room for improved accuracy of sire and MGS evaluations. Evaluations of dams could improve because REL for dams often are <60%. Larger changes would occur for solutions for unknown-parent groups because a new grandprogeny record could be the only source of information. For simplicity, the PA could be assumed to be constant and the new progeny data to be used only to update the estimated MS of the animal. Alternatively, an SI could be applied to update PA and animal MS simultaneously.

Regressed MS results in simpler SI formulas, whereas deregressed MS results in simpler mixed model equations. Suppose two separate BLUP predictions of MS ($\hat{u}_1$ and $\hat{u}_2$) are available:

$$\hat{u}_1 = PTA_1 - PA_1, \text{ and}$$

$$\hat{u}_2 = PTA_2 - PA_2.$$

Variances of the two predictions (diagonals of variance matrix ***V***) are less than the variance of PTA because of the subtraction of PA:

$$\mathrm{Var}(\hat{u}_1) = (REL_1 - REL_{PA_1})\mathrm{Var}(TA), \text{ and}$$

$$\mathrm{Var}(\hat{u}_2) = (REL_2 - REL_{PA_2})\mathrm{Var}(TA),$$

where TA = true transmitting ability. Vector ***c***, the covariance of the two predictions with true MS (u), is easy to obtain because covariance of predictions and true effects equals variance of predictions:

$$\mathrm{Cov}(\hat{u}_1, u) = \mathrm{Var}(\hat{u}_1), \text{ and}$$

$$\mathrm{Cov}(\hat{u}_2, u) = \mathrm{Var}(\hat{u}_2).$$

Off-diagonals of ***V*** are approximated with algebra similar to that of Weigel et al. (1998) and Harris and Johnson (1998). The main difference is the use of MS instead of PTA as data. Also, $\hat{u}_1$ and $\hat{u}_2$ are assumed to estimate the same trait u; formula changes for multiple traits are shown in the section “Correlated Traits.” If $\hat{u}_1$ and $\hat{u}_2$ are obtained from completely independent sets of progeny, then

$$\mathrm{Cov}(\hat{u}_1, \hat{u}_2) = \mathrm{Var}(\hat{u}_1)\mathrm{Var}(\hat{u}_2)/\mathrm{Var}(u).$$

If the two sets of progeny are not independent, a constant d is introduced to account for their correlation as in Weigel et al. (1998). This constant depends on D_a for each estimate (D_{a1}, D_{a2}), the number of DE in common ($D_{a1,2}$), and the variance ratio k. Because a genetic correlation of 1, equal heritabilities, and equal error variances are assumed for the single trait in the two progeny datasets:

$$d = 1 + kD_{a1,2}/(D_{a_1}D_{a2}).$$

The constant d is multiplied by $\mathrm{Cov}(\hat{u}_1, \hat{u}_2)$ for independent progeny sets to account for lack of independence between progeny sets:

$$\mathrm{Cov}(\hat{u}_1, \hat{u}_2) = d\mathrm{Var}(\hat{u}_1)\mathrm{Var}(\hat{u}_2)/\mathrm{Var}(u).$$

Note that d would have been 1 if the progeny sets had been independent because $D_{a1,2}$ would have been 0; therefore, the formula for $\mathrm{Cov}(\hat{u}_1, \hat{u}_2)$ for data with correlated errors reduces to the formula for independent data.

Weigel et al. (1998) presented covariance formulas equivalent to those equations except that estimates of true transmitting abilities were combined instead of estimates of MS. Harris and Johnson (1998) presented formulas equivalent to the $\mathrm{Cov}(\hat{u}_1, \hat{u}_2)$ formula for independent data except that they considered genetic correlations of <1, which is addressed in the section “Correlated Traits.”

Correlated Traits

The predictions $\hat{u}_1$ and $\hat{u}_2$ may be estimates of correlated traits (u_1 and u_2) instead of the same trait (u). Most formulas of the previous section remain unchanged, but a few formulas must be modified to account for correlations of <1. Covariance of the two true effects (g_{12}) replaces $\mathrm{Var}(u)$. The ratio of error covariance to genetic covariance for the two traits ($c_{1,2}$) and the constant d are obtained from the h^2 of the two traits (h_1^2, h_2^2), their phenotypic correlation, and their genetic correlation:

$$c_{1,2} = 4[\mathrm{Corr}(y_1, y_2)/(h_1^2 h_2^2)^{0.5}] - \mathrm{Corr}(u_1, u_2), \text{ and}$$

$$d = \mathrm{Corr}(u_1, u_2) + c_{1,2}D_{a_{1,2}}/D_{a1}D_{a2}.$$

Harris and Johnson (1998) tested a similar SI procedure to compute REL of MACE evaluations. For this case, no daughters are tested for both traits; therefore, $D_{a1,2} = 0$, and the formula is simpler. Their estimated REL were correlated to true REL by 0.99 and were higher on average by only 1%.

With more than two traits, subsets of the traits may already have been evaluated with multitrait methods. For example, multitrait PTA for milk, fat, and protein may account for correlations within that subset of traits, and PTA for type traits may account for correlations within the type traits; however, correlations among the two subsets of traits were ignored. For any two traits included in the same multitrait system of equations, covariance of the estimate for trait i and the true MS for trait j is set equal to the covariance of the estimates for traits i and j. This causes elements of ***c*** and $\boldsymbol{V}^{-1}$ to cancel so that PTA are not updated for correlations with other traits that already were included in a multitrait analysis.

Table 2. Comparison of single-trait and multitrait evaluations of productive life.

Evaluation method	Breed	Gender	Birth year or animal status	Evaluation year	Mean PTA Single-trait	Mean PTA Multi-trait	Mean reliability Single-trait	Mean reliability Multi-trait
					--------(mo)-------		--------(%)--------	
Previous SI[1,2]	Holstein	Bulls	1989 through 1990	1994	0.83	1.19	50	53
MACE[3,4]	Holstein	Bulls	1989	1996	0.83	1.00	54	73
New SI	Jersey	Bulls	1990 through 1995	1999	0.66	0.62	52	58
			Active AI	1999	1.69	2.12	53	63
	Holstein	Bulls	1990 through 1995	2000	0.60	0.50	58	65
			Active AI	2000	0.85	1.10	56	66
		Cows	1995 through 1997	2000	0.61	0.66	28	31
			Elite	2000	1.36	1.58	33	39

[1] Selection index.

[2] Weigel et al., 1998.

[3] Multitrait, across-country evaluation.

[4] Weigel, 1996.

DATA

International Data

Eight of the national evaluation centers listed in Table 1 provided sire and dam evaluations and sire and dam REL for their bulls that were included in February 2000 Interbull evaluations. The Interbull Centre supplied the national input records for February 2000 and applied the current MACE methods to the eight-country subset. Bull evaluations for the eight countries were then computed by the new SI method to investigate differences for protein yield. A few bulls were not included in the SI approach because of missing sire or dam evaluations or REL. Comparisons of the two approaches included 35,414 bulls that had data in the same number of countries for both SI and BLUP.

Correlated Trait Data

Single-trait evaluations for PL, yield, SCS, and composite type traits are combined into multitrait PL beginning with August 2000 evaluations. Since July 1994, PL, yield, and type evaluations have been combined into multitrait PL evaluations (Weigel et al., 1998) by Holstein Association USA (Brattleboro, VT). The calculations can now be moved to the Animal Improvement Programs Laboratory (**AIPL**), ARS, USDA (Beltsville, MD), because Holstein composite traits will be sent to AIPL before release day for use in computing the net merit index. The composite trait evaluations are actually multitrait evaluations and include correlated information from other type traits but not from yield, PL, or SCS.

New SI programs based on the methods of Weigel et al. (1998) were applied to both bull and cow evaluations. Major differences from the previous SI programs used by Holstein Association USA are that PTA for SCS are included in predictions and that predictions of PL begin with PA for PL and only adjust the MS for information from correlated traits of progeny. Minor differences are that the udder composite, foot and leg composite, and body size composite are used in predictions instead of all 17 individual linear traits. Also, all three yield traits (milk, fat, and protein) are used in predictions instead of the two traits (milk and fat) used previously.

RESULTS

International Results

For the 35,414 Holstein bulls from eight countries, MACE evaluations using the SI procedure required 1.5 min of computation for each trait (milk, fat, and protein yields). Correlations between SI and BLUP protein evaluations of bulls ranged from 0.989 to 0.993 on the eight-country scales. The SI evaluations were more consistent across countries; correlations for all country pairs ranged from 0.994 to 0.999 as compared with correlations of 0.987 to 0.996 with BLUP. The use of a linear regression across time instead of estimation of separate unknown-maternal granddam groups within time periods could explain this difference.

Bull REL from the SI approach were higher than Interbull REL by a mean of 6%, and REL from the two methods were correlated by only 0.908 to 0.977 on the eight-country scales. As a test of differences, dam REL was limited to a maximum of 25%, which would have been the maximum possible if MGS REL had been used as a substitute for dam REL. Mean difference in REL declined to about 3%; correlations increased greatly and ranged from 0.977 to 0.993. As another test, conversion formulas were applied to bulls evaluated in only one country, and an SI was applied to bulls evaluated in multiple countries. The converted REL (foreign REL multiplied by genetic correlation squared) were closer than SI REL to official REL. Mean difference between converted and official bull REL was 3% when dam REL was included and <1% when dam REL was limited to 25%.

Simple conversion formulas gave nearly the same evaluations as the SI method for most bulls. Advantages for an SI are greatest when two or more countries each provide evaluations with moderate REL. Some other differences among conversion formulas, SI, and BLUP may deserve further investigation, but use of either conversion formulas or the SI approach to provide combined international evaluations for cows seems feasible. Combined cow evaluations could be provided but would require minimum standards for publication, and the rankings provided would be less accurate than for progeny-tested bulls.

Correlated Trait Results

Evaluations for PL from single-trait and approximate multitrait procedures are compared in Table 2. The gain in REL from the new SI procedure is higher than from the previous SI method (Weigel et al., 1998) and is closer to the REL from MACE reported by Weigel (1996). The REL from MACE reported by Weigel (1996) could be too large because the correlated traits were assumed to be from independent daughters instead of from the same daughters as for PL. The previous SI programs for PL did consider the covariances among traits measured on the same daughters but used regression on PTA without removing parent contribution. The REL from this approach was lower because the indirect evaluations of parents replaced their direct evaluations whenever indirect traits of daughters were included. The MACE approach uses the direct pedigree index and regression of the bull to adjust for the difference of the correlated traits from pedigree index. The new SI programs use PA instead of the pedigree index and then apply regressions to the MS.

For bulls in active AI service, multitrait PTA for PL were higher than single-trait PTA as expected. However, for all bulls and cows, little difference was found in mean PTA between single- and multitrait evaluations. For the new SI method, single-trait and multitrait PTA were correlated by 0.85; the corresponding correlation for the previous SI method was 0.95. The previous multitrait PTA were correlated by only 0.88 to the new multitrait PTA. Those correlations are consistent with the larger gains in REL from the new SI procedure. With the previous SI approach, any use of indirect PL for daughters also forced the use of indirect PL for the parents. This use of indirect PL for parents limited the gain in bull REL because most sires had a direct REL of 99%, whereas their indirect REL might have been only 60%.

Because conformation traits and SCS are missing for some relatives, the new programs were also tested for upgrading single-trait PTA for SCS and udder composite to multitrait PTA using correlated information from all other traits. For bulls, the mean REL increased only from 68.6 to 68.9% for SCS and from 77.9 to 78.1% for udder composite. For cows, REL went from 32.8 to 33.2% for SCS and from 30.0 to 31.6% for udder composite. The small gains in evaluation accuracy for those traits did not justify the added computing complexity and disk storage that would be required for routine evaluations. Except for PL, a multitrait evaluation for any trait was computed only when an animal had no records and no progeny and, therefore, no single-trait evaluation for that trait. Comparisons in Table 2 reflect genetic correlations used for August 2000 computations rather than the revised genetic correlation matrix used in November 2000. Advantages of the new methods were less in subsequent evaluations when genetic correlations were reduced.

The time required to obtain PA for the eight traits, to estimate MS for PL from MS of correlated traits, to adjust progeny PTA for PL for multitrait PTA of parents, and to compute net merit for all bulls and cows was 17 h. Evaluations of all eight traits were loaded into memory at the start of the program because disk access to parent evaluations was too slow (nearly 3 d). All of those steps were completed in one pass of the data that were ordered by age of the animals, but the SI method also can be applied to upgrade single-trait to multitrait evaluations for each animal separately.

CONCLUSIONS

An SI is a simple and accurate method to combine information from separate sources. For any number of traits, single-trait evaluations can be combined into multitrait evaluations. When estimates of MS are used as the data source, environmental effects and genetic trend already are removed and thus few fixed effects need to be estimated. The matrices used in a SI approach are smaller than those used in BLUP if the data vector is shorter than the solution vector. In MACE, solutions may be needed for 25 or more nations even though most bulls have progeny in just one country.

Methods to combine national evaluations using sire and dam information with an SI method were compared with current procedures that use sire and MGS information with BLUP procedures. Differences were fairly small, and correlations were about 0.99 for the scale of each country. Bull REL that included dam contribution instead of only MGS information were higher and should agree more closely with national REL from animal models.

The SI approach could be used to provide MACE evaluations for cows and could provide a closer connection between national and international evaluations. The current BLUP model includes information from foreign daughters but excludes information from foreign dams. However, many more bulls have foreign dams than foreign daughters. A MACE evaluation system for cows would allow foreign information to be transferred among the national evaluations without relying on a single international animal model. In either case, centralized processing of female evaluations by Interbull should be more efficient than two-way exchange of data files between each of the national centers.

Multitrait evaluations of longevity for US bulls and cows were improved through a new SI method. Gains in REL were larger than for the previous SI method because the new approach could include both the direct PL evaluations of parents and the correlated traits from progeny and the records of the animal.

The SI method is approximate and may not account for the effects of selection as precisely as a combined analysis of all data. If separate datasets are combined, more uniform statistical methods can be applied. If data are analyzed separately and then results combined, different models that are better adapted to the needs of each trait or country can be applied. Both methods can include information from several sources instead of just one. Meta-analysis and approximate methods are useful if exact methods to combine all data are difficult.

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