Identification of Factors Causing Heterogeneous Within-Herd Variance Components Using a Structural Model for Variances

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ABSTRACT

Many applications of mixed linear statistical models for genetic evaluation of dairy cattle assume that genetic and residual components of variance are each constant across environments. However, this assumption is violated for production and conformation traits, which can reduce accuracy of selection and cause biases in the proportions of breeding animals chosen from each environment. Best linear unbiased prediction can accommodate heterogeneous variances if the appropriate variance components are known. Variance components may need to be estimated within individual herds using Bayesian or empirical Bayes methods, but such approaches may not yet be computationally feasible on a national basis. For this study, a structural log-linear model for sire and residual variances was used to identify various management factors associated with differences in within-herd variance components. Increases of herd size and within-herd mean were associated with significant increases of within-herd residual variance for milk and fat yields, but residual variance of milk yield decreased slightly as the proportion of registered animals in the herd increased. Type of milking system, silage storage system, DHI testing program, use or nonuse of a TMR, and use or nonuse of automatic milking machine removal devices also significantly affected residual variances. However, differences in sire variances across levels of management factors were not significant. (**Key words**: variance components, model)

Abbreviation key: **AM-PM** = a.m.-p.m., **DHIR** = Dairy Herd Improvement Registry, **PHR** = proportion of herd that is registered, **RHA** = rolling herd average.

INTRODUCTION

Differences in within-herd variance components have been reported for economically important traits of dairy cattle [e.g., (4, 22, 23, 31)]. If not properly taken into account, heterogeneous variances across levels of classifications of the data can cause biases in BLUP breeding value predictions for individuals performing in environments with above or below average variances. However, BLUP can properly account for differences in within-subclass variances if all necessary variance components are known [e.g., (10)]. Unfortunately, this method may require estimation of a large number of variance components with very little information contributing to each component. In such a situation, likelihood-based methods, such as REML, which rely on an asymptotic justification, may fail to provide sufficiently accurate estimates (26, 31).

Some authors (3, 5) advocated stratification of the data by within-herd means and estimation of variance components within each stratum. Although this strategy increases the amount of information available for variance estimation, any heterogeneity that is due to effects other than the association between the mean and variance will be concealed. Famula (7) cautioned that estimates of genetic variances obtained in this manner may be biased

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by selection, because the strategy used to classify herds into groups is analogous to selection on sire progeny group means if sires are nonrandomly used across herds. Visscher (24) contended that such biases will likely be small, particularly if considerable environmental variation exists among herds.

Recent developments have focused on three topics. First, because phenotypic variances can be estimated more accurately than genetic variances with limited data, methods have been developed to pool within- and across-subclass phenotypic variance estimates (4, 12, 13, 29, 30). Estimates obtained in this manner have been used to standardize records in national genetic evaluations (13, 30). However, these methods do not properly model the covariance structure of the data, and differences in heritability or repeatability across environments cannot be detected.

Second, Gianola et al. (11) presented an empirical Bayes method for estimating within-herd genetic and residual components of variance using across-herd REML estimates as priors. Accuracy of resulting within-herd variance component estimates was improved greatly by incorporating across-herd information, particularly for the genetic component (28). Although this method could be implemented on an individual herd basis (28), it would be computationally taxing if relationships across a large number of herds were considered.

Third, Foulley et al. (8, 9) and San Cristobal et al. (20, 21) derived a procedure based on a generalized linear model (1, 16) that allows construction of a log-linear model for variance components (15) such that factors causing heterogeneity of genetic and residual variances can be identified and their effects quantified. Their (8, 9, 20, 21) method offers a potential computational advantage relative to procedures for within-herd variance estimation because it can be applied to a random subset of the data. Resulting estimates of effects of herd management factors on within-herd components of variance can be used to standardize records from other herds with similar management practices.

Keown (14) conducted an extensive survey of management practices on midwestern dairy farms, and phenotypic variation of herd mean milk yield was significantly associated with differences in nutritional programs, management practices, and facilities (2, 14). In addition, Padilla (18) and Padilla and Keown (19) reported differences in heritability estimates when the data were stratified by levels of herd management factors.

The objective of this study was to apply the structural log-linear model approach of Foulley et al. (8, 9) and San Cristobal et al. (20, 21) to the production and management data of Keown (14) 1) to identify management factors causing heterogeneity of within-herd genetic and residual variances for first lactation milk and fat yields and 2) to assess implications for breeding value prediction and selection associated with this method of accounting for heterogeneous within-herd variances.

MATERIALS AND METHODS

Management Data

A dairy management survey was conducted in 1985 and 1986 by Keown (14) using herds enrolled in DHI testing programs in Arkansas, Illinois, Iowa, Kansas, Missouri, Nebraska, North Dakota, Oklahoma, and South Dakota. Seven aspects of the dairy operation were assessed (14): 1) housing and facilities; 2) milking operation; 3) types of grains and forages fed and methods for storing and dispensing feed; 4) feeding of newborn calves; 5) additives and supplements fed to heifers and cows; 6) management practices, such as grouping of heifers and milking cows, computer usage, veterinary programs, estrus detection, mastitis control, and DHI usage; and 7) AI and methods of sire selection.

Padilla (18) and Padilla and Keown (19) found significant differences in within-herd phenotypic variances across levels of housing system, type of silage fed in the summer, and use or nonuse of a TMR or a buffer supplement. In addition to these factors, various other management characteristics were considered for the present study as possible causes of heterogeneous genetic and residual variances, including frequency of concentrate and roughage feeding, use or nonuse of AI, type of storage system for silage, type of milking system, type of DHI test, enrollment or nonenrollment in a veterinarian-supervised herd health program, type of dry hay fed in summer and

winter, presence or absence of automatic takeoff (milking machine removal) devices, DHI rolling herd average (**RHA**) for milk or fat yield (depending on the trait under consideration), state, herd size, and proportion of cattle in the herd that were registered (**PHR**). These management factors were described in detail by Keown (14).

Production Data

Production data, consisting of mature equivalent, twice daily milking, 305-d DHI milk and fat records from first lactation Holstein cows calving between June 1, 1984 and December 31, 1985 in the nine Midwestern states listed previously, were merged with the management data. Records of cows <18 mo or >40 mo of age at first calving were deleted. In addition, records <2500 kg of milk or 100 kg of fat or >18,000 kg of milk or 900 kg of fat, as well as records less than 40 d in length, were eliminated. Only herds containing ≥10 cows and sires having ≥5 progeny were considered. Data from 6503 progeny of 385 sires in 465 herds remained for the analysis. Year-season subclasses were assigned by date of calving using a 5-mo summer season (May through September) and a 7-mo winter season (October through April).

Statistical Analysis

The structural log-linear model approach of San Cristobal et al. (20, 21), which is an extension to genetic components of the procedure of Foulley et al. (8, 9) for modeling residual variances, was used to assess the effects of various herd management factors on within-herd genetic and residual variances of first lactation milk and fat yields. Because the methods were presented in detail by San Cristobal et al. (21), only a brief summary is given herein.

Following the notation of San Cristobal et al. (21), the data were assumed to arise from an overall population stratified into I herds, such that

$$\mathbf{y}_i = \mathbf{X}_i\boldsymbol{\beta} + \mathbf{Z}_i\mathbf{u}_i + \mathbf{e}_i \qquad i = 1, 2, \ldots, I \qquad [1]$$

where

$\mathbf{y}_i$ = data vector for herd i,
$\mathbf{X}_i$ = $n_i \times p$ incidence matrix for fixed effects,
$\boldsymbol{\beta}$ = $p \times 1$ vector of fixed effects,
$\mathbf{Z}_i$ = $n_i \times q_i$ incidence matrix for random effects,
$\mathbf{u}_i$ = $q_i \times 1$ vector of additive genetic effects (random) for herd i, and
$\mathbf{e}_i$ = $n_i \times 1$ vector of residuals.

Further, we assumed that

$$\mathbf{u}_i \sim \mathbf{N}(\mathbf{0}, \mathbf{A}_i\sigma^2_{u_i}) \qquad [2]$$

and

$$\mathbf{e}_i \sim \mathbf{N}(\mathbf{0}, \mathbf{I}_i\sigma^2_{e_i}), \qquad [3]$$

where

$\mathbf{A}_i$ = $q_i \times q_i$ additive genetic relationship matrix for herd i;
$\mathbf{I}_i$ = $n_i \times n_i$ identity matrix;
$\sigma^2_{u_i}$ and $\sigma^2_{e_i}$ = variance components corresponding to genetic and residual effects, respectively, in herd i; and
$\text{cov}(\mathbf{u}_i, \mathbf{e}_j') = 0$ for all i, j.

Now, let the vector of genetic values corresponding to herd i be written as

$$\mathbf{u}_i = \sigma_{u_i}\mathbf{S}_i\mathbf{u}^* \qquad [4]$$

where

$\mathbf{S}_i$ = $q_i \times q$ incidence matrix mapping the q_i animals in herd i (or sires used in herd i, for a sire model) to the q animals (sires) present in the population, and
$\mathbf{u}^*$ = $q \times 1$ vector of standardized genetic effects (random) for all animals present in the population,

assuming

$$\mathbf{u}^* \sim \mathbf{N}(\mathbf{0}, \mathbf{A}) \qquad [5]$$

where

$\mathbf{A}$ = q × q additive relationship matrix for all animals in the population.

The mixed model equations corresponding to Model [1] are

$$\begin{bmatrix} \mathbf{X'R^{-1}X} & \mathbf{X'R^{-1}Z^*} \\ \mathbf{Z^{*\prime}R^{-1}X} & \mathbf{Z^{*\prime}R^{-1}Z^*} + \mathbf{A^{-1}} \end{bmatrix} \begin{bmatrix} \hat{\boldsymbol{\beta}} \\ \hat{\mathbf{u}}^* \end{bmatrix} = \begin{bmatrix} \mathbf{X'R^{-1}y} \\ \mathbf{Z^{*\prime}R^{-1}y} \end{bmatrix} \quad [6]$$

where

$$\mathbf{X} = [\mathbf{X}_1'\mathbf{X}_2' \ldots \mathbf{X}_I']',$$
$$\mathbf{Z}^* = [(\sigma_{u_1}\mathbf{Z}_1\ \mathbf{S}_1)'\ (\sigma_{u_2}\mathbf{Z}_2\mathbf{S}_2)' \ldots (\sigma_{u_1}\mathbf{Z}_I\mathbf{S}_I)']', \text{ and}$$
$$\mathbf{R} = \text{Diag}\ (\mathbf{I}_i\sigma^2_{e_i}).$$

The structural model for variances involves the use of a log-link function (16), such that the transformed variance components can be described using a linear model, e.g.,

$$\ln\ (\sigma^2_{e_i}) = \mathbf{w}'_{e_i}\boldsymbol{\gamma}_e \qquad i = 1, \ldots, I \quad [7]$$

$$\ln\ (\sigma^2_{u_i}) = \mathbf{w}'_{u_i}\boldsymbol{\gamma}_u \qquad i = 1, \ldots, I \quad [8]$$

where

$\mathbf{w}_{e_i}$ = k_e × 1 incidence vector for herd i;
$\boldsymbol{\gamma}_e$ = k_e × 1 vector of fixed effects for the residual variance model;
$\mathbf{w}_{u_i}$ = k_u × 1 incidence vector for herd i, and
$\boldsymbol{\gamma}_u$ = k_u × 1 vector of fixed effects for the genetic variance model.

A log-link function implies that factors affecting variance components act in a multiplicative manner. Now, letting $\boldsymbol{\gamma} = [\boldsymbol{\gamma}'_e\boldsymbol{\gamma}'_u]'$, estimation of parameters for the variance model involved maximization of $L(\boldsymbol{\gamma}|\mathbf{y})$, which is the log-marginal likelihood of $\boldsymbol{\gamma}$ after integration of $\boldsymbol{\beta}$ and $\mathbf{u}$. A first-order expectation-maximization algorithm, which is presented in detail by San Cristobal et al. (21), was used for parameter estimation.

In the present study, the model for observations (Model [1]) was of the following form:

$$y_{ijkl} = H_i + YS_j + s_k + e_{ijkl} \quad [9]$$

where

y_{ijkl} = an observation of progeny l of sire k, arising in herd i and year-season j,
H_i = fixed effect of herd i (i = 1, 2, . . ., 465),
YS_j = fixed effect of year-season j (j = 1, 2, . . . , 4),
s_k = additive genetic effect of sire k (k = 1, 2, . . . , 385), and
e_{ijkl} = random residual (l = 1, 2, . . . , n_{ijk}).

Although use of an animal model would have been theoretically preferable, a sire model (Equation [9]) was chosen for computational simplicity. Because the inverse of the mixed model coefficient matrix in Equation [6] is required at each round of iteration, this procedure can become quite costly computationally, particularly when a large number of preliminary variance component models are used during the model selection process. Three generations of relationships among sires were considered for construction of the relationship matrix in Equation [5].

Initial screening of management factors as possible causes of heterogeneous within-herd variances was performed using Levene's test, which involved a one-way ANOVA on absolute deviations of observations from the means of their respective levels for each management variable (17). This preliminary test was used to investigate the null hypothesis of homogeneous phenotypic variances across herds, states, year-seasons, and levels of each categorical management variable. Levene's test was approximate in this case because correlations among observations that were due to genetic relationships and differences in variances that were due to fixed effects, other than the management factor being tested, were ignored.

For computational simplicity, selection of models for residual and sire variances was performed using a random subset of the full data. Herds with even-numbered DHI herd codes were chosen, and data were edited as described previously; the remaining data contained 232 sires, 239 herds, and 3078 records. Model [9] was used for the observations in all cases, and model selection for the within-herd variance components involved a two-stage procedure (21). First, the most suitable residual variance model for milk yield was chosen in a forward stepwise manner (using a likelihood ratio test) under the assumption of homogeneous sire variances. Second, the residual variance model was held constant, and differing models for within-herd sire variances were implemented. Once an overall model for sire and residual variances was chosen for this subset of the data, it was applied to an independent subset of the data consisting of herds with odd-numbered DHI herd codes (200 sires, 225 herds, 2857 records). This subset of the data was used to check normality and independence of residuals and to check whether significant effects of management factors on variance components were consistent across subsets. The resulting variance model was applied to milk yield for the full data.

Following the first stage of the model selection procedure, Model [7] for within-herd residual variances for milk yield contained the following parameters:

$$\gamma = [\mu_{(e)}\ DHIT_1\ DHIT_2\ MS_1\ MS_2\ ATO_1\ ATO_2\ TMR_1\ TMR_2\ STO_1\ STO_2\ \alpha_{RHA}\ \alpha_{HS}\ \alpha_{PHR}]' \quad [10]$$

where

$\mu_{(e)}$ = effect common to all herds;
DHIT = effect of DHI test type;
MS = effect of milking system;
ATO = effect of presence or absence of automatic takeoff devices;
TMR = effect of use or nonuse of a TMR;
STO = effect of silage storage system; and
α_{RHA}, α_{HS}, and α_{PHR} = regressions on rolling herd average, herd size, and proportion of animals in the herd that were registered, respectively.

A description of individual levels of management factors is given in Tables 1 and 3, and participation in each level is given in Table 1. Levels of management factors that contained very few observations were combined with those levels representing similar management practices whenever possible. To

TABLE 1. Description of relevant management and production factors.

Factor	Herds
State	(no.)
Illinois	158
Iowa	35
Missouri	75
North Dakota	9
South Dakota	30
Nebraska	57
Kansas	80
Arkansas	1
Oklahoma	20
DHI Test type	
DHIR,[1] Official DHI, AM-PM component	395
AM-PM with timer	70
Milking system	
Pipeline, bucket	338
Parlor	127
Automatic takeoff devices	
Yes	121
No	344
Silage storage system	
Conventional silo, bags, trench, other	322
Oxygen-limiting storage system	143
TMR	
Yes	103
No	362
Year-season records	
June 1, 1984 to September 30, 1984	3078
October 1, 1984 to April 30, 1985	2806
May 1, 1985 to September 30, 1985	549
October 1, 1985 to December 31, 1985	70
Covariates	$\bar{X}$
DHI Rolling herd average for milk, kg	7595
DHI Rolling herd average for fat, kg	277
Herd size, no. cows on DHI test	83
Proportion of animals in herd that were registered	.59

[1]DHIR = DHI Registry, AM-PM = a.m.-p.m.

render the model as simple as possible, levels that were thought, a priori, to be similar were combined if corresponding estimates of effects on variances components were similar. The preceding model was also applied to fat yield data; two management factors, TMR and PHR, did not significantly affect residual variances for fat yield and were removed from the model for this trait.

All factors in Equation [10] for residual variances, as well as several other management characteristics that were hypothesized to cause differences in additive genetic variation, were individually incorporated into the model for within-herd sire variances. Because no significant relationships were detected, Model [8] for within-herd sire variances for milk and fat yields contained only the overall mean, e.g.,

$$\gamma_u = [\mu_{(u)}] \qquad [11]$$

where $\mu_{(u)}$ = effect common to all herds. Equation [11] implies homogeneity of sire variances. However, the selection of a homogeneous model for sire variances (Equation [11]) and a heterogeneous model for residual variances (Equation [10]) does not necessarily imply that significant differences in heritability existed across herds, and this hypothesis was not tested explicitly.

Given solutions to the residual and sire variance models in Equations [10] and [11], respectively, within-herd variance component estimates were obtained as

$$\hat{\sigma}^2_{e_i} = \exp\,[\mathbf{w}'_{e_i}\hat{\gamma}_e] \qquad [12]$$

and

$$\hat{\sigma}^2_{u_i} = \exp\,[\hat{\mu}_{(u)}]. \qquad [13]$$

For example, for milk yield of a herd on DHI Registry (**DHIR**) test using a pipeline milking system, no automatic takeoff devices, a TMR, oxygen-limiting silage storage, RHA for milk yield = 7500 kg, herd size = 60 cows, and PHR = .8,

$$\mathbf{w}_{e_i} = [1\ 1\ 0\ 1\ 0\ 0\ 1\ 1\ 0\ 0\ 1\ 7500\ 60\ .8]'.$$

At convergence of the variance model, solutions to Equation [6] using $\sigma^2_{e_i} = \hat{\sigma}^2_{e_i}$ and $\sigma^2_{u_i} = \hat{\sigma}^2_{u_i}$ are empirical Bayes estimates and predictions of β and $\mathbf{u}^*$, respectively. Changes of standardized PTA (e.g., elements of $\hat{\mathbf{u}}^*$ for the heterogeneous model or, equivalently, $(1/\sigma_u)\,\hat{\mathbf{u}}$ for the homogeneous model) and rankings of sires were examined to assess effects on sire selection associated with accounting for heterogeneous within-herd variances using the structural model. As a check for nonrandom allocation of sires to environments with differing variances, a one-way ANOVA was used to examine the association between sire progeny groups and the natural logarithms of within-herd residual variance estimates obtained using Equation [12] for those herds in which the sires had progeny.

RESULTS AND DISCUSSION

As shown in Table 2, significant heterogeneity of phenotypic variances was detected across individual herds and states using Levene's test (17). A 10-fold range of estimated within-herd phenotypic standard deviations was observed. In agreement with Brotherstone and Hill (4), who suggested that factors causing heterogeneous within-herd phenotypic variances remain relatively constant over time, heterogeneity across year-seasons was not detected. However, the data for the present study spanned only 19 mo. Heterogeneity of phenotypic variances was also observed for several management factors, including type of DHI test, milking system, presence or absence of automatic takeoff devices, and silage storage system. However, differences in phenotypic variances that were due to nutritional factors, such as type of dry hay or silage fed and use or nonuse of a TMR or a buffer supplement, were generally small.

The structural log-linear model for variance components was first implemented for the homogeneous case, i.e., assuming that $\sigma^2_{e_i} = \sigma^2_e$ and $\sigma^2_{u_i} = \sigma^2_u$ for all i. In the homogeneous case, the first-order algorithm presented by San Cristobal et al. (20, 21) is equivalent to REML via the estimation-maximization algorithm. Estimates of dispersion parameters for milk yield under the homogeneous model were

$$\hat{\sigma}^2_e = \exp\,(14.334) = 1{,}679{,}489$$

TABLE 2. Probabilities associated with the null hypothesis of homogeneity of phenotypic variances across herds, states, year-season subclasses, and across levels of each of the herd management factors using Levene's test.

Management factor	P > F	
	ME[1] Milk	ME Fat
Herd	.0001	.0001
State	.0011	.044
Year-season	.95	.10
DHI Test type	.048	.01
Type of housing system	.17	.63
Type of milking system	.088	.055
Use or nonuse of automatic takeoff devices	.0001	.0001
Type of silage storage system	.016	.0009
Use or nonuse of a TMR	.58	.13
Use or nonuse of a buffer supplement	.36	.90
Type of dry hay fed in winter	.40	.61
Type of dry hay fed in summer	.54	.82
Type of silage fed in summer	.47	.60
Frequency of concentrate feeding	.08	.09
Frequency of roughage feeding	.22	.06
Use or nonuse of a herd health program	.94	.93
Use or nonuse of AI	.27	.21

[1]Mature equivalent, 305-d lactation, twice daily yield.

and

$$\hat{\sigma}_u^2 = \exp(11.695) = 119{,}970.$$

Similarly, the homogeneous model for fat yield gave the following estimates:

$$\hat{\sigma}_e^2 = \exp(7.589) = 1976$$

and

$$\hat{\sigma}_u^2 = \exp(4.765) = 117.$$

Heritability estimates for milk and fat yields were .267 and .224, respectively, for the homogeneous model.

As shown in Table 3, eight herd management characteristics were identified that significantly influenced within-herd residual variances for first lactation milk yield. Among covariates, within-herd residual variances for milk and fat yields increased as RHA increased, as suggested in previous studies (3, 5). A positive relationship between residual variance and herd size was also observed. For milk yield, residual variance decreased slightly as the proportion of registered animals in the herd increased. This relationship may be because of differences in management of registered and grade cattle, differing selection goals between the registered and grade populations, or a greater incidence of pedigree recording errors in grade herds (27).

Among categorical management factors, residual variances differed among types of DHI testing programs. In particular, herds enrolled in DHIR, official DHI, and a.m.-p.m. (**AM-PM**) component testing schemes, in which all milk weights in a 24-h period are recorded, had lower residual variances than herds on AM-PM test with a timer, in which only one milk weight per month is recorded on an alternating basis (6). This difference most likely reflects greater accuracy of measurement among testing plans in which all milkings are recorded. The difference in residual variances among DHI testing plans was slightly smaller for fat yield, perhaps because herds on AM-PM component testing may have larger residual variance than those on DHIR or official DHI. However, levels of management variables were pooled in the same manner for milk and fat yields to simplify interpretation of results.

Herds using a pipeline or bucket milking system had smaller residual variances than herds using a milking parlor, although the

reason for this difference is unclear. In addition, herds using automatic takeoff devices had smaller residual variances; these differences may be due to a more consistent time of milking machine removal when automatic takeoff devices are used.

Herds using a TMR had larger residual variances for milk yield, and herds using oxygen-limiting silage storage had larger residual variances than herds using conventional silos, trenches, or other types of silage storage. These differences may be due, in part, to higher means for herds with more progressive management practices.

Effects of state and housing type were not significant ($P < .05$) after the other factors were accounted for in Model [10]. Some confounding may likely exist, both among factors included in Model [10] and among other unidentified factors that affect residual variances. For example, herds housed in free stalls are more likely to use a parlor milking system, automatic takeoff devices, and group feeding, which can lead to difficulties in interpretation of results. Furthermore, several models may be constructed for variances that contain widely different management factors but that describe a similar portion of the variation among within-herd variance components.

No difference in sire variances were significant across levels of the management factors; however, the relatively small size of the present data set may preclude detection of such differences. In addition, Visscher (25) suggested that likelihood ratio tests may lack sufficient power to detect differences in within-herd genetic variances or heritability, particularly with limited data. Furthermore, because this study was relatively short and because all data were from a common geographical region, heterogeneity of sire variances may possibly exist with respect to time or regions even though the structure of the present data precluded its detection.

TABLE 3. Estimates of significant ($P < .05$) effects of herd management factors on within-herd residual and sire components of variance for milk and fat yield using the structural log-linear model for variances.

Factor	Description	ME[1]Milk	ME Fat
	Residual variance		
$\mu_{(e)}$	Intercept	13.31[2]	6.446
$DHIT_1$	DHIR,[3] Official DHI, AM-PM component	−.158	−.137
$DHIT_2$	AM-PM with timer	0	0
MS_1	Pipeline or bucket milking system	−.08	−.112
MS_2	Parlor milking system	0	0
ATO_1	Automatic takeoff devices used	−.108	−.071
ATO_2	Automatic takeoff devices not used	0	0
TMR_1	TMR used	.046	. . .
TMR_2	TMR not used	0	. . .
STO_1	Conventional silo, bags, trench, other	−.108	−.107
STO_2	Oxygen-limiting silage storage	0	0
α_{RHA}	Regression on rolling herd average	.000141	.000158
α_{HS}	Regression on herd size	.00163	.00155
α_{PHR}	Regression on proportion registered	−.0248	. . .
	Sire variance		
$\mu_{(u)}$	Intercept	11.7	4.769

[1]Mature equivalent, 305-d lactation, twice daily yield.

[2]Using the structural model for log variances, within-subclass variance components of, e.g., milk yield for a herd on DHIR test using a pipeline milking system, no automatic takeoff devices, a TMR, oxygen-limiting silage storage, rolling herd average for milk yield of 7500 kg, and herd size of 60 cows, 80% of which are registered, can be calculated as

$$\hat{\sigma}^2_{e_i} = \exp[13.31 - .158 - .08 + 0 + .046 + 0 + .000141\,(7500) + .00163\,(60) - .0248\,(.8)] = \exp(14.253) = 1{,}549{,}526$$

and

$$\hat{\sigma}^2_{s_i} = \exp(11.7) = 120{,}572.$$

[3]DHIR = DHI Registry, AM-PM = a.m.-p.m.

In Figure 1, the average of residual variance estimates for herds in which each sire was used, weighted by the number of progeny per herd by sire subclass, is plotted versus the total number of progeny of the sire. A threefold range in average residual variance estimates was observed across sire progeny groups, which is indicative of nonrandom use of sires across variance levels, particularly for sires with relatively few total progeny. Sires with ≥50 progeny, many of which would likely be popular AI sires, were apparently used, on the average, in herds with above average residual variances (Figure 1). Furthermore, the null hypothesis of constant residual variances across sire progeny groups was rejected ($P < .001$) within each of four progeny group categories (<10, 10 to 24, 25 to 49, or ≥50 total progeny), using a one-way ANOVA of the relationship between sire progeny group and ln ($\hat{\sigma}^2_{e_i}$) for the herd in which each progeny was housed.

Sires' standardized PTA, $\hat{u}^*$, before and after accounting for heterogeneous variances, are shown in Figure 2. Product-moment and rank correlations between sires' standardized PTA under the two models were >.99, which suggests that the overall impact on sire selection would be small. However, changes of PTA for individual sires may be somewhat larger.

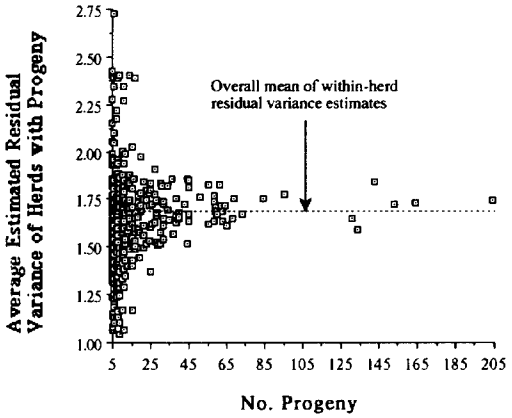

Figure 1. Number of progeny for each sire plotted versus the weighted average of within-herd residual variance estimates (million square kilograms), using the structural log-linear model, for milk yield for herds in which the sire's progeny performed.

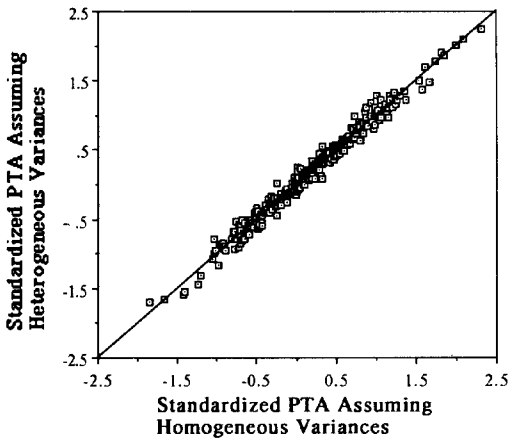

Figure 2. Plot of sires' standardized PTA, $\hat{u}^*$, for milk yield before and after accounting for heterogeneous variances using estimates from the structural log-linear model.

In Table 4, standardized PTA and rankings of the top 5% of sires, based on standardized PTA under the homogeneous model, are given. Some shuffling of the top sires occurred when heterogeneous within-herd residual variances were taken into account; for example, sires 133 and 79 dropped 6 and 10 places, respectively, and sires 79, 86, and 210 dropped from the top 5%. As shown in Table 5, an average rank change of 10, with a maximum of 72, was observed when the 385 sires were ranked by standardized PTA assuming either homogeneous or heterogeneous within-herd variances.

In Figure 3, the change of standardized PTA when heterogeneous variances were taken into account is shown as a function of the average estimated within-herd residual variance for herds in which the sire's progeny were housed. In Figure 3A, for sires for which standardized PTA was ≥1 under the homogeneous model, standardized PTA increased for sires for which progeny, on average, were housed in low variance environments and decreased for sires for which progeny were kept in high variance environments. This trend was reversed for sires for which standardized PTA under homogeneity was ≤−1, as shown in Figure 3B. This result supports the hypothesis that, when heterogeneity is ignored, superior sires used primarily in high variance environments are over-

TABLE 4. Standardized PTA for milk yield and rankings of the top 5% of sires before and after accounting[1] for heterogeneous within-herd variances.

Sire	No. of progeny	Homogeneous[2]			Heterogeneous[3]		
		PTA	SEP	Rank	PTA	SEP	Rank
46	45	2.31	.53	1	2.25	.53	1
155	84	2.09	.44	2	2.09	.44	2
175	61	1.99	.47	3	2.02	.47	3
110	143	1.86	.35	4	1.87	.35	5
138	204	1.83	.30	5	1.91	.30	4
59	55	1.75	.51	6	1.78	.51	6
338	6	1.68	.84	7	1.48	.87	9
250	6	1.61	.83	8	1.69	.81	7
11	7	1.58	.84	9	1.38	.86	10
73	30	1.53	.61	10	1.50	.59	8
133	13	1.38	.71	11	1.24	.71	17
70	164	1.35	.33	12	1.35	.33	11
132	10	1.31	.77	13	1.30	.76	13
183	73	1.27	.44	14	1.23	.43	19
79	19	1.25	.68	15	1.16	.66	25
210	14	1.25	.74	16	1.19	.75	21
208	10	1.24	.81	17	1.26	.80	16
233	5	1.22	.90	18	1.34	.89	12
86	58	1.20	.47	19	1.12	.47	27

[1]SEP = Standard errors of prediction.

[2]Assuming homogeneous variances.

[3]Accounting for heterogeneous residual variances using estimates from the structural model.

evaluated, and, similarly, inferior sires in high variance herds are underevaluated. In Figure 3, the coefficients of regression of change in sires' PTA on average within-herd estimated residual variance were significant ($P < .01$). Thus, biases in PTA of individual sires that were due to nonrandom use of sires across herds with differing variances may have been reduced by using within-herd variance estimates from the structural model.

TABLE 5. Changes of PTA for milk yield and rankings of the 385 sires present in the study when heterogeneous within-herd residual variances were either ignored or accounted for using estimates from the structural log-linear model.

Criterion	Value
Average absolute change in standardized PTA	.063
Average change in rank	10
Maximum absolute change in standardized PTA	.285
Maximum change in rank	72
Correlation between sires' PTA	.991
Rank correlation among sires	.992

CONCLUSIONS

The structural model for variance components succeeded in identifying management factors that cause heterogeneity of within-herd residual variances. However, differences in within-herd sire variances were not detected, and parameter estimates from the heterogeneous sire variance model were not very accurate. For this reason, shrinkage procedures may be desirable (21) when factors affecting genetic variances are estimated, particularly if the amount of data is limited. However, larger differences in within-herd genetic and residual variances may be expected for data that span a wider geographical range or a longer time than the data of the present study.

Identification of factors affecting within-herd sire and residual variances using the structural model (8, 9, 20, 21) may be more feasible computationally on a large scale than methods for direct estimation of within-herd variance components (11) because the structural model can be applied to a random subset of the data rather than to all US dairy herds. Estimates of factors affecting genetic and

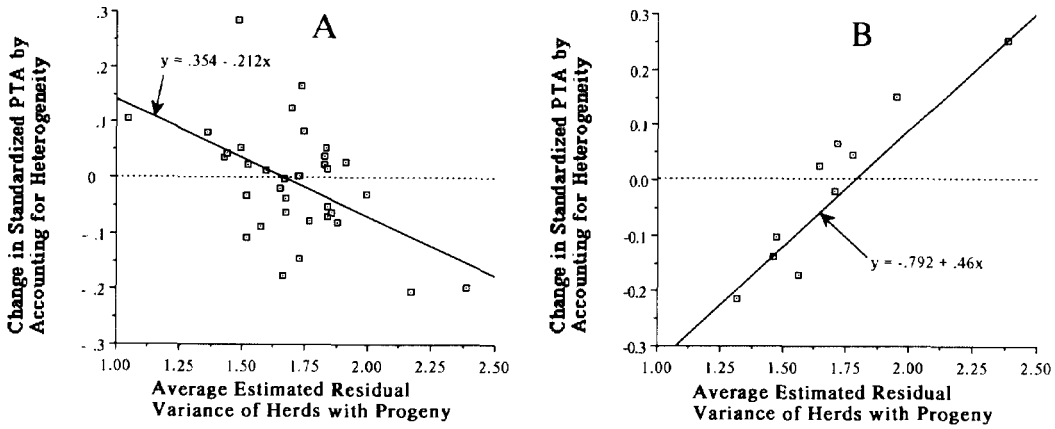

Figure 3. Change of standardized PTA of milk yield when heterogeneity was accounted for using residual variance estimates from the structural model versus the weighted average of residual variance estimates (million square kilograms) for herds in which the sire's progeny performed: A) for those sires for which standardized PTA assuming homogeneity was ≥1; B) for those sires for which standardized PTA assuming homogeneity was ≤–1.

residual variances could be used to approximate within-herd variance components for other herds for which management practices are known.

The overall effect of accounting for heterogeneous within-herd residual variances using the structural model on sire selection and accuracy of prediction was small. However, changes of rankings for individual sires occurred, which may be important with regard to young sires for which progeny are nonrandomly distributed across herds with differing variances. In addition, changes in PTA and rankings of cows could be larger, because a cow's own records and records of her maternal relatives are usually made within a single herd. Therefore, even though the impact on genetic progress of the population may be limited, an increase in "fairness" of genetic evaluations with respect to individual herds or animals may result.

The potential value of the methodology employed herein as a solution to the heterogeneous variance problem in national genetic evaluation procedures will depend on two considerations. First, sufficient management information for individual herds must be available to allow estimation of adjustment factors for variance components and approximation of within-herd variances for other herds with similar management practices (G. R. Wiggans, 1992, personal communication). Information regarding factors such as DHI test type, herd production, herd size, and PHR is readily available; however, data regarding on-farm facilities and specific management practices may be difficult and costly to obtain on a large scale. Second, an adequate proportion of the total variability of residual and genetic variance components must be explained by factors in the variance model. Development of a statistic analogous to the coefficient of determination would be useful to assess the proportion of variation of variance components accounted for by the structural model. Perhaps this statistic could be crudely approximated phenotypically by regressing the usual unbiased within-herd sample variance (sum of squared deviations from the within-herd mean/(number of observations – 1)) on $\hat{\sigma}^2_{P_i} = \hat{\sigma}^2_{e_i} + \hat{\sigma}^2_{u_i}$; $\hat{\sigma}^2_{e_i}$ and $\hat{\sigma}^2_{u_i}$ can be estimated using Equations [12] and [13]. (This procedure gave an approximate R^2 for variances of .11 when applied to the full heterogeneous model in the present study.) Presumably, this procedure could also be used with a model containing a subset of the parameters such that the increase in the proportion of variation of variances that is due to inclusion of an additional parameter could be calculated.

If sufficient data can be obtained and a large proportion of the variation of within-herd

variances can be explained by the structural model, useful adjustment factors for within-herd variances could probably be computed. However, if the majority of differences in within-herd variance components are due to random variation or due to management characteristics that are unknown, it may be desirable to estimate variance components within herds using Bayesian methods (11, 28) or approximations based on phenotypic variances (4, 30).

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