The Effective Daughter Contribution Concept Applied to Multiple Trait Models For Approximating Reliability of Estimated Breeding Values

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Introduction

Recent development of international genetic evaluation has been focused on using performance records, instead of deregressed national estimated breeding values (EBV) (Weigel et al., 2000). Lactation yield deviations (LYD) on a 305-day basis, which have been adjusted for all fixed effects and heterogeneous herd variances within each country, can be used as an alternative to raw performance records for international evaluations. Since lactations can have variable length, a measure of accuracy of LYD needs to be developed. For the purpose of approximating reliability of EBV in large scale national genetic evaluation, daughter equivalents (DE) concept (VanRaden and Wiggans, 1991) has been shown to be reasonably accurate. In recent years several new methods have been proposed, e.g. information source method (Harris and Johnson, 1998), effective daughter contribution (Interbull, 2000; Fikse and Banos, 2001), and progeny equivalents (Koots et al., 1997; Jamrozik et al., 2000), but they are indeed closely related to DE. Although effective daughter contribution (EDC) or DE have been widely used for single trait models, its extension to multiple trait models is either limited to special cases (Gengler and Misztal, 1996; Strabel et al., 2001) or the information from multiple traits is combined at a rather early stage (Graser, 1997; Jamrozik et al., 2000), which leads to unnecessary loss of information. Therefore, the objectives of this research are to develop a general EDC concept for multiple trait models to approximate reliability of EBV, and to apply it to compute accuracy of LYD from genetic evaluations with test day models and to compare EDC from single and multiple trait models.

Methods

The theory of EDC or DE is based on the concept of equivalent animal and sire models. A multiple trait animal model can be written in a general form:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Za} + \mathbf{e} \qquad [1]$$

where $\mathbf{y}$ is a vector of phenotypic values of t traits for an animal, $\mathbf{b}$ represents all fixed effects affecting the traits, $\mathbf{X}$ is the design matrix for $\mathbf{b}$, $\mathbf{a}$ is a vector of additive genetic effects of the animal, $\mathbf{Z}$ is the design matrix for $\mathbf{a}$, and $\mathbf{e}$ is a vector of residual effects that contains all random effects but $\mathbf{a}$. Let $\mathbf{G_0}$ and $\mathbf{R_0}$ represent (co)variance matrices for additive genetic and residual effects of the t traits, respectively. The animal model [1] can be re-written into an equivalent sire model:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Z_s s} + \varepsilon \qquad [2]$$

where $\mathbf{s}$ is a vector of additive genetic effects of the sire, $\mathbf{Z_s}$ is the design matrix for $\mathbf{s}$, and ε is a vector of residual effects of the sire model. Let $\mathbf{G_s}$ and $\mathbf{R_s}$ represent respectively (co)variance matrices for sire and residual effects of the sire model. Assuming that models [1] and [2] are equivalent, $\mathbf{G_s} = \frac{1}{4}\mathbf{G_0}$ and $\mathbf{R_s} = \frac{3}{4}\mathbf{G_0} + \mathbf{R_0}$. According to the EDC concept, all animals are treated as if they were a *standard sire*, which is defined as an animal having no known parents and no own performance records but only daughter information, in order to approximate reliability of EBV. Further it is assumed that the whole population is comprised of a single half-sib

family and all daughters of the sire have their dams missing for estimating EBV of the sire. Thus the mixed model equations (MME) for estimating breeding values of the sire, after absorbing all fixed effects and other random effects, are:

$$(\mathbf{Z_s'W_sZ_s + G_s^{-1})\hat{s} = Z_s'W_sy} ,$$

where $\mathbf{W_s = R_s^{-1} - R_s^{-1}X(X'R_s^{-1}X)^- X'R_s^{-1}}$.

Let $\mathbf{C = (Z_s'W_sZ_s + G_s^{-1})^{-1}}$, then reliability values of multiple trait EBV for this sire are:

$$\begin{aligned}
\mathfrak{R}_s &= \mathbf{G_s^{-1}(G_s - C) = I - G_s^{-1}C =} \\
&\quad \mathbf{I - G_s^{-1}(Z_s'W_sZ_s + G_s^{-1})^{-1} =} \quad [3]\\
&\quad \mathbf{I - (Z_s'W_sZ_sG_s + I)^{-1}}
\end{aligned}$$

The equivalent form of equation [3] for single trait models is:

$$R^2 = 1 - \sigma_s^{-2}(n\sigma_e^{-2} + \sigma_s^{-2})^{-1} = n/(n+k) \qquad [4]$$

where $k = \sigma_e^2/\sigma_s^2$, and σ_s^2 and σ_e^2 are sire and residual variances of a single trait sire model, respectively.

Multiple trait reliabilities can be transformed back to EDC using:

$$\mathbf{\Psi = Z_s'WZ_s = [(I - \mathfrak{R}_s)^{-1} - I]G_s^{-1}} \qquad [5]$$

From equation [5] it can be seen that EDC for multiple trait model is no longer a scalar but a matrix that contains, e.g. effective numbers of daughters weighted by proper variance. For single trait models, equation [5] is equivalent to:

$$n\sigma_e^{-2} = (1/(1-R^2) - 1)\sigma_s^{-2} \qquad [6]$$

Simplifying equation [6] gives: $n = k\,R^2/(1-R^2)$ for single trait models.

Multiple trait reliability matrix $\mathfrak{R}_s$ is asymmetric, and it usually has non-zero off-diagonal elements. $\mathfrak{R}_s$ has a row of zeros corresponding to a missing trait. In contrary to $\mathfrak{R}_s$, multiple trait EDC matrix Ψ is symmetric. For a missing trait Ψ has a row and a column of zeros. EDC from different sources can be added together.

In order to approximate the reliability of an animal's EBV, the amount of information from each of the three sources needs to be computed: parental average (PA), own performance records (Y), and progeny information adjusted for mates (P-M). The total EDC for an animal (Ψ_T) is the sum of EDC from the three sources:

$$\Psi_T = \Psi_{PA} + \Psi_Y + \sum \Psi_{P\text{-}M} \qquad [7]$$

Based on Ψ_T animal's reliability matrix $\mathfrak{R}_T$ is calculated as:

$$\mathfrak{R}_T = \mathbf{I} - (\Psi_T\,\mathbf{G_s + I})^{-1} \qquad [8]$$

An animal's EDC contributed by its own performance records (Ψ_Y) is calculated based on its reliability ($\mathfrak{R}_Y$) which is computed after absorbing all relevant effects, e.g. fixed effects and permanent environmental effects, into genetic effects:

$$\mathfrak{R}_Y = \mathbf{I} - (\Psi_d\mathbf{G_0 + I})^{-1} \qquad [9]$$

where Ψ_d is the left hand side of MME after absorbing all but genetic effects. EDC contributed by animal's own performance is:

$$\Psi_Y = [(\mathbf{I} - \mathfrak{R}_Y)^{-1} - \mathbf{I}]\mathbf{G_s^{-1}} \qquad [10]$$

An animal's EDC contributed by a progeny adjusted for mate ($\Psi_{P\text{-}M}$) is calculated from the reliability provided by that progeny (VanRaden and Wiggans, 1991), assuming that it is the animal's only source of information:

$$\mathfrak{R}_{P\text{-}M} = \tfrac{1}{4}[\mathbf{E} - \mathbf{E}(\mathbf{E} + (\mathbf{I} - \tfrac{1}{4}\mathfrak{R}_M^*)^{-1})^{-1}\mathbf{E}] \qquad [11]$$

where $\mathfrak{R}_M^*$ is mate's reliability with EDC from this progeny excluded, and

$$\mathbf{E} = (\mathbf{I} - \mathfrak{R}_P^*)^{-1} - \mathbf{I} \qquad [12]$$

with $\Re_{P}^{*}$ being the progeny's reliability including information from its performance and its progeny but not from its parents. EDC for the animal contributed by each of the animal's progeny is calculated as:

$$\Psi_{\text{P-M}} = [(\mathbf{I} - \Re_{\text{P-M}})^{-1} - \mathbf{I}]\mathbf{G}_s^{-1} \qquad [13]$$

Note that if $\Re_M^* = \mathbf{0}$, $\Re_{\text{P-M}} = \frac{1}{4}\Re_P^*$. For derivation of formula [11], see Appendix I. The formula corresponding to [12] for single trait models is $R^2/(1+R^2)$, that is the major component of daughter or record equivalents (VanRaden and Wiggans, 1991).

Like EDC concept for single trait model (VanRaden and Wiggans, 1991), an animal's Ψ_{PA} is a function of parental reliabilities after EDC contributed to parents by this animal are subtracted. Subtraction of EDC contributed by this animal is necessary to avoid double counting. Formulae [11] and [13] are used to compute the animal's contribution to parents. If $\Re_{sire}^*$ and $\Re_{dam}^*$ are reliability matrices of sire and dam calculated from their total EDC minus EDC contributed by this animal, then the reliability that the animal receives from parents excluding information it contributed to them is:

$$\Re_{\text{PA}} \approx \frac{1}{4}(\Re_{sire}^* + \Re_{dam}^*) \qquad [14]$$

and the corresponding EDC is:

$$\Psi_{\text{PA}} = [(\mathbf{I} - \Re_{\text{PA}})^{-1} - \mathbf{I}]\mathbf{G}_s^{-1} \qquad [15]$$

The same sequence of reliability calculation is applied for multiple trait models as for single trait models (VanRaden and Wiggans, 1991). First, reliability contributed by performance records is computed by processing data file for animals with records. Second, EDC contributed by progeny are collected by processing pedigree file from the youngest to oldest animals. Third, reliability contributed by parents is computed starting from the oldest, once EDC from all progeny have been accumulated. At the end, EDC from the three sources of information are summed to calculate final reliability. A detailed description of the reliability calculation is illustrated for a random regression test day model (Liu et al., 2001).

The multiple trait EDC concept enables computing relative weights (Liu et al., 1999) on all information sources contributing to EBV as a by-product. The relative weights for estimating animal's EBV are: $\mathbf{W_Y} = \Psi_T^{-1}\Psi_Y$, $\mathbf{W_{PA}} = \Psi_T^{-1}\Psi_{PA}$, and $\mathbf{W_P} = \Psi_T^{-1}(\sum \Psi_{P-M})$ for animal's own records, parental information and progeny contribution, respectively. Using the above weights EBV can be re-constructed with: $\tilde{\mathbf{a}} = \Psi_T(\mathbf{W_Y q} + \mathbf{W_{PA} p} + \mathbf{W_P d})$, where $\tilde{\mathbf{a}}$ is a vector of re-constructed EBV of the animal, $\mathbf{q}$ is a vector of animal's yield deviations, $\mathbf{p}$ is a vector of pedigree indexes that are free of contribution by the animal, and $\mathbf{d}$ is a vector of daughter yield deviations.

Results and Discussion

Verification of the formulae: Accuracy of the multiple trait EDC method can be examined by simulation. Also practical application of this method must be performed to study its efficiency. Since the presented formulae are applicable to multiple trait models, they must yield to identical formulae as those in VanRaden and Wiggans (1991) for single trait models when they are simplified to a single trait case. This derivation can be regarded as a verification of the multiple trait EDC concept.

As shown in Methods, formulae [4] and [6] for single trait models are equivalent forms of formulae [3] and [5] for multiple trait models. The equivalent form of $\mathbf{E}$ for single trait models is: $e = R^2/1 - R^2$. Let R_{P-M} and R_M^* represent the animal's reliability contributed by a progeny adjusted for the animal's mate and the mate's reliability with EDC from this progeny excluded for single trait models, respectively, formula [11] for single trait models is:

$$R_{\text{P-M}} = \frac{1}{4}[e - e(e + \frac{1}{1 - \frac{1}{4}R_M^*})^{-1}e]$$

$$= \frac{R^2}{4 - R^2 R_M^*} \quad ,$$

which is identical to $\text{REL}^*_{\text{anim}}$ used by VanRaden and Wiggans (1991).

Computing accuracy of LYD: Computing the contribution by animal's own performance records is illustrated with the accuracy of LYD. For international genetic evaluation using performance records, LYD on a 305-day basis can be served as a common trait among countries that apply either lactation or test day models in national genetic evaluations. Accuracy of LYD derived from lactation models can be approximated using Interbull's EDC method (Interbull, 2000; Fikse and Banos, 2001). The following formulae for computing LYD and its accuracy are applicable for countries using test day models in national genetic evaluations.

Yield deviation of a test day record is computed as the test day yield, that has been adjusted for heterogeneous herd variances, minus estimates of fixed effects from a genetic evaluation using a test day model: $y_i = Y_i - \hat{\beta}$ with y_i being yield deviation of the i-th test day records of a lactation, Y_i being yield of the i-th test day record that has been adjusted for heterogeneous herd variance, and $\hat{\beta}$ being estimates of all fixed effects. Suppose that a lactation has m test day records, best prediction method (VanRaden, 1997) can be used to compute 305-day LYD based on yield deviations of the m test day records with phenotypic (co)variance matrix: $y_{lact} = \mathbf{1}'\mathbf{C}\mathbf{V}^{-1}\mathbf{y}$, where y_{lact} is estimated LYD, $\mathbf{y} = \begin{bmatrix} y_1 & ... & y_m \end{bmatrix}'$ is a vector containing m test day yield deviations, $\mathbf{V}$ is phenotypic (co)variance matrix of the m test day yield deviations, $\mathbf{C}$ is phenotypic covariance matrix between the m test day yield deviations and all 305 days, and $\mathbf{1}$ is a vector of 1s. Note that this formula makes projection of 305-day lactation yield deviation if a lactation is still in progress. For a fixed regression test day model, the above formula is simplified to:

$$y_{lact} = \sum_{i=1}^{m} y_i + (305-m)\frac{r}{1+(m-1)r} \sum_{i=1}^{m} y_i ,$$

with r being phenotypic correlation between test days. Due to the complex structure of the phenotypic (co)variance matrix, random regression models do not have a closed form for the formula for LYD.

Variance of LYD is:

$$\text{Var}(y_{\text{lact}}) = \text{Var}(\mathbf{1}'\mathbf{C}\mathbf{V}^{-1}\mathbf{y}) = \mathbf{1}'\mathbf{C}\mathbf{V}^{-1}\mathbf{C}'\mathbf{1} .$$

A complete lactation from a monthly testing programme consisting n test day records is assumed to be a *standard lactation*. Relative accuracy of LYD can be defined as the ratio of its variance to the variance of the standard lactation:

$$R^2 = \text{Var}(y_{lact})\big/\text{Var}(y_{lact}^{BASE}) ,$$

where $\text{Var}(y_{lact}^{BASE})$ is variance of LYD of the standard lactation. For a fixed regression model the accuracy of LYD can be simplified as: $R^2 = \frac{m}{n}\frac{1+(n-1)r}{1+(m-1)r}$. Note that R^2 can be greater than one for testing programmes more accurate than monthly testing.

Comparison of EDC from single and multiple trait models: Based on the EDC formula [11] for progeny contribution, a *standard daughter* can be defined. If dam of the daughter is missing ($\mathfrak{R}^*_{\text{M}} = \mathbf{0}$), then if $\mathbf{\Psi}_{\text{P-M}} = \mathbf{R}_{\text{s}}^{-1}$, $\mathfrak{R}^*_{\text{P}} = \mathbf{H} = 4(\mathbf{G_s} + \mathbf{R_s})^{-1}\mathbf{G_s}$. For single trait models the aforementioned formula becomes $R^2 = h^2$. Thus a standard daughter in multiple trait EDC is defined as having one record in all traits with an infinite number of management group mates, and the other parent missing with zero reliability. This definition is an extension of Interbull's EDC (Interbull, 2000) but differs slightly from VanRaden and Wiggans (1991) in the assumption of the other parent. However the two definitions are equivalent, because the variance ratios differ accordingly too. For traits with repeated records, such as lactations with repeated test day records, *one record* means a complete lactation according to the multiple trait EDC definition.

Two models are compared: a single trait repeatability model applied to lactation average somatic cell scores (SCS) and a multiple lactation random regression model (Liu et al., 2000) applied to test day SCS. The repeatability model is assumed to have a heritability of 0.1 and

repeatability of 0.35, whereas the heritability of lactation average SCS is c.a. 0.2 for the test day model (Liu et al., 2000). Table 1 shows EDC of both models throughout lactations. When the cow has completed her first three lactations, EDC of the repeatability model is 8.3, which is greater than EDC of the test day model, 5.2. The phenomenon of smaller EDC from multiple trait models than from single trait models was also observed in Interbull's EDC for bulls at the same age from different countries. This can be explained by different definitions of one EDC, which is resulted from different definitions of breeding objectives, in single and multiple trait models and different genetic parameters.

The presented multiple trait EDC approach extends the single trait DE (VanRaden and Wiggans, 1991) to general multiple trait models. The basic building blocks of this approach are matrices of the order equal to the number of traits, therefore its RAM usage is limited and much less than its corresponding solving program. The CPU consumption of this approach is approximately equivalent to that of one to two rounds of iteration in solving program. Summarising, the proposed approach is efficient in terms of RAM as well as CPU usage. In addition, this approach eliminates the needs for special handling of missing traits as it is by Gengler et al. (1996) and Strabel et al. (2001). In the proposed approach the problem of non-random distribution of relatives in contemporary groups is not addressed, however, it is possible to implement a method similar to the approach (Interbull, 2000) for multiple trait models. The multiple trait EDC can be applied to multiple trait models with correlated genetic effects, e.g. maternal effects model (Strabel et al., 2001). The correlated genetic effects must be considered jointly as a unit with this approach.

Table 1. Comparison of EDC of a single and multiple trait model, illustrated with a cow in a monthly testing programme.

Own performance records of the cow	EDC of the example cow from	
	the repeatability model	the test day model
Three tests from first lactation	1.6	1.2
Six tests from first lactation	2.9	1.8
First lactation completed with 10 tests	4.3	2.4
First two lactations completed	6.7	4.1
First three lactations completed	8.3	5.2

Summary

A general EDC approach was developed for approximating reliabilities of EBV for multiple trait models. It combines genetic theory with computational techniques, therefore it is efficient in RAM and CPU consumption. Formulae identical to a single trait EDC method were obtained, when the multiple trait EDC approach was applied to single trait models. Application of this approach is illustrated with two examples: calculating accuracy of 305-day lactation yield deviations for test day models and comparing EDC from single and multiple trait models. Further improvements and extensions of this approach are also indicated.

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APPENDIX I. Derivation of the formula for computing reliability contributed by progeny adjusted for mate

Formula [11] is for the calculation of animal's reliability contributed by a progeny adjusted for mate. To derive the formula the same method is used here as VanRaden and Wiggans (1991) did for single trait models. Let $\mathbf{y}*$ represent a vector of the progeny's trait values in which the true values of all fixed effects and other random effects than additive genetic effects are subtracted, instead of predictions of these effects. Let $\mathbf{y}^O$ represent $\mathbf{y}*$ adjusted for the effect of mate for the animal. Then a sire model can be used to predict the animal's breeding values from only this progeny's information: $\mathbf{y}^O = \mathbf{Za}_s + \Delta$, with $\mathbf{a}_s$ being a vector of animal's breeding values as the progeny's sire, and Δ is a vector of residual effects containing progeny's Mendelian sampling and error effects. If $\mathbf{y}*$ were the progeny's only source of information for estimating its breeding values ($\mathbf{a}_P$), then $(\mathbf{Z'R^{-1}Z} + \mathbf{G_0^{-1}})\hat{\mathbf{a}}_P = \mathbf{Z'R^{-1}y}*$.

The progeny's reliability contributed only by its own information is:

$$\mathfrak{R}_P^* = \mathbf{I} - \mathbf{G_0^{-1}}(\mathbf{Z'R^{-1}Z} + \mathbf{G_0^{-1}})^{-1} = \mathbf{I} - (\mathbf{Z'R^{-1}ZG_0} + \mathbf{I})^{-1}.$$

As a result of adjusting for EBV of the animal's mate, the genetic variance of $\mathbf{y}^O$ is reduced to $\mathbf{G_0^0} = \mathbf{G_0}(\mathbf{I} - \frac{1}{4}\mathfrak{R}_M^*)$. The following equations are used in derivation: $\mathbf{Z'R^{-1}Z} = [(\mathbf{I} - \mathfrak{R}_P^*)^{-1} - \mathbf{I}]\mathbf{G_0^{-1}}$,
$\mathbf{Z'R^{-1}ZG_0} = (\mathbf{I} - \mathfrak{R}_P^*)^{-1} - \mathbf{I}$,
$\mathbf{Z'R^{-1}Z} + (\mathbf{G_0^0})^{-1} = [(\mathbf{I} - \mathfrak{R}_P^*)^{-1} - \mathbf{I}]\mathbf{G_0^{-1}} + (\mathbf{G_0^0})^{-1} = [(\mathbf{I} - \mathfrak{R}_P^*)^{-1} + (\mathbf{I} - \frac{1}{4}\mathfrak{R}_M^*)^{-1} - \mathbf{I}]\mathbf{G_0^{-1}}$, and
$(\mathbf{Z'R^{-1}Z} + (\mathbf{G_0^0})^{-1})^{-1} = \mathbf{G_0} [(\mathbf{I} - \mathfrak{R}_P^*)^{-1} + (\mathbf{I} - \frac{1}{4}\mathfrak{R}_M^*)^{-1} - \mathbf{I}]^{-1}$.

The following (co)variances are also used in the derivation: $\mathrm{var}(\mathbf{y}^O) = \mathbf{V_0} = \mathbf{R} + \mathbf{ZG_0^0Z'}$ and $\mathrm{cov}(\mathbf{a}_s, \mathbf{y}^O) = \mathbf{ZG_s}$. Since $\mathbf{V_0^{-1}} = (\mathbf{R} + \mathbf{ZG_0^0Z'})^{-1} = \mathbf{R^{-1}} - \mathbf{R^{-1}Z}(\mathbf{Z'R^{-1}Z} + (\mathbf{G_0^0})^{-1})^{-1}\mathbf{Z'R^{-1}}$ (Harville 1997), $\mathbf{Z'V_0^{-1}ZG_0} = \mathbf{Z'R^{-1}ZG_0} - \mathbf{Z'R^{-1}Z}(\mathbf{Z'R^{-1}Z} + (\mathbf{G_0^0})^{-1})^{-1}\mathbf{Z'R^{-1}ZG_0}$.

Animal's breeding values based on the information from only this progeny are calculated (Henderson 1990): $\hat{\mathbf{a}}_s = \mathbf{G_sZ'V_0^{-1}y}^O$. Because $\mathrm{var}(\hat{\mathbf{a}}_s) = \mathbf{G_sZ'V_0^{-1}ZG_s}$, the animal's reliability contributed by this progeny adjusted for mate is:

$$\mathfrak{R}_{P-M} = \mathbf{G_s^{-1}G_sZ'V_0^{-1}ZG_s} = \tfrac{1}{4}\mathbf{Z'V_0^{-1}ZG_0}.$$

Because $\mathbf{Z'R^{-1}ZG_0} = (\mathbf{I} - \mathfrak{R}_P^*)^{-1} - \mathbf{I} = \mathbf{E}$,
$$\begin{aligned}
\mathfrak{R}_{P-M} &= \tfrac{1}{4}[\mathbf{Z'R^{-1}ZG_0} - \mathbf{Z'R^{-1}Z}(\mathbf{Z'R^{-1}Z} + (\mathbf{G_0^0})^{-1})^{-1}\mathbf{Z'R^{-1}ZG_0}] \\
&= \tfrac{1}{4}[\mathbf{E} - [(\mathbf{I} - \mathfrak{R}_P^*)^{-1} - \mathbf{I}][(\mathbf{I} - \mathfrak{R}_P^*)^{-1} + (\mathbf{I} - \tfrac{1}{4}\mathfrak{R}_M^*)^{-1} - \mathbf{I}]^{-1}\mathbf{E}] \\
&= \tfrac{1}{4}[\mathbf{E} - \mathbf{E}(\mathbf{E} + (\mathbf{I} - \tfrac{1}{4}\mathfrak{R}_M^*)^{-1})^{-1}\mathbf{E}].
\end{aligned}$$

The above formula was derived for progeny with performance records. In case that progeny has no actual records, $\mathbf{Z'R^{-1}Z}$ is replaced the progeny's EDC. Whether EDC or $\mathbf{Z'R^{-1}Z}$ are considered, the same formula for $\mathfrak{R}_{P-M}$ can be obtained.