

# Derivation, Calculation, and Use of National Animal Model Information

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## ABSTRACT

New terms and definitions were developed to explain national USDA genetic evaluations computed by an animal model. An animal's PTA combines information from its own records and records of all its relatives through a weighted average of 1) average of parents' evaluations, 2) half of its yield deviation, and 3) average across progeny of twice progeny evaluation minus mate's evaluation. Yield deviation is a weighted average of a cow's lactation yields minus solutions for management group, herd-sire, and permanent environmental effects. Bulls do not have yield deviations; however, a weighted average of daughter yield deviations adjusted for mates' merit can provide a useful, unregressed measure of daughter performance. Reliability is the squared correlation of predicted and true transmitting ability. An animal's parents, own records, and progeny each contribute amounts of information measured in daughter equivalents. Reliability of USDA evaluations then is computed as (total daughter equivalents)/(total daughter equivalents + 14).

(Key words: animal model, genetic evaluation, reliability)

Abbreviation key: DE = daughter equivalent, DYD = daughter yield deviation, MCC = Modified Contemporary Comparison, MCD = modified contemporary deviation, MD = management group deviation, PA = parent average, PC = progeny contribution, PPA = predicted producing ability, RE = record equivalent, REL = reliability, TA = transmitting ability, YD = yield deviation.

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## INTRODUCTION

Animal model evaluations use information from all known relationships among animals to predict each animal's genetic merit. New terminology and explanations were needed to provide animal model information to users. Simple explanations were provided by Wiggans and VanRaden (9), but derivations of some terms were not given.

Methods to summarize accuracy provided by the additional sources of information included in evaluations also were needed. Powell (5) presented formulas to measure accuracy obtained by incorporating daughter and son information into Modified Contemporary Comparison (MCC) cow evaluations, but these formulas assumed that all daughters had equal numbers of records, that all sons had equal numbers of daughters, and that there was no adjustment for merit of mates. Meyer (3) approximated accuracy reasonably well in an animal model by adjusting diagonals for off-diagonal elements. Misztal and Wiggans (4) obtained more precise measures of the accuracy of individual evaluations using an iterative procedure that was computationally affordable but lacked easy interpretation.

This article explains how PTA, yield deviation (YD), daughter yield deviation (DYD), reliability (REL), and daughter equivalents (DE) are calculated and how they interrelate.

## MATERIALS AND METHODS

### Model

In matrix notation, the current USDA animal model can be represented as

$$y = Mm + Za + ZA_{gg} + Pp + Cc + e$$

where  $y$  represents standardized milk, fat, or protein yield;  $m$ ,  $a$ ,  $g$ ,  $p$ , and  $c$  are vectors of effects for management group, random portion of additive genetic merit, unknown-parent group, permanent environment, and herd-sire

interaction, respectively;  $M, Z, ZA_g, P,$  and  $C$  are incidence matrices for these effects; and  $e$  is error. The matrix  $A_g$  relates animals to unknown-ancestor groups and is equivalent to  $A_{10}Q$  as reported by Wiggans et al. (7).

Vectors  $a, p, c,$  and  $e$  are mutually uncorrelated with variances  $A\sigma_a^2, I\sigma_p^2, I\sigma_c^2,$  and  $R\sigma_e^2,$  respectively. The matrix  $A$  is the additive rela-

tionship matrix among all animals in  $a,$  and  $R^{-1}$  is a diagonal matrix with diagonals equal to  $w_{len},$  lactation length weights (8). Mixed model equations were given in scalar form for this model (8) and in matrix notation for a similar model with  $Var(e) = I\sigma_e^2$  (7). With  $Var(e) = R\sigma_e^2,$  mixed model equations are:

$$\begin{bmatrix} M'R^{-1}M & & & & & & \\ Z'R^{-1}M & Z'R^{-1}Z + A^{-1}k_a & & & & & \\ 0 & -A'_gA^{-1}k_a & A'_gA^{-1}A_gk_a & & & & \\ P'R^{-1}M & P'R^{-1}Z & 0 & P'R^{-1}P + Ik_p & & & \\ C'R^{-1}M & C'R^{-1}Z & 0 & C'R^{-1}P & C'R^{-1}C + Ik_c & & \end{bmatrix} \begin{bmatrix} \hat{m} \\ \hat{u} \\ \hat{g} \\ \hat{p} \\ \hat{c} \end{bmatrix} = \begin{bmatrix} M'R^{-1}y \\ Z'R^{-1}y \\ 0 \\ P'R^{-1}y \\ C'R^{-1}y \end{bmatrix}$$

where  $k_a = \sigma_e^2/\sigma_a^2, k_p = \sigma_e^2/\sigma_p^2, k_c = \sigma_e^2/\sigma_c^2,$  and  $u = a + A_gg$  (total genetic merit including fixed and random portions). Values assigned to  $k_a, k_p,$  and  $k_c$  are 1.8, 2.8, and 3.2, respectively.

These equations are solved as a singular system, and a genetic base is imposed later. Alternatively, constraints on  $g$  could impose a base during solution, but this slows convergence (Van Vleck, personal communication,

1988). Procedures used to construct  $A^{-1}$  assume that parents are noninbred (2), and this assumption continues for all procedures. Many of the results released to the dairy industry for individual animals are functions of solutions to these equations: e.g., PTA =  $\hat{u}_i/2,$  predicted producing ability (PPA) =  $\hat{u}_i + \hat{p}_i + \hat{c}_i,$  and YD =  $y_i - (\hat{m}_i + \hat{p}_i + \hat{c}_i),$  where  $i$  refers to an individual animal. Subsequent discussion deals mainly with equations for  $u,$  which can be rewritten as

$$(Z'R^{-1}Z + A^{-1}k_a)\hat{u} = A'_gA^{-1}k_a \hat{g} + Z'R^{-1}(y - M\hat{m} - P\hat{p} - C\hat{c}) \tag{1}$$

**Yield Deviations and Management Group Deviations**

Information from lactation records of a cow is included in the cow's PTA through her YD. A cow's YD is the element of  $Z'R^{-1}(y - M\hat{m} - P\hat{p} - C\hat{c})$  for that cow divided by the corresponding diagonal of  $Z'R^{-1}Z;$  i.e., a weighted average of the cow's yields adjusted for all effects other than genetic merit and error. Management group deviation (MD) is defined as an element of  $Z'R^{-1}(y - M\hat{m})$  divided by the corresponding diagonal of  $Z'R^{-1}Z;$  i.e., a weighted average of the cow's yields adjusted for management group effects. Subtraction of permanent environmental and herd-sire interaction solutions from the cow's yields causes YD to have smaller variance than MD. Also, MD

is more similar to a cow's modified contemporary deviation (MCD) from the MCC system than is YD (Powell, personal communication, 1989).

Management group solutions include information from all cows in the management group, whereas MCD measured differences from contemporaries that did not include the cow herself or her paternal half-sibs. In the case of a herd containing only one cow with one record, MCD would be undefined, whereas both YD and MD would equal twice the cow's PTA. For such cows, permanent environmental and herd-sire interaction solutions would be 0; management group solution then would equal the cow's record minus twice her PTA, which would be computed from information on her

parents and progeny. Records with no management group mates are deleted, and consequently such YD are not reported. However, if group sizes are small, information from parents and progeny will have some influence on the cow's YD and MD because management group solutions are adjusted for average genetic merit, which includes the cow's own genetic merit.

Averages of management group solutions and MD are not reported for individual cows but can be constructed from variables provided. Subtraction of twice an animal's PTA ( $PTA_{anim}$ ) from the animal's PPA gives the total of solutions for permanent environment and herd-sire interaction. This total can be added to YD to obtain MD:

$$MD = YD + PPA - 2PTA_{anim}$$

Weighted average of management group solutions for a cow can then be computed as the weighted average of her standardized yield minus MD.

#### Predicted Transmitting Abilities

The matrix  $A^{-1}$  has nonzero off-diagonals only for an animal's parents, progeny, and mates (2), and coefficients of  $A_g A^{-1}$  are nonzero if an animal's parents or mates are unknown (6). Because PTA are elements of  $\hat{u}$  divided by 2, division of both sides of Equation [1] by 2 and transfer of off-diagonal terms of  $A^{-1}$  to the right side of Equation [1] gives

$$[\text{diag}(Z'R^{-1}Z + A^{-1}k_a)]PTA_{anim} =$$

$$\begin{aligned} & k_a q_{par}(PTA_{sire} + PTA_{dam}) \\ & + [\text{diag}(Z'R^{-1}Z)]YD/2 \\ & + .5k_a \Sigma q_{prog}(2PTA_{prog} - PTA_{mate}) \end{aligned} \quad [2]$$

where  $q_{par}$  equals 1 if both parents are known, 2/3 if one is known, and 1/2 if neither is known, and  $q_{prog}$  equals 1 if progeny's other parent is known and 2/3 if unknown. Appropriate genetic group solutions divided by 2 replace  $PTA_{sire}$ ,  $PTA_{dam}$ , and  $PTA_{mate}$  if any are unknown. An analogous formula using breeding value instead of PTA was given by Wiggins et al. (8).

Equation [2] can be simplified by defining parent average (PA) as average of parents' PTA and progeny contribution (PC) as weighted average of twice  $PTA_{prog}$  minus  $PTA_{mate}$  or

$$PC = \Sigma q_{prog}(2PTA_{prog} - PTA_{mate})/\Sigma q_{prog} \quad [3]$$

Then, substituting  $\Sigma w_{len} + 2k_a q_{par} + .5k_a \Sigma q_{prog}$  for  $\text{diag}(Z'R^{-1}Z + A^{-1}k_a)$  ( $W_{len}$  = lactational length weight) and dividing both sides of Equation [2] by this quantity gives

$$PTA_{anim} = w_1 PA + w_2 (YD/2) + w_3 PC, \quad [4]$$

where  $w_1$ ,  $w_2$ , and  $w_3$  are weights that sum to 1. The numerator of  $w_1$  is  $2k_a q_{par}$ ; the numerator of  $w_2$  is  $\Sigma w_{len}$  for the cow; and the numerator of  $w_3$  is  $.5k_a \Sigma q_{prog}$ . The denominator of all three  $w$  is the diagonal of  $Z'R^{-1}Z + A^{-1}k_a$ , which equals the sum of the three numerators. These weights were derived directly from the mixed model equations but may be interpreted more easily if numerators and denominators are each divided by  $k_a$ .

Evaluations computed by an animal model are interpreted more easily if the three components of Equation [4] are reported along with  $PTA_{anim}$ . The term  $2PTA_{prog} - PTA_{mate}$  is reported by USDA individually for daughters of bulls and is labeled "contribution to bull" on the Bull Evaluation and Daughter List. Contributions to bull are used directly to calculate the bull's PTA. However, when interpreting these contributions, it must be remembered that  $PTA_{prog}$  is also a function of  $PTA_{anim}$ ; i.e., daughter contribution to bull includes some information contributed by the bull to his daughter.

To illustrate, suppose the mixed model equations include some progeny with no records or descendants. For such progeny,  $PTA_{prog}$  would equal the progeny's PA or  $(PTA_{anim} + PTA_{mate})/2$ , and contribution to bull then would equal  $2[(PTA_{anim} + PTA_{mate})/2] - PTA_{mate}$ , which reduces to  $PTA_{anim}$ . Such progeny obviously do not contribute new information but simply reflect back information received. Similarly, progeny providing little new information to their sire's evaluation likely will have contributions close to his PTA.

Because Equation [4] is solved iteratively, an animal's PTA may affect and be affected by all relatives. The YD of daughters are much less dependent on the bull's PTA, and a weighted average of YD of daughters adjusted for  $PTA_{mate}$  can be used to construct PTA of bulls that do not have grandprogeny.

### Daughter Yield Deviations

Information from YD of progeny ( $YD_{prog}$ ) is included in  $PTA_{anim}$  only indirectly after  $YD_{prog}$  is combined with information from the progeny's progeny and parents by the proge-

ny's PTA equation. Thus, PC is a regressed and not independent measure of progeny performance because  $PTA_{anim}$  is directly included in  $PTA_{prog}$ . A more independent and unregressed measure of progeny performance is DYD.

The PTA equation of any daughter without progeny can be written as

$$PTA_{prog} = w_{1_{prog}}[(PTA_{anim} + PTA_{mate})/2] + w_{2_{prog}}[YD_{prog}/2] \quad [5]$$

where  $w_{1_{prog}}$  and  $w_{2_{prog}}$  are  $w_1$  and  $w_2$  of progeny. Substitution of Equation [5] into Equation [3] allows PC to be expressed as

$$PC = \Sigma q_{prog}(w_{1_{prog}}PTA_{anim} + w_{1_{prog}}PTA_{mate} + w_{2_{prog}}YD_{prog} - PTA_{mate})/\Sigma q_{prog}$$

Because these progeny have no progeny of their own,  $w_{3_{prog}}$  equals 0 and  $w_{1_{prog}}$  equals  $1 - w_{2_{prog}}$ . Therefore,

$$\begin{aligned} PC &= \Sigma q_{prog}[(1 - w_{2_{prog}})PTA_{anim} + w_{2_{prog}}(YD_{prog} - PTA_{mate})]/\Sigma q_{prog} \\ &= PTA_{anim} + [\Sigma q_{prog}w_{2_{prog}}(-PTA_{anim} + YD_{prog} - PTA_{mate})]/\Sigma q_{prog} \end{aligned} \quad [6]$$

Substituting Equation [6] into Equation [4] and accumulating all terms involving  $PTA_{anim}$  to the left side gives

$$(1 - w_3 + w_3\Sigma q_{prog}w_{2_{prog}}/\Sigma q_{prog})PTA_{anim} = w_1PA + w_2(YD/2) + w_3\Sigma q_{prog}w_{2_{prog}}(YD_{prog} - PTA_{mate})/\Sigma q_{prog}$$

Next, by replacing  $1 - w_3$  with  $w_1 + w_2$ , removing the common denominator of the  $w$  from both sides, and defining DYD as

$$DYD = \Sigma q_{prog}w_{2_{prog}}(YD_{prog} - PTA_{mate})/\Sigma q_{prog}w_{2_{prog}}$$

$PTA_{anim}$  can be rewritten as

$$PTA_{anim} = x_1PA + x_2(YD/2) + x_3DYD$$

where  $x_1$ ,  $x_2$ , and  $x_3$  are weights that sum to 1. Numerators of  $x_1$  and  $x_2$  equal numerators of  $w_1$  and  $w_2$ ; numerator of  $x_3$  is  $.5k_a\Sigma q_{prog}w_{2_{prog}}$ , which was derived as the numerator of  $w_3$  times  $\Sigma q_{prog}w_{2_{prog}}/\Sigma q_{prog}$ . The denominator for all three  $x$  is the sum of the numerators. Because  $w_{2_{prog}}$  is always less than 1,  $x_3$  is always less than  $w_3$ , which reflects that DYD is an unregressed measure of progeny performance, whereas PC is a regressed measure. The DYD may be helpful in explaining evaluations and

also as a dependent variable in statistical tests and calculation of conversions across countries.

Currently, DYD is provided to the dairy industry for bulls with 10 or more daughters, but not for cows. For bulls with granddaughters, DYD does not include all information from descendants because information from granddaughters and sons is excluded. For each daughter with daughters of its own,  $w_{2_{prog}}$  is calculated as if granddaughter information did not exist and is not the actual  $w_2$  of the bull's daughter. For all daughters of the bull,  $w_{2_{prog}}$  used in calculating DYD is

$$\Sigma w_{len}/(\Sigma w_{len} + 2k_aq_{prog})$$

Otherwise, presence of granddaughters would reduce weight given to that daughter's YD.

Values of  $w$  and  $x$  for a specific animal provide only an imprecise measure of how much information came from its PA, YD, and PC or DYD. The three terms used to construct PTA may have large part-whole correlations, and important factors such as parent REL, number of management group mates, and mate REL do not enter into calculation of either  $w$  or  $x$ . More precise measurement of the influence of PA, YD, and PC can be obtained by examining their contributions to REL.

#### Reliability

The measure of accuracy of an evaluation, REL, is the squared correlation of an animal's predicted and true transmitting abilities (TA). An equivalent definition of REL is variance of the animal's PTA divided by variance of its TA. Selection is ignored for computing REL, i.e., correlations and variances are derived from unselected rather than selected population parameters. Exact REL usually must be replaced by approximations if matrices are too large to invert.

Like PTA, REL can account for information from all relatives by only directly including terms for parents, self, and progeny adjusted for mates. Misztal and Wiggans (4) accurately estimated REL by adding information from these three sources. They expressed information in record equivalents (RE) because this is the natural unit of information for a cow in mixed model equations. Interpretation of RE is difficult because only one sex has records, because RE increase nonlinearly with additional records as the result of permanent environmental effects, and because large numbers of records are not biologically possible.

Daughter equivalents were selected for the USDA animal model implementation because of simpler interpretation and the tradition of relating accuracy of sire evaluations to number of daughters. One DE is the amount of information contributed to a parent by a standard daughter. For USDA evaluations, a standard daughter was defined as having one record, an infinite number of management group mates, and the other parent with perfect REL. Total DE for an animal ( $DE_{anim}$ ) is the sum of DE from PA ( $DE_{PA}$ ), own yield ( $DE_{yield}$ ), and progeny adjusted for mates ( $\Sigma DE_{prog-mate}$ ):

$$DE_{anim} = DE_{PA} + DE_{yield} + \Sigma DE_{prog-mate}$$

Each animal's REL ( $REL_{anim}$ ) is calculated from  $DE_{anim}$ :

$$REL_{anim} = DE_{anim}/(DE_{anim} + k_d),$$

where  $k_d$  is a variance ratio calculated as  $(4 - 2h^2)/h^2$ , which can be interpreted using sire model terms as the ratio of error to sire variance with dam variance removed from error variance or  $(\sigma_e^2 + \sigma_p^2 + \sigma_c^2 + .5\sigma_a^2)/(.25\sigma_a^2)$ . For USDA evaluations,  $k_d = 14$ . The previous equation can be reversed to calculate  $DE_{anim}$  from  $REL_{anim}$ :

$$DE_{anim} = k_d(REL_{anim})/(1 - REL_{anim}).$$

*Daughter Equivalents from Parents.* An animal's  $DE_{PA}$  is a simple function of parent REL after DE contributed to parents by this animal are subtracted. Subtraction of DE contributed by this animal is necessary to avoid including information twice; formulas to compute the animal's contribution to parents follow in the next section. If  $REL_{sire}^*$  and  $REL_{dam}^*$  are REL of sire and dam calculated from their total DE minus DE contributed by this animal, then REL that the animal receives from parents (8) excluding information it contributed to them ( $REL_{PA}^*$ ) is

$$REL_{PA}^* = (REL_{sire}^* + REL_{dam}^*)/4$$

and

$$DE_{PA} = k_d(REL_{PA}^*)/(1 - REL_{PA}^*).$$

This formula for  $DE_{PA}$  is simpler but equivalent (proof of equivalence in Appendix) to the formula of Misztal and Wiggans (4) and Meyer (3) for RE from parents.

*Daughter Equivalents from Yield.* An animal's  $DE_{yield}$  is calculated from  $REL_{yield}$ , the REL provided by the animal's own records with information from relatives excluded. For animals with an infinite number of management group mates,  $REL_{yield}$  can be calculated by the familiar formula:

$$REL_{yield} = n_{rec}h^2/[1 + (n_{rec} - 1)r_{yield}]$$

where  $n_{rec}$  is number of records, and  $r_{yield}$  is yield repeatability. Actual formulas to calculate  $REL_{yield}$  account for lactation length weights of the cow and her management group mates and also number and average REL of sires of management group mates. After accounting for these effects with formulas given by Wiggans et al. (8),

$$DE_{yield} = k_d(REL_{yield})/(1 - REL_{yield}).$$

*Daughter Equivalents from Progeny.* An animal's  $DE_{prog-mate}$  from each progeny is calculated from the REL provided by that progeny, assuming that it is the animal's only source of information ( $REL_{anim}^*$ ):

$$REL_{anim}^* = REL_{prog}^*/(4 - REL_{prog}^*REL_{mate}^*)$$

where  $REL_{prog}^*$  is the progeny's REL including information from its yield and its progeny but not from its parents, and  $REL_{mate}^*$  is mate's REL with DE from this progeny excluded. Then  $DE_{prog-mate}$  for each of the animal's progeny is calculated as

$$DE_{prog-mate} = k_d(REL_{anim}^*)/(1 - REL_{anim}^*).$$

The equations for  $REL_{anim}^*$  and  $DE_{prog-mate}$  can be derived (see Appendix) from formulas of Misztal and Wiggans (4) and also from selection index procedures as follows. Yield information from a progeny that has no progeny of its own is summarized as  $YD_{prog} - PTA_{mate}$ . To simplify calculations, let  $YD_{prog}^*$  be a  $YD_{prog}$  in which true values for management group, permanent environment, and herd-sire interaction are subtracted instead of predictions of these effects. Then

$$YD_{prog}^* = TA_{anim} + TA_{mate} + s + (\sum w_{len} e_i)/\sum w_{len}$$

where  $TA_{anim}$  and  $TA_{mate}$  are true TA of the animal and its mate,  $s$  is Mendelian sampling of progeny, and  $e_i$  is an element of  $e$ . If  $YD_{prog}^*$

were the progeny's only source of information, then  $REL_{prog}^*$  could be calculated as variance of the progeny's breeding value divided by variance of  $YD_{prog}^*$ , or

$$REL_{prog}^* = \sigma_a^2/(\sigma_a^2 + \sigma_e^2/\sum w_{len}).$$

Let  $PTA_{anim}^*$  be a prediction of  $TA_{anim}$  from just this progeny and  $PTA_{mate}^*$  be a prediction of  $TA_{mate}$  from all information excluding this progeny. Because  $Cov(TA_{anim}, YD_{prog}^* - PTA_{mate}^*)$  equals  $Var(TA_{anim})$ , REL that the animal receives from just this progeny adjusted for mate ( $REL_{anim}^*$ ) can be calculated as

$$\begin{aligned} REL_{anim}^* &= Var(TA_{anim})/Var(YD_{prog}^* - PTA_{mate}^*) \\ &= (\sigma_a^2/4)/[\sigma_a^2 + (\sigma_e^2/\sum w_{len}) - (REL_{mate}^*\sigma_a^2/4)] \\ &= 1/[(4/REL_{prog}^*) - REL_{mate}^*]. \end{aligned}$$

A more convenient expression may be

$$REL_{anim}^* = REL_{prog}^*/(4 - REL_{prog}^*REL_{mate}^*).$$

These formulas to calculate REL from a sum of DE provide good approximations (4) but are not exact because some covariances assumed to be 0 may not be, e.g., if relatives are compared in the same management group or herd or if an animal has several progeny by the same mate.

*Daughters in the Same Herd.* Inclusion of herd-sire interaction in the animal model limits information contributed to a sire by daughters located in any one herd. Formulas to account for herd-sire interaction in USDA-DHIA animal model evaluations were given by Wiggans et al. (8), but these included an assumption of no adjustment for merit of mates. Adjustment for mates can be included in formulas of Wiggans et al. (8) by subtracting  $REL_{mate}^*\sigma_a^2/4$  from variance assigned to progeny information [specifically from  $\sigma_x^2$  in the daughter weight

formula of Wiggans et al. (8)]. With this adjustment, formulas of Wiggans et al. (8) can be reexpressed as

$$\text{REL}_{\text{anim}}^* = .25\sigma_a^2 / [.25\sigma_a^2 + \sigma_c^2 + (\sigma_p^2 + .5\sigma_a^2 + \sigma_e^2)/d]$$

where  $d$  accumulates information from daughters in one herd. If daughters of an infinite number of other sires are present in each management group,  $d$  can be calculated as

$$d = \Sigma\{(\sigma_p^2 + .5\sigma_a^2 + \sigma_e^2)/[\sigma_p^2 + (.75 - .25 \text{REL}_{\text{mate}}^*)\sigma_a^2 + \sigma_e^2/\Sigma w_{\text{len}}]\}$$

Actual formulas adjust for number of management group mates and number and average REL of their sires by replacing  $\Sigma w_{\text{len}}$  by a sum of lactation weights (8) times  $\sigma_e^2$ . The term  $\sigma_p^2 + .5\sigma_a^2 + \sigma_e^2$  could be factored out but achieves scaling so that  $d$  is simply the number of daughters if each daughter is a standard daughter.

Replacement of  $\sigma_a^2$ ,  $\sigma_p^2$ ,  $\sigma_c^2$ , and  $\sigma_e^2$  by their numeric values and transformation from  $\text{REL}_{\text{anim}}^*$  to  $\text{DE}_{\text{prog-mate}}$  leads to a simple formula to compute the DE that a sire receives from daughters in just one herd:

$$\text{DE}_{\text{prog-mate}} = 1 / (.16 + .84/d)$$

*Sequence of Reliability Calculations.* Because  $\text{REL}_{\text{anim}}$  is a function of parent, progeny, and mate REL and because those in turn are functions of  $\text{REL}_{\text{anim}}$ , an iterative strategy could be used to calculate REL (4). The USDA programs avoid iteration by starting with REL computed in the previous evaluation and processing animals twice in age order. The first step is to collect  $\text{DE}_{\text{yield}}$  for all cows with records by processing the yield file in herd order. At the same time, DE contributed by daughters to sires are computed using formulas of Wiggans et al. (8) that account for herd-sire interaction. These contributions reflect only information from records of a bull's daughters; progeny of these daughters currently do not

contribute to the bull's reported REL. Next, animals are processed from youngest to oldest to collect  $\text{DE}_{\text{prog-mate}}$  from the other three pathways (daughters to dams and sons to parents), which ensures that DE from all progeny of an animal will have been summed before calculating that animal's contribution to its parents.

Once DE from all progeny have been accumulated, REL is computed starting with the oldest animals. This ensures parent REL is available before progeny REL is calculated. Because  $\text{REL}_{\text{PA}}^*$  rather than  $\text{REL}_{\text{PA}}$  is required for computing  $\text{DE}_{\text{PA}}$ , REL of each parent without this animal's contribution must be determined. Using the animal's  $\text{DE}_{\text{yield}}$  and  $\Sigma \text{DE}_{\text{prog-mate}}$  and REL of the other parent, DE that the animal contributes to each parent are computed, and these DE are subtracted from the parent's total DE to obtain  $\text{REL}_{\text{sire}}^*$  and  $\text{REL}_{\text{dam}}^*$ . Then  $\text{REL}_{\text{PA}}^*$  is used to obtain  $\text{DE}_{\text{PA}}$ , which is combined with  $\text{DE}_{\text{yield}}$  and  $\Sigma \text{DE}_{\text{prog-mate}}$  to compute  $\text{REL}_{\text{anim}}$ .

*Relatives in the Same Management Group.* The preceding formulas assume that an animal's parents, its own records, and its progeny each contribute independent information about  $\text{TA}_{\text{anim}}$ . If records of relatives are compared directly in the same management group, this assumption of independence no longer is valid. For example, an animal's YD contributes information to its own PTA but not to its sire's PTA if the animal's records are compared only with those of its paternal half-sibs. Formulas of Dickinson et al. (1) and Wiggans et al. (8) account for this reduction in information provided to the sire if paternal half-sibs are management groupmates. If full-sibs, maternal half-sibs, cousins, etc., are compared directly, information also is reduced, but adjustment for this is not made. Thus, reported REL could be too large and genetic gains less than expected if management groups include many embryo transfer progeny from the same dam.

## RESULTS AND DISCUSSION

### Examples

An individual animal's total DE can be approximated by summing values of  $\text{DE}_{\text{PA}}$ ,

TABLE 1. Example daughter equivalents (DE) contributed to cow reliability (REL) by various sources of information.

Relative	Information available	DE
Parents <sup>1</sup>	Sire with 70% REL, dam with 30% REL	4.7
	Sire with 99% REL, dam with 50% REL	8.3
	Sire with 99% REL, dam with 99% REL	14.0
Self <sup>2</sup>	1 lactation record	4.7
	3 lactation records	7.8
	5 lactation records	9.0
Daughter <sup>2,3</sup>	1 lactation record	1.0
	3 lactation records	1.5
	5 lactation records	1.7
Son <sup>3</sup>	1 daughter with 1 lactation record	.2
	10 daughters in 10 herds, each with 1 lactation record	1.8
	50 daughters in 50 herds, each with 1 lactation record	4.4
	100 daughters in 100 herds, each with 1 lactation record Evaluation with 99% REL	5.4 7.0

<sup>1</sup>Parent REL excluding information contributed by this offspring.

<sup>2</sup>Lactation records with infinite number of management group mates.

<sup>3</sup>Other parent assumed to have 99% REL.

DE<sub>yield</sub>, and DE<sub>prog-mate</sub> in Table 1. These values were computed with assumptions that parent REL are adjusted for the animal's contribution and of perfect REL for mate, but they usually are good approximations of DE even if these assumptions are not met. Examples of DE<sub>prog-mate</sub> contributed to sire if daughters are in the same herd are in Table 2. Sire's REL then is obtained from DE from all herds plus DE<sub>PA</sub>.

Calculation of PTA, DYD, and REL will be demonstrated for an example cow, although DYD is reported only for bulls. Suppose the

example cow has a YD based on three records of +1000 kg, a PA of -500 kg, and two daughters with one record each. The first daughter has a YD of -300 kg, and her sire's PTA is -200 kg. The second daughter has a YD of +400 kg and an unknown sire; an unknown-group solution of +100 kg is substituted for her sire's PTA. The cow's DYD can then be computed as

$$\begin{aligned} \text{DYD} &= [.2174(-300 + 200) \\ &\quad + .2941(2/3)(400 - 100)] / \\ &\quad [.2174 + .2941(2/3)] \\ &= 90 \text{ kg} \end{aligned}$$

where .2174 and .2941 are  $w_{2_{\text{prog}}}$  for the first and second daughters, respectively. The cow's PTA can then be computed from PA, YD, and DYD as

$$\begin{aligned} \text{PTA} &= .516(-500) + .431(1000/2) \\ &\quad + .053(90) \\ &= -38 \text{ kg} \end{aligned}$$

where  $x_1 = .516$ ,  $x_2 = .431$ , and  $x_3 = .053$ . Because the two daughters have no progeny of their own, their PTA can be obtained fairly easily and equal -126 kg and 81 kg, respectively. Then, the cow's PC is

TABLE 2. Example daughter equivalents (DE) contributed to sire reliability (REL) by daughters in the same herd.

Number of daughters in herd	DE <sup>1</sup> contributed to sire REL	DE/daughter
1	1.0	1.00
2	1.7	.86
5	3.0	.61
10	4.1	.41
25	5.2	.21
50	5.7	.11
100	5.9	.06

<sup>1</sup>Calculated by  $1/[.16 + (.84/d)]$ , where d is number of standard daughters in the herd and a standard daughter has one record, infinite management group mates, and the other parent with perfect REL.



$$\begin{aligned} \text{PC} &= \{[2(-126) + 200] + (2/3)[2(81) \\ &\quad - 100]\}/[1 + (2/3)] \\ &= -6 \text{ kg.} \end{aligned}$$

The cow's PTA also can be computed as a weighted average of PA, YD, and PC with the weights in Table 3. For comparison, values of  $x$  and DE provided by parents, self, and progeny expressed as fractions of total DE also are given. Values of  $DE_{\text{PA}}$ ,  $DE_{\text{yield}}$ , and  $DE_{\text{prog - mate}}$  were 8.3, 7.8, and 1.93, respectively. Assumptions were that the cow's dam had 50% REL after removing cow's contribution to dam and that the cow's sire and the sire of her first daughter both had 99% REL. The second daughter with unknown sire contributed .93 DE, a situation not included in Table 2. The cow's total DE is 18.03, which results in  $REL_{\text{anim}} = 18.03/(18.03 + 14) = .56$ .

#### Implementation

The PTA, REL, and deviation variables for about 14 million cows and 100,000 bulls have been computed semiannually since the first release of animal model information in July 1989. The new evaluations and terminology generally have been accepted well by the dairy industry. A few complaints were received. Some dairy producers disliked that REL for bulls has a more limited range than did Repeatability and that PTA cannot be approximated easily from data available on the farm. Others would have preferred that MD rather than YD be reported.

#### CONCLUSIONS

Animal model evaluations combine information from an animal and all relatives using optimum statistical techniques but can be explained easily without matrix algebra. The cow's own information is summarized by her YD, a weighted average of yields adjusted for effects other than genetic merit and error. Each cow's PTA combines information from her YD with information from her parents (PA) and her progeny (adjusted for genetic merit of mates) through a simple weighted average. If progeny do not have progeny of their own, PTA also can be computed as a weighted average of PA, half of YD, and DYD.

The total amount of information provided by records of the animal and all its relatives is

TABLE 3. Weights assigned to parent, self, and progeny information and proportion of daughter equivalents (DE) contributed by each for an example cow.

Weighting factor	Parents	Self	Progeny
w	.445	.370	.185
x	.516	.431	.053
DE/Total DE	.460	.433	.107

summarized by REL through a simple function of total DE from parents, own yield, and progeny adjusted for mates. As with PTA, information from more distant relatives is incorporated through parents and progeny. Daughters located in the same herd provide less information and fewer  $DE_{\text{prog - mate}}$  to their sire than if each were located in a different herd. Computed REL do not equal true REL but do account for estimation of management group effects, herd-sire interaction, and correction for merit of mates. Further refinements such as reduction of  $DE_{\text{prog - mate}}$  contributed to dam if daughters are in the same management group and inclusion of maternal granddaughter information for bulls also may be possible.

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#### APPENDIX

Formulas for  $DE_{PA}$  and  $DE_{prog - mate}$  are equivalent to the appendix formulas of Misztal and Wiggans (4) for RE from parents and progeny. Proofs follow. Formulas of Meyer (3) for information from parents are identical to those of Misztal and Wiggans (4), but Meyer's (3) formulas for information from progeny did not adjust for  $REL_{mate}^*$ .

Let  $b_a$  represent total amount of information for animal a expressed in RE rather than in DE. Define  $q_a$  as RE for a with parents' contributions excluded,  $q_s$  as RE of a's sire with the contribution of progeny a excluded,  $q_d$  as the corresponding statistic for progeny a's dam, and  $\alpha$  as the ratio  $\sigma_e^2/\sigma_a^2$ . Then, RE contributed to progeny a by sire s and dam d ( $RE_{a_{s+d}}$ ) in the notation of Misztal and Wiggans (4) are

$$\begin{aligned} b_a - q_a &= \alpha - [\alpha^2(1.5\alpha + q_s) - \alpha^3 + \alpha^2(1.5\alpha + q_d)] / [(1.5\alpha + q_s)(1.5\alpha + q_d) - .25\alpha^2] \\ &= \alpha - (2\alpha^3 + \alpha^2q_s + \alpha^2q_d) / (2\alpha^2 + 1.5\alpha q_s + 1.5\alpha q_d + q_s q_d) \\ &= (2\alpha^3 + 1.5\alpha^2q_s + 1.5\alpha^2q_d + \alpha q_s q_d - 2\alpha^3 - \alpha^2q_s - \alpha^2q_d) / (2\alpha^2 + 1.5\alpha q_s + 1.5\alpha q_d + q_s q_d) \\ &= (.5\alpha^2q_s + .5\alpha^2q_d + \alpha q_s q_d) / (2\alpha^2 + 1.5\alpha q_s + 1.5\alpha q_d + q_s q_d) \\ &= (\alpha^2q_s + \alpha^2q_d + 2\alpha q_s q_d) / (4\alpha^2 + 3\alpha q_s + 3\alpha q_d + 2q_s q_d) \\ &= \alpha(\alpha q_s + \alpha q_d + 2q_s q_d) / [4(\alpha^2 + \alpha q_s + \alpha q_d + q_s q_d) - \alpha q_s - \alpha q_d - 2q_s q_d] \\ &= \alpha[q_s(\alpha + q_d) + q_d(\alpha + q_s)] / [4(\alpha + q_s)(\alpha + q_d) - q_s(\alpha + q_d) - q_d(\alpha + q_s)] \\ &= \alpha[q_s/(\alpha + q_s) + q_d/(\alpha + q_d)] / [4 - q_s(\alpha + q_s) - q_d(\alpha + q_d)]. \end{aligned}$$

Thus,

$$RE_{a_{s+d}} = \alpha(REL_s^* + REL_d^*) / (4 - REL_s^* - REL_d^*).$$

Similarly, RE contributed to sire s by progeny a ( $RE_s$ ) can be calculated as

$$\begin{aligned} b_s - q_s &= .5\alpha - [.25\alpha^2(2\alpha + q_a) - \alpha^3 + \alpha^2(1.5\alpha + q_d)] / [(1.5\alpha + q_d)(2\alpha + q_a) - \alpha^2] \\ &= .5\alpha - (\alpha^3 + .25\alpha^2q_a + \alpha^2q_d) / (2\alpha^2 + 2\alpha q_d + 1.5\alpha q_a + q_a q_d) \\ &= (\alpha^3 + \alpha^2q_d + .75\alpha^2q_a + .5\alpha q_a q_d - \alpha^3 - .25\alpha^2q_a - \alpha^2q_d) / (2\alpha^2 + 2\alpha q_d + 1.5\alpha q_a + q_a q_d) \\ &= .5(\alpha^2q_a + \alpha q_a q_d) / (2\alpha^2 + 2\alpha q_d + 1.5\alpha q_a + q_a q_d) \\ &= (\alpha^2q_a + \alpha q_a q_d) / (4\alpha^2 + 4\alpha q_d + 3\alpha q_a + 2q_a q_d) \\ &= \alpha q_a / [(4\alpha^2 + 3\alpha q_a + 4\alpha q_d + 3q_a q_d - q_a q_d) / (\alpha + q_d)] \\ &= \alpha q_a / [4\alpha + 3q_a - q_a q_d / (\alpha + q_d)] \\ &= \alpha q_a / \{4(\alpha + q_a) - q_a[1 + q_d/(\alpha + q_d)]\} \\ &= [\alpha q_a / (\alpha + q_a)] / \{4 - [q_d/(\alpha + q_a)][1 + q_d/(\alpha + q_d)]\}. \end{aligned}$$

Thus:

$$\begin{aligned} RE_{s_a} &= \alpha[REL_a^* / (4 - REL_a^*(1 + REL_d^*))] \\ &= \alpha[REL_a^* / (4 - REL_a^*REL_d^*)] / \{[4 - REL_a^*(1 + REL_d^*)] / (4 - REL_a^*REL_d^*)\} \\ &= \alpha REL_s^* / (1 - REL_s^*). \end{aligned}$$

Corresponding algebra for the dam results in RE contributed by progeny a to dam d ( $RE_d$ ) of

$$RE_d = \alpha REL_d^* / (1 - REL_d^*).$$

Therefore, equivalence of the formulas to compute DE and RE is demonstrated, giving the simple identity  $DE = (k_a/\alpha)RE$ .