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L. Dale Van Vleck

University of Nebraska-Lincoln, dvan-vleck1@unl.edu

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Contemporary Groups for Genetic Evaluations

L. D. VAN VLECK
Department of Animal Science
Cornell University
Ithaca, NY 14853

ABSTRACT

Contemporary groups are used to remove biases from genetic evaluations due to differential effects such as management associated with the grouping. Numerous groups, however, can result in small numbers of records per subclass with associated loss of effective number of daughters for sire evaluation and increased prediction error variance. Thus, in practice, mean square error, bias squared plus prediction error variance, may be more meaningful than bias alone or prediction error variance. Considering contemporary groups as fixed removes bias due to association between effects corresponding to contemporary groups and sires. If contemporary groups are considered random, then effective number of daughters is increased at the expense of possible bias. Various compromises may be effective for increasing genetic gain. Arbitrary definition of contemporary groups can include herd-year-season of freshening, lactation number, registered or nonregistered, sampling or postsampling daughters, and special treatments among others. The assumption of homogeneous genetic and residual variances is likely to be incorrect. Alternative methods include simple transformations, a two-step transformation, and multiple trait modeling. Multiple trait analyses may include the assumption of genetic correlations of unity, common genetic and heterogeneous residual variances, and joint estimation of genetic values and variances.

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INTRODUCTION

The objectives of this paper are 1) to review the basic principles involved in building models to adjust for effects common to contemporary groups, 2) to speculate on factors to consider in defining contemporary groups, and 3) to recommend areas in need of research.

Single trait evaluation will be considered throughout. Multiple trait evaluation involves most of the same problems with the added requirement of having to know the genetic and phenotypic covariances.

DISCUSSION

Models

The true model for a vector of records, y , can be written in general as:

$$y = f(g, e, \text{people})$$

This formulation emphasizes the obvious fact that records are influenced by joint effects of genotype, environment, and the people who manage the cows and that the form of this function is not known. Usually a linear model is assumed to be a reasonable approximation to the true model because of ignorance of the true model and for computing simplicity:

$$y = X\beta + Zu + e$$

where:

β is a vector that contains fixed effects of various factors including effects of management and effects common to contemporaries,

X is the matrix associating effects in β to y ,
 u is a vector of random genetic values in an animal model (or transmitting abilities in a sire model),

Z is the matrix associating effects in u to y , and

e is a vector of random residuals.

The effects of people on records usually are assumed to be accounted for by elements of β .

The expectations of y , u , and e are assumed to be:

$$E \begin{bmatrix} y \\ u \\ e \end{bmatrix} = \begin{bmatrix} X\beta \\ 0 \\ 0 \end{bmatrix}$$

If selection has occurred, which is the desired result of genetic evaluation, then it is unlikely that $E[u] = [0]$. The properties of best linear unbiased prediction (and selection index with perfect knowledge of β) as shown by Henderson (6) and others include unbiased prediction of u even when selection has occurred provided that records on which selection was based are included in the analysis and that all pertinent genetic relationships are specified correctly.

A basic principle of genetic evaluation is not to include records after selection unless the records on which selection was based are properly included in the analysis. This topic requires a full symposium in itself and will not receive any more attention in this presentation.

The assumption of no covariance between genetic and residual effects is also made:

$$V \begin{bmatrix} u \\ e \end{bmatrix} = \begin{bmatrix} G & 0 \\ 0 & R \end{bmatrix}$$

The linear model can accommodate nonzero covariances between elements of u and e as shown by Schaeffer and Henderson (17), but estimation of the covariances between elements of u and e appears nearly impossible.

Several simplifying assumptions are generally made about G and R . The consequences of each assumption not being true should be carefully considered. Often an assumption for the animal model is:

$$G = A\sigma_g^2$$

where:

A is the numerator relationship matrix, and σ_g^2 is the additive genetic variance ($\sigma_g^2/4$ for the sire model).

This genetic variance structure assumes:

- 1) only additive genetic effects are important (mixed model procedures can accommodate dominance and epistatic genetic effects [e.g., see Henderson (9)]),
- 2) genetic values are all from the same distribution and have a common genetic variance (the assumption may be adequate within a breed and region but across breeds and locally adapted strains the assumption is not likely to be true), and
- 3) genetic differences are the same when expressed in the presence of any fixed factors (e.g., in heifers and cows or in poorly and well-managed herds).

The last assumption may be incorrect in some cases and on some scales of measurement.

The residual covariance is often assumed to be:

$$R = I\sigma_e^2$$

where:

- I is the identity matrix of order the number of records, and σ_e^2 is the residual variance.

The implied assumptions are:

- 1) no covariances among the residual effects (in some cases this assumption is not satisfactory, for example, in the modified contemporary comparison evaluation, an environmental covariance among paternal half-sibs in the same herd is considered; similarly, variance due to sire by herd interaction can be accounted for by appropriate off-diagonal terms in R),
- 2) residual variance is not influenced by genetic value (e.g., this assumption would be violated if some sires had daughters with more uniform production than other sires), and
- 3) residual variances are expressed to the same extent for all fixed or management

factors (more variation, however, is usually observed in later lactations than in first lactations and in high producing herds than in low producing herds).

Some consequences of violations of the homogeneity of variance assumptions were discussed by Hill (11), Lofgren et al. (13), Van Vleck (19), and as part of this symposium by Vinson (22).

The mixed model equations for the general linear model assuming $cov(u, e) = 0$ are:

$$\begin{bmatrix} X'R^{-1}X & X'R^{-1}Z \\ Z'R^{-1}X & Z'R^{-1}Z + G^{-1} \end{bmatrix} \begin{bmatrix} \hat{\beta} \\ \hat{u} \end{bmatrix} = \begin{bmatrix} X'R^{-1}y \\ Z'R^{-1}y \end{bmatrix}$$

The variance-covariance matrix of prediction errors (PEV) of genetic values, $V(\hat{u}-u)$, under the assumption of the linear model being correct and for R and G known, is the lower right block of a generalized inverse of the coefficient matrix for the mixed model equations (6).

The goal of genetic evaluation is often thought to be to minimize PEV. In practice, however, the linear model may be a compromise between accounting for possible fixed effects and PEV. Thus, consideration of mean square error (MSE) would be appropriate for evaluating a model where as is well-known:

$$MSE = (Bias)^2 + PEV$$

For the genetic evaluation of animal i :

$$MSE_i = [E(\hat{u}_i - u_i)]^2 + V(\hat{u}_i - u_i)$$

In practice, true parameter values for the true model are required to evaluate bias. Limits for bias, however, might be approximated for some models for comparison with PEV.

Bias can arise for various reasons. Selection and assortative mating can be sources of bias. Biases can occur from failure of the model to account properly for fixed factors as well as from deliberate or unintentional preferential treatment. However, inclusion of unnecessary fixed factors in β will result in increased PEV but not increased bias.

Determining Contemporary Groups

A contemporary group effect is included in models to account for similar conditions and management practices. A usual way of attempting to identify such an effect is by herd and year and season (HYS) of calving with season somewhat arbitrarily defined. Addition of lactation number would be logical for analyses with a mixture of first and later lactation records. Herd-year-season effects have characteristics of both random and fixed effects. For mixed model evaluation either way is computationally similar. In addition to the difficult problem of whether to assume the HYS effects are fixed or random, there are more important considerations.

The advantage of considering HYS effects to be fixed in the mixed model equations is that the expectation of the solutions for genetic values does not include fixed effects, i.e.,

$$E(\hat{u}) \neq f(\beta)$$

This result can be shown algebraically even though the result is generally well-known. That $E(\hat{u})$ does not include terms included in β (whether fixed or random) can be shown by taking the expected value of the solution vector for \hat{u} for the mixed model equations after absorbing equations for β . For the case where $R = I$ and H^{-} is a generalized inverse of H :

$$\hat{u} = [Z'Z + G^{-1} - Z'X(X'X)^{-1}X'Z]^{-1} [Z'y - Z'X(X'X)^{-1}X'y]$$

To show that $E(\hat{u})$ does not include terms in β , substitute $X\beta$ for y in the last of the two terms and show that:

$$[Z'X\beta - Z'X(X'X)^{-1}X'X\beta] = 0$$

Factor to:

$$Z'[X - X(X'X)^{-1}X']\beta$$

Because $(X'X)^{-1}X' = X^{-}$ and $XX^{-}X = X$, the expression becomes:

$$Z'(X - XX^{-}X)\beta = Z'(X - X)\beta = 0$$

Thus, if nonrandom association occurs

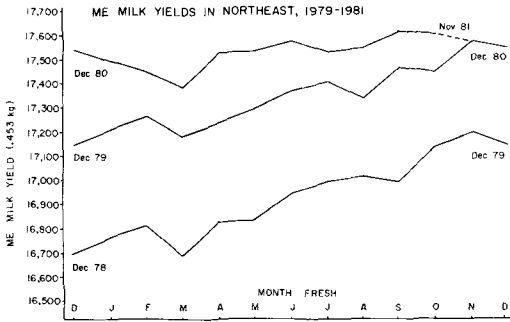


Figure 1. Average mature equivalent (ME) milk yields for first lactation Holsteins by month of freshening in the northeastern United States from December 1979 through November 1981 (K. Agyemang, 1984, personal communication).

between animals and effects considered fixed, then those effects do not introduce bias to genetic comparisons. Such associations can arise, e.g., from some sires being used primarily in high production herds or seasons and other sires in low production situations. If the HYS effects are treated as random, then the model for the genetic solutions contains functions of those effects with the corresponding potential for biased genetic evaluations.

The assignment of calendar day of freshening to a seasonal group is arbitrary. Often assignment is based on historical data. Means by calendar month of calving are examined to find sequences of months with similar production. Like sequences of months, however, may be different in different climatic conditions and may shift from year to year.

Figure 1 is a plot by calendar month of first freshening for 3 yr for records adjusted from previously estimated factors for age and month. The figure illustrates the difficulty of assigning calendar months to seasonal periods. A logical case could be made to have each calendar month represent a season of similar conditions. Even then cows freshening on February 28 would be assigned to a different season from cows freshening on March 1.

If a season is defined as a short period of time, e.g., a single calendar day, week, or month, another problem arises due to the limited number of animals of the same lactation freshening on a particular calendar day, week, or month. If no other animal freshens

TABLE 1. The fraction of herd-year-seasons (HYS) with only a single sire and fraction of records lost from Holstein sire evaluation for different groupings of months of freshening into arbitrary sets of two and three seasons per year for first freshenings from December 1979 through November 1981 in the northeastern United States. (K. Agyemang, 1984, personal communication).

	Single sire HYS	Records lost
	(%)	
Three seasons		
Aug to Nov		
Dec to Mar	27.5	7.2
Apr to Jul		
Jul to Oct		
Nov to Mar	29.5	8.0
Apr to Jun		
Two seasons		
May to Nov	21.2	4.1
Dec to Apr		
Jul to Nov	20.4	2.5
Dec to Jun		

in that season, then that record has no contemporary records available for comparison (Table 1). Thus, bias due to failure to adjust properly for seasonal conditions must be balanced against increase in prediction error variance due to loss of effective number of daughters.

Effective Number of Daughters

Effective number of daughters is often the term applied to the diagonal coefficient of the least squares matrix corresponding to, for example, a sire after absorption of the HYS equations. In fact, the inverse of the diagonal coefficient often is used to approximate prediction error variance. If the coefficient matrix after absorption is inverted, the diagonal term corresponds to PEV. Because off-diagonal elements also affect the inverse, and also are generated by absorption, the inverse of the effective number of daughters can be considered only as an approximation to PEV.

As an example of the effect of number of contemporaries on effective number of daughters, assume HYS are treated as fixed effects. Assume a bull has n daughters in a HYS with

m daughters of other bulls. The daughters of the bull in that HYS contribute n^* to the diagonal of the bull equation after absorption of the HYS equation with:

$$n^* = n - n^2 / (n + m) = nm / (n + m)$$

with corresponding terms subtracted from diagonals of equations of other bulls and off-diagonals for joint occurrence in the HYS. In this form, it is obvious that if m is zero, then the HYS adds nothing to effective number of daughters no matter how many daughters a bull has in that HYS. The third column of Table 2 also shows that when the number of comparisons is only one, i.e., $m = 1$, then the effective number of daughters in that HYS is $n^* = n / (n + 1)$, which is less than 1 no matter how large n is. As the number of contemporaries having other sire(s), m, increases, the effective number of daughters increases. The effect on PEV for all sires obviously also depends on the number of sires represented by the m contemporaries.

Because PEV is related to accuracy of evaluation and therefore to genetic gain from selection, i.e., $PEV = (1 - r_{uu}^2) \sigma_u^2$, the importance of the effective number of daughters contributed by each HYS comparison depends on whether $\sum_1 n_1^*$ is large or small. When $\sum_1 n_1^*$ is small, then each comparison is more important than when $\sum_1 n_1^*$ is large because the plot of r_{uu}^2 against $\sum_1 n_1^*$ for many models approaches 1.00 as $\sum_1 n_1^*$ becomes large.

TABLE 2. Effective number of daughters, n^* , when a sire has n daughters compared with m daughters of other sires when herd-year-season effect is considered fixed or random ($\gamma = \sigma_e^2 / \sigma_h^2 = 2$).

n	m	Fixed n^*	Random n^*
1	0	0	2/3
2	0	0	1
10	0	0	5/3
∞	0	0	γ
1	1	1/2	3/4
1	10	9/10	12/13
n	1	$n / (n + 1)$	$m\gamma / (n + 1 + \gamma)$
n	m	$nm / (n + m)$	$n(m + \gamma) / (n + m + \gamma)$

Thus, in balancing bias due to failure to adjust completely for contemporary effects against PEV, total effective number of daughters is important. If biases are randomly associated with daughters of sires, sire evaluation may not be greatly affected although evaluation and selection of bull dams may be seriously affected. However, systematic association of seasons or herd averages with sires may be important for sire evaluation and more important with a large number of daughters than with a small number. For example, if one bull had all daughters freshening in March and a second bull had all daughters freshening in June with both months assigned to the same season, and if both bulls had daughters that were equal genetically, then after adjustment for herd-year effects the mean daughter production would differ by about 100 kg (Figure 1). With many effective daughters, this difference is not regressed much toward 0 but with few daughters, the bias of 100 kg in the means is regressed considerably toward 0.

If HYS are treated as random effects, then in mixed model equations n_1^* is not 0 even when a daughter of a sire has no contemporaries. If $\sigma_e^2 / \sigma_h^2 = \gamma$ is the ratio of residual to HYS variance, then:

$$n^* = n - n^2 / (n + m + \gamma) = n(m + \gamma) / (n + m + \gamma)$$

Unless γ is very large, n^* approaches n much more rapidly as m increases than when HYS are considered fixed effects. When $m = 0$ and $n = 1$ with $\gamma = 2$, $n^* = 2/3$ as compared with 0 when HYS are fixed (Table 2). However, even when n becomes very large with $m = 0$, n^* only approaches γ so that the effective number of daughters is limited by the ratio, γ .

In a situation with small herd sizes, the need to balance bias from association with management or season against effective number of daughters becomes important. During the discussion, a compromise was proposed (C. R. Henderson, personal communication, 1986) for such situations. If γ is chosen to be 0, the effect is to treat HYS as fixed. Therefore, if γ^* is chosen to be smaller than σ_e^2 / σ_h^2 but not 0, then the result is intermediate between consideration of HYS as fixed and as random. How to determine γ^* to balance potential

bias and effective number of daughters may require simulation corresponding to a particular data set.

Another way to increase effective number of daughters is to assume that adjacent HYS effects are correlated. Certainly if HYS effects are random, those for adjacent year-seasons for a herd are likely to be correlated. This procedure salvages records in small HYS. What is involved is adding the inverse of the covariance matrix for the adjacent HYS effects, H_i^{-1} to the coefficients in $X'R^{-1}X$ corresponding to the whole herd, i.e., the diagonal block of $X'R^{-1}X$ for cows in the same herd would be $X_i'R_i^{-1}X_i + H_i^{-1}$ corresponding to elements of β_i for the i^{th} herd [e.g. (21)]. Such a procedure may also be indicated for other types of contemporary group effects, e.g., registered and unregistered subgroupings or cows treated or not treated with growth hormone in the same HYS. A variation of this procedure (Rudolph Preisinger, 1986, personal communication) is to consider herds as fixed effects and year-seasons within herds as random, correlated effects. A question to be answered is what length of a sequence of year-seasons for a herd should have nonzero covariances. In either case, estimation of the covariance matrix is necessary. An approximate covariance matrix may be satisfactory and could also allow for a compromise between treating the effects as random or as fixed.

Contemporary Groups

Thus far, principles for determining contemporary groups and some methods for analysis have been discussed. The contemporary group now commonly used, HYS of freshening grouping, has been used in examples with only brief mention of other groupings. Many alternatives for grouping in addition to time period are obvious. These can be treated as identifying either fixed effects or random and possibly correlated effects.

- 1) Subgroup by lactation number or groups of lactations such as 1st vs. non-1st, 1st vs. 2nd vs. later than 2nd, etc. When all lactations are included in a HYS group, the assumption is that the quantitative effect of management at the same time period is the same magnitude for all cows,

e.g., the same for 2-yr-olds as for mature cows for records expressed on a mature equivalent basis.

- 2) Subgroup by registered and nonregistered. The assumption is that herds with both kinds may treat the groups differently. There may not, however, be many herds with many cows in both groups.
- 3) Subgroup by whether the cows are sampling daughters of unproved bulls or are daughters of previously tested bulls. A variation of this would be to treat daughters of bulls with different priced semen as different groups. The bookkeeping needed for analysis may not be worth any reduction in bias.
- 4) Subgroup by management string or milking parlor within the farm. Again, keeping track of the cows might be difficult.
- 5) A very obvious and timely question is whether to subgroup cows treated with growth hormone separately from untreated cows in the same HYS. Burnside (1) has thoroughly discussed various options in the first presentation in this symposium.
- 6) Subgroup by various combinations of 1) to 5). The effective number of daughters, however, may be greatly reduced if such a combined contemporary group is treated as fixed.
- 7) The reason for any subgrouping is to remove effects of differential management. Often only the dairy herd manager can determine appropriate subgroupings. If an outsider can determine the potential for specific preferential treatment, a politically difficult decision may be to exclude such records completely.

Contemporaries

Perhaps the characteristics of the contemporaries as well as the management of contemporaries should be considered in the model. Previously, consideration to group sampling daughters separately from daughters resulting after bulls are proved was suggested. Another approach to consider would be to include different sire effects for the same bull. The effect might be considered random for sampling

daughters and fixed for daughters after the bull is proved (12, 14, 15, 18). Variations of this approach include: random for unregistered daughters and fixed for registered daughters; random for all records made before a proof is established and fixed for all others including later records of sampling daughters. The "official" proof would be based on evaluation of the random effect; records of daughters when the bull is "fixed" would provide connections and the "fixed" solution would not be published. The computational difficulties of adding extra sire effects will not be considered, but equations for such effects probably could be absorbed.

Contemporary Groups—Variances

Most genetic evaluation procedures assume all records come from the same population with constant genetic, σ_g^2 , and residual, σ_e^2 , variances. Vinson (22) in this symposium has reviewed evidence for and consequences of heterogeneous variances. Considerable evidence has accumulated that both genetic and residual variances are not always constant for all herds even within populations defined by short time spans and limited region (e.g., 12, 15, 16, 20). Differences in variances have been associated with production level herd and time period, although time is generally related somewhat to changes in production level. Figure 2 demonstrates the relationships of production level with sire and residual variances commonly found for milk records and for logarithmic transformation of milk records (2). The same pattern was also found for records made in 1976 and in 1984. Lactation yields associated with different parities have different variances even when adjusted to mature equivalents. Records of registered cows may have different variances from those of nonregistered cows. Records of cows in different housing, feeding, or milking systems may have different variances. Certainly cows on growth hormone or similar treatments may exhibit more or less variation than untreated cows. Combinations of factors such as identified here may have specific effects on the magnitude of variation. Differences in variation may be in either or both genetic and residual variances associated with any such factors.

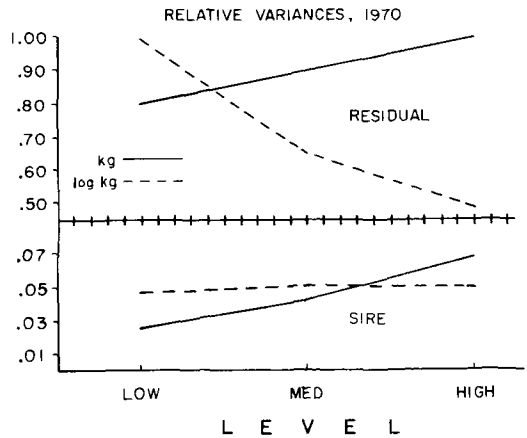


Figure 2. Sire and residual variances relative to the largest residual variances estimated for milk records and for logarithms of milk records of first lactation Holstein cows freshening in 1970 in herds classified as low, medium, and high for production (2).

A key question for dairy cattle breeders is not whether differences in genetic or residual variation occur but whether the assumption of homogeneous variances that is usually made results in an important reduction in genetic gain. Sensitivity analyses for situations that adequately mimic real situations may provide answers (4, 7, 11, 19).

What are some approaches for dealing with heterogeneous variances? The first is to ignore indications of heterogeneity and use average genetic and residual variances. This approach is generally used and can be a basis for comparison of other approaches. A second approach is to do a transformation of records, e.g., logarithmic, square root, or other power transformation and then to assume average genetic and residual variances are representative of all records. This approach simply substitutes the transformed record for the original record and does not require any new computer programs. One problem is how to explain and publish the evaluations. Another problem is how to decide what transformation is best.

A third approach fits the linear model for multiple traits (5, 10). The expression of a genotype in one environment is treated as a different trait from the expression in another environment (2, 3). Environments can be defined in many ways, but the method of de-

inition is assumed to put records into environments in which variances are homogeneous. One method is to define production levels as environments and to use different average genetic and residual variances for each environment. Options with this approach include assuming genetic correlations among genetic expression in different environments are 1 or are less than 1.

The fourth procedure is a modification of the general multiple trait method and would be easy to implement in most current evaluation methods and was discussed in detail by Hill (11) and in the review by Vinson (22). A constant genetic variance and genetic correlations of 100% are assumed, but the residual variances are assumed to be different. Basically the \mathbf{R} matrix is now not $I\sigma_e^2$ but is diagonal with possibly different $\sigma_{e_i}^2$. Computationally, for single trait models each record would be divided by σ_{e_i} , the appropriate residual standard deviation that may be arbitrarily assigned according to characteristics of the i th contemporary group. Again, the question of how to present the genetic evaluations to producers with different management characteristics must be answered.

Double standardization was proposed by Weller et al. (23) in which a linear change in genetic variance and a different linear change in residual variation are assumed for changes in an indicator characteristic. The first step of the method is to divide each record by the appropriate genetic standard deviation to force the genetic variance to be unity for all records. Then the phenotypic variance of the resulting record is calculated so that the second step is to divide by the new phenotypic standard deviation. Implicit in this method is the assumption of genetic correlations of unity across environments. Again, a question is how to scale the evaluations for producers.

Another class of methods uses data from individual herds to estimate genetic and residual variances appropriate for that herd. Such an approach generally assumes perfect genetic correlation between genotypic expression in different herds and thus is a multiple trait procedure. Evaluations standardized in this way, in theory, should be scaled for use in the individual herds. Many potential difficulties seem likely in estimating variances

for individual contemporary groups. One method would be to assume a constant genetic variance or a constant ratio of genetic to residual variance and to estimate only the residual variance. The ratio also could be allowed to change with characteristics of the contemporary group or herd. Estimates of variances from few records are unreliable. Therefore, a likely approach is to weight estimates for the contemporary group with prior values (5, 8, 11) obtained from pooled estimates for contemporary groups with similar characteristics, for example, production level and lactation number. Even with a weighting procedure, the question must be asked: what time period will be used for estimation of the herd or contemporary group variances?

Simulation to mimic a likely population may be one approach to answer the question of whether any of these rather difficult methods provides for important extra genetic gain as compared with simpler methods that assume constant variances or constant variances for all records in contemporary groups assigned to three or four subpopulations by production level or other characteristic (4).

SUMMARY AND CONCLUSIONS

The best model to approximate the true model for milk records is not easy to define. Genetic evaluations from linear models can be biased by selection and by inadequate adjustment for contemporary effects. Bias, however, must be balanced against prediction error variance. Choice of characteristics to define contemporary groups is not trivial and whether to treat effects associated with contemporary groups as fixed or random must consider both bias and PEV. Contemporary groupings that may need consideration as well as HYS of freshening are lactation number, registered and unregistered, whether sire was in sampling or was proved, and any special management conditions.

Research is required to determine how to deal with heterogeneous genetic and residual variances. Sensitivity analysis may show whether the assumption of common genetic and residual variances would be expected to result in an important reduction in genetic gain as compared with alternative evaluation methods. Alternative ways of grouping contem-

poraries or methods of handling heterogeneous variances must take into account that the goal is increased genetic gain per year and not necessarily reduced bias or PEV.

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