Approximate Reliability of Genetic Evaluations Under an Animal Model

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ABSTRACT

A method was developed for calculating approximate reliability for national systems of evaluation. The method combined the reliability of three information sources: parent average, animal's own records, and progeny records. This method provided good approximation to the actual values with minimal upward bias and was considerably better than the current national method of New Zealand genetic evaluation or Meyer's method for all accuracy measures. Our method had an average absolute bias of 0.006 compared with 0.026 and 0.035 for the current national method and Meyer's method, respectively. Our method was less computationally demanding than the current New Zealand method. One of the major advantages of the method is that it can be extended to accommodate more complex models by altering the selection index equations within the method. An example is given for which the method was extended to account for a genetic correlation other than unity between an incomplete lactation and a complete lactation yield.

(**Key words**: animal model, reliability, continuous evaluation)

Abbreviation key: **AM** = animal model, **IS** = information source, **ISNG** = IS method for genetic correlations other than unity, **MME** = mixed model equations, **NZ** = New Zealand, **PEV** = prediction error variance.

INTRODUCTION

For national genetic evaluation of dairy cattle, animal model (**AM**) BLUP is widely used. In most instances, the genetic evaluation of an animal is provided along with a measure of the reliability of the genetic evaluation. The reliability is a measure of the amount of information that has contributed to the genetic evaluation and can be used to derive confidence intervals for the estimated breeding value. The

reliability is directly related to the prediction error variance (**PEV**). The PEV in theory can be obtained from the diagonal elements of the inverse of the mixed model equations (MME). The MME for most national genetic evaluations range from 100,000 to 20,000,000 equations. Inversion of systems of equations of this size is generally not feasible because of their magnitude or because of loss of numerical precision. Four methods have been advanced for approximating the PEV under AM BLUP (1, 6, 7, 10). These methods are based on the approximation of the diagonal element of the inverse MME for each animal by absorbing information through the relationship matrix. Koots et al. (5) have presented a method using an equivalent number of progeny; however, the details of this method were not given. VanRaden and Wiggans (10) demonstrated an equivalent way to incorporate information via relationships for their method and the methods of Meyer (6) and Misztal et al. (7). Boichard and Lee (1) extended the method of Meyer to account for close inbreeding, covariance among contemporaries, and distribution of relatives among herds. The method of Boichard and Lee reduced the upward bias in the approximate PEV compared with that of the Meyer method (6). However, the method of Boichard and Lee is not extendable to repeatability AM BLUP or other more general implementations of AM BLUP.

This study developed a method for computing the approximate reliability of the estimated breeding values that would be suitable across a number of different AM BLUP implementations, in particular, with a repeatability single-trait AM BLUP that is currently used for national genetic evaluations in New Zealand (NZ) (3). To adapt to the continuous genetic evaluation system employed in NZ, the method had to be extended to include a genetic correlation other than one between lactation yields that were calculated from varying numbers of herd test samples. The current method for computing reliability uses lactation weight information (3); however, the reliability estimates are overstated for sires and cows with evaluations based on incomplete lactation information. A reduction in the upward bias in the reliability from that of current methods would be

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desirable. The method was required to be computationally feasible for large systems of MME equations (>10,000,000).

MATERIALS AND METHODS

The actual reliability for a breeding value estimate from a repeatability single-trait AM BLUP is calculated as

$$R = 1 - \lambda_g c^{ii}$$

where $\lambda_g = (1 - r)/(h^2)$, c^{ii} is the diagonal element of the inverse of MME for animal i, and r is repeatability. A method is proposed that uses the reliability of three information sources: parent average, animal's own records, and progeny records. Two general equations are required; first, the reliability of two pieces of information (x and y) could be expressed in terms of the individual reliabilities as

$$R(x + y) = \frac{R(x) + R(y) - 2R(x)R(y)}{1 - R(x)R(y)}.$$
 [1]

This relationship holds when two information sources from selection index theory are combined. Second, by a rearrangement of Equation [1], the reliability of one piece of information (x) given the reliability of two pieces of information (x and y) and the reliability of the other single piece of information (y) is calculated as

$$R(x) = \frac{R(x + y) - R(y)}{R(x + y)R(y) + 1 - 2R(y)}.$$
 [2]

The calculation of the AM BLUP reliability requires four steps:

- 1. Calculate reliability based on own records.
- 2. Calculate reliability based on progeny records.
- 3. Incorporate information on progeny's progeny.
- 4. Incorporate information on parent reliability.

Step 1. To calculate reliability based on an animal's own records, selection index equations can be used. First, the major fixed effect (e.g., herd-year-age-season) is absorbed from each record when the effective number of records (n) are computed for an animal:

$$n = \sum_{i=1}^{l} (1 - \frac{1}{ncg_i})$$

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where $ncg_i = number$ of records in contemporary group i, and l = number of repeated measures. The reliability based on animal's own records assuming a simple repeatability model is calculated as

$$R(o) = \frac{nh^2}{1 + (n - 1)r}.$$
 [3]

Step 2. While the reliability based on own records is being calculated, the number of progeny with records and the number of records on each progeny are accumulated for each parent. The reliability based on progeny is calculated using selection index as

$$R(p) = \frac{\bar{n}h^2m}{4 + (m - 1)\bar{n}h^2 + 4(\bar{n} - 1)r}$$
[4]

where \bar{n} = average number of records per progeny adjusted for the major fixed effect, and m = number of progeny with records. The reliability based on progeny does not include grandprogeny, great grandprogeny, or other generations of progeny. This information can be incorporated by updating the reliability based on the animal's progeny for the progeny reliability of each progeny of the animal (i.e., grandprogeny information). The process works from the youngest parent to the oldest parent to allow all generations to be incorporated. The progeny reliability of each parent is updated for each offspring as

$$R(p) = \frac{R(p) + \frac{1}{4}R_{i}(p) - \frac{1}{2}R(p)R_{i}(p)}{1 - R(p)\frac{1}{4}R_{i}(p)}$$
[5]

where $R_i(p)$ is the progeny reliability for offspring i of that animal. This process is repeated for each offspring of the animal.

Step 3. The reliability based on all progeny and own records is combined. The reliability based on own records and progeny is calculated as

$$R(o + p) = \frac{R(o) + \frac{1}{4}R(p) - \frac{1}{2}R(o)R(p)}{1 - R(o)\frac{1}{4}R(p)}$$

Step 4. The final step is to include information on the parents in the reliability of the animal. The process works from the oldest animal to the youngest animal to allow all generations to be incorporated. For a given animal, the reliability of a parent (pt) of that animal includes information on the animal's own records and the progeny of the animal. In order to calculate the contribution to the reliability of the animal from the parent average (pa), this information must first be removed from the parent reliability:

$$R_{i}(pt) = \frac{R_{i}(pa + o + p) - \frac{1}{4}R(o + p)}{R_{i}(pa + o + p)\frac{1}{4}R(o + p) + 1 - \frac{1}{2}R(o + p)}$$

where i is sire or dam. The parent average reliability is calculated as (assuming the sire and dam are unrelated)

$$R(pa) = \frac{1}{4} (R_{sire}(pt) + R_{dam}(pt))$$

The total reliability of the animal with one or two parents known and including all information is calculated as

$$\frac{R(pa + o + p) =}{\frac{R(o + p) + R(pa) - 2R(pa)R(o + p)}{1 - R(o + p)R(pa)}}$$

For the oldest animals, the sire and dam are unknown, and R(pa + o + p) = R(o + p) because R(pa) = 0 (unknown parents).

The calculation of the reliability for the producing ability of a cow, the sum of estimated breeding value and the estimated permanent environmental effect, can be easily calculated from the equations just given by adding one more step, as is shown in Appendix 1.

Computing Strategy

Two passes of the data file are required. First, the diagonal elements for the major fixed effect were built, and the sire and dam identifications were stored in memory; second, the reliability based on an animal's own records (step 1) is computed. At the same time, the number of progeny and the total number of progeny records are accumulated for the parent animals. The reliability based on the immediate progeny is computed from each parent. Next, the progeny information from future generations is incorporated (step 2) iterating from the youngest to oldest animal; the sire and dam identifications were retrieved from memory. The reliability from progeny information and own records are combined (step 3). Each animal updates the reliability of its parents if that animal has progeny. Finally, the parent information is incorporated (step 4) by iterating from the oldest to youngest animal ignoring animals for which both parents were unknown; the sire and dam identifications were retrieved from memory.

Accounting for Incomplete Lactation Records in Continuous Evaluation

The procedure just described assumes that each record contributes an equal amount of information. This assumption is not true when yields are based on varying numbers of herd tests that are extended to complete lactation yields. The genetic correlation between the true lactation yield and a prediction of that yield, based on a number of herd tests, approaches unity as the number of tests increases. With four or five tests spread evenly over the lactation, the genetic correlation is close to 1, but, for a single herd test, the genetic correlation could be typically around 0.88, depending on the stage of lactation (4). The reliability of the breeding value should not exceed the square of the genetic correlation (0.77 for the single test example). The advent of continuous national genetic evaluation in NZ combined with the seasonal calving pattern required that the proposed method be extended to account for the genetic correlations for partial lactation so that, in particular, sire reliabilities were not overstated at the start of the season. To account for this situation, Equations [3] and [4] were altered to accommodate a multivariate approach to selection. This alteration was achieved by classifying records according to the number of herd tests making up that record and using covariances appropriate to partial lactation information. The reliability based on animal's own records (R(o)) is

$$R(o) = g'_{own} P^{-1}_{own} g_{own},$$
$$g_{own} = \begin{bmatrix} g_{1q}h \\ \vdots \\ h \end{bmatrix},$$

and

$$P_{own} = \begin{bmatrix} \frac{x_i + (n_1 - 1)r}{n_1} & \dots & r \times g_{1q} \\ \vdots & \ddots & \vdots \\ r \times g_{q1} & \dots & \frac{x_q + (n_q - 1)r}{n_q} \end{bmatrix}$$

where x_i = expansion factor used to expand a partial lactation yield based on i herd tests to a complete lactation yield (4), g_{ij} = genetic correlation between a lactation yield based on i herd tests and a lactation yield based on j herd tests, and q = the number of partial lactation categories. The reliability based on progeny using Equation [4] was calculated within the partial lactation categories. Equation [5] was used within partial lactation categories to include the reliability information on grandprogeny, great grandprogeny, or other generations of progeny. The progeny reliabilities (R(p)) calculated with partial lactation categories were combined, taking into account the genetic correlations by

 $R(p) = g' \cdot P^{-1} \cdot g$

where

$$g = \begin{bmatrix} g_{1q}R_1(p) \\ \vdots \\ g_{jq}R_j(p) \\ \vdots \\ R_q(p) \end{bmatrix},$$

and

$$P = \begin{bmatrix} R_1(p) & \cdots & g_{1j}R_1(p)R_j(p) & \cdots & g_{1q}R_1(p)R_q(p) \\ & \ddots & & \vdots \\ g_{1j}R_1(p)R_j(p) & R_j(p) & g_{qj}R_q(p)R_j(p) \\ & \ddots & \vdots \\ g_{1q}R_1(p)R_q(p) & \cdots & g_{jq}R_j(p)R_q(p) & \cdots & R_q(p) \end{bmatrix}$$

Step 3 was used to combine the animal's own records with progeny, and the parent reliabilities were included using step 4.

TABLE 1. Data set characteristics.

Characteristics	Number	
Animals	5005	
Males	614	
Females	4391	
Records	13,556	
Levels of major fixed effect	391	
Parentage		
Known sire and dam	2009	
Known sire only	896	
Known dam only	208	
Unknown sire and dam	1892	
Males progeny number		
1 to 5	515	
6 to 10	40	
11 to 20	29	
>20	30	
Females		
Records only	2255	
Progeny only	1068	
Records and progeny	1068	

TABLE 2. Accuracy of the approximation methods 1 for calculating reliability.

	Meyer	National	IS
Average reliability ²	0.448	0.407	0.411
Average absolute bias	0.035	0.026	0.006
Regression slope ³	0.950	0.983	0.999
Correlation with true value	0.975	0.974	0.998
Standard deviation of the bias	0.049	0.054	0.014

 $^1\!Meyer$ = Method based on Meyer (6), National = current method used for genetic evaluation in New Zealand, and IS = information source method.

²Actual average = 0.414.

 $^{3}\text{Coefficient}$ for simple linear regression with the intercept constrained to 0.0.

Materials

The proposed method, denoted as the information source (IS) method, was compared with the method of Meyer (6) allowing for the absorption of the permanent environmental effects (8), the current method used for the NZ national genetic evaluation system (3), and actual reliabilities computed from the direct inverse of the MME. The current calculation of reliability in NZ is based directly on Meyer's method but ignores relationships that are not connected to records to reduce the upward bias. The data consisted of 13,556 lactation records from 1986, 1987 to 1997, and 1998 and 5005 animals from NZ herds with a history of artificial insemination usage. The 5005 animals included all recorded ancestors back to 1940. The contemporary group size ranged from 2 to 98, and the average group size was 36.2. The amount of missing pedigree information and the contemporary group sizes and distributions were consistent with the national NZ data set used for genetic evaluation. The main characteristics of the data are given in Table 1. Heritability was set at 0.35, and repeatability was set at 0.60.

The national NZ data set was used to compare the adjustment for incomplete lactations with the current national method and the IS method. The national data set comprised 10,262,807 animals and 622,025 contemporary groups for herd-year-season-age. The current method used for the NZ national genetic evaluation system and the method of Meyer accounted for the lactation weight information (4) to calculate the diagonal after absorption of the permanent environment and contemporary group effects.

RESULTS

Table 2 shows the accuracy of each approximation method. Clearly, the IS method is considerably better

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TABLE 3. Trends in average absolute bias as actual reliability increased. $^{\rm 1}$

Range	Number	Meyer	National	IS
00-10	550	0.096	0.039	0.015
10-20	622	0.072	0.057	0.013
20-30	309	0.084	0.078	0.010
30-40	207	0.041	0.049	0.011
40-50	528	0.016	0.014	0.004
50-60	2126	0.012	0.012	0.003
60-70	629	0.011	0.011	0.003
70-80	18	0.039	0.019	0.010
80-100	18	0.021	0.013	0.005

 1 Meyer = Method based on Meyer (6), National = current method used for genetic evaluation in New Zealand, and IS = information source method.

than the current NZ national method and Meyer's method in all of the accuracy measures. The current NZ national method provides an improvement in the average absolute bias and regression slope over Meyer's method but is as efficient as Meyer's method for the other accuracy measures. The measures of accuracy for the Meyer and NZ national methods show greater loss in efficiency than those reported by Boichard and Lee (1); however, the inclusion of repeated records rather than single records results in a greater number of terms being ignored in the approximations.

The trends in the average absolute bias as reliability increased were examined. Table 3 provides the average absolute bias for the three methods for 0.10 increments in the average actual reliability. Biases were greater in the low reliability ranges. In all cases, the biases were larger for animals without records and no immediate progeny, but with grandprogeny. This result is consistent with results of Boichard and Lee (1); in this study, the bias in reliability approximations increased as the number of known parents and the number of generations of ancestry increased. Meyer's method overestimated the reliability of these animals, and the national method underestimated the reliability. In all cases, the bias in reliability was lowest for cows with lactation records and for sires with large numbers of progeny.

Table 4 provides a comparison of the current NZ national method, IS method, and the IS method accounting for a genetic correlation other than unity (**ISNG**) between a yield from an incomplete lactation and a yield from complete lactation. All methods were computationally feasible when used on large amounts of data. Because the IS method only required two passes of the data, IS was the most efficient in terms of computer time and memory; the ISNG method was the least efficient because of the large number of matrix inversions (12 million 4×4 matrices) assuming four partial lactation categories. The average reliability for all of the animals was similar for all methods. The average reliabilities for three groups of animals affected most by the inclusion of genetic correlations, other than unity, among incomplete lactations and complete lactation yield are given in Table 4. The average number of herd tests was 1.15 tests per cow for 1997-1998 season compared with 3.79 herd tests for lactations in the 1996-1997 season. The ISNG method produced the lowest average reliabilities for the three classes of animals, and the national and IS methods provided similar average values. The largest decrease in average reliability between ISNG and the other two methods occurred for reevaluated sires, who had 50 to 90 daughters with complete lactations and up to 35,000 second-crop daughters with incomplete lactations in the season 1997 to 1998. Compared with the ISNG method, the other two methods do not bound the information from the second-crop daughters to the square of the genetic correlation between the incomplete and complete lactation, a value of 0.77 for lactation yields based on one herd test. The correlations between the reliabilities produced by the three methods (Table 4) ex-

TABLE 4. Comparison of methods¹ for calculating approximate reliability using the New Zealand national data set.

	National	IS	ISNG
Computer time, min:s ²	7:07	4:06	8:27
Memory requirements, MB	178	169	223
Average reliability all animals	0.428	0.427	0.401
Average reliability first			
lactation cows ³	0.418	0.414	0.346
Average reliability first			
evaluation sires ³	0.466	0.452	0.422
Average reliability reevaluated			
sires ³	0.944	0.920	0.857
Correlation first lactation cows			
National		0.99	0.99
IS			0.99
Correlation first evaluation sires			
National		0.98	0.95
IS			0.99
Correlation reevaluated sires			
National		0.92	0.90
IS			0.98

 1 National = Current method used for genetic evaluation in New Zealand, IS = information source method, and ISNG = IS method accounting for genetic correlations other than unity between incomplete lactation yields and complete lactation yields.

²Elapsed processing time.

³Based on lactation information up to the end of October 1997 containing on average 1.15 herd tests per cow in the season 1997 to 1998.

hibited a consistent trend; the highest values were between the IS and ISNG methods, and the lowest values were between the national and ISNG methods for the three classes of animals. The correlations suggest that relative ranking of animals on reliability with IS and ISNG methods are close; however, the average is reduced by the ISNG method.

DISCUSSION

A method has been outlined for calculating the approximate reliability for national evaluation systems based on combining the reliability of three information sources, parent average, animal's own records, and progeny records. The method provides a good approximation with minimal upward bias compared with methods that use adjusted diagonal elements of the MME to approximate reliability. When applied to a repeatability AM, the method was computationally less demanding than current approximate methods for the NZ national genetic evaluation, which comprise over 10 million animals. The method does not account for inbreeding or the distribution of relatives in contemporary groups, which were addressed by Boichard and Lee (1) for a single record AM. The IS method may be less suitable for applications where there are a large number of small contemporary groups containing related animals or in populations with a large number of inbred animals.

One of the major advantages of this method is the ease with which it can be extended to accommodate more complex models by altering the selection index equations. An example has been provided of such an extension, which made it possible to account for genetic correlations other than unity among incomplete lactation and complete lactation yields. Another possible extension would be the application of this method to multiple across-country evaluations (9). The selection index equations would be used to calculate the reliability for a sire based on daughter information in a number of countries, taking into account the genetic correlations among countries. The progeny information and then the parent information would be combined as described, adjusting the coefficients in the equations for use with a maternal grandsire rather than a dam. This procedure would be repeated country by country to compute the reliabilities for a sire in each country. This approach would have the advantage in that the reliability for sires without information in the country of interest would be bounded by a function of the square of the betweencountry genetic correlations in which the sires had information. The approach could be compared with a method discussed by Graser and Tier (2) as a multiple-trait sire model.

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APPENDIX 1

Reliability of Producing Ability

Having calculated the reliability for the breeding value, calculating the reliability of producing ability is a simple task. The reliability for the breeding value is subdivided into two components, reliability of own records and reliability of parents and progeny:

$$R(pa + p) = \frac{R(pa + o + p) - R(o)}{R(pa + o + p)R(o) + 1 - 2R(o)}$$

The reliability of the producing ability based on own records is calculated using selection index equations as

$$R_{pab}(o) = \frac{nr}{1 + (n - 1)r}$$

The complete reliability of the producing ability is calculated by combining the reliability of the producing ability based on own records with the reliability based on progeny and parent information using Equation [1].

$$\frac{R_{pab}(pa + o + p) =}{\frac{h^2}{r}R(p + pa) + R_{pa}(o) - 2\frac{h^2}{r}R_{pab}(o)R(p + pa)}{1 - \frac{h^2}{r}R(p + pa)R_{pab}(o)}$$