Heterogeneous Variances of Canadian Bull EBVs Over Time

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Introduction

Canadian Dairy Network is responsible for the calculation of genetic evaluations for all traits of interest in Canadian dairy breeds. As part of the regular validation of national evaluations, it is important to examine trends in estimated breeding values (EBVs) across birth years.

Average bull EBVs across birth years can be used to reflect genetic progress of bulls as they are proven and may include parent averages of young bulls tested in more recent years. Variances or standard deviations (SD) of bull EBVs across birth years can also be useful information. As intensity of selection increases, the young bulls entering A.I. testing programs become more alike and the variance of their resulting EBVs is reduced accordingly. Italian research has shown that heterogeneous variances of bull EBVs across birth years can have a significant impact on international evaluations calculated using the MACE procedure (1,3). Consequently, a procedure for standardizing the variance of de-regressed bull proofs across birth years was recently introduced in the national genetic evaluation system in Italy (2).

The objectives of this study were to estimate trends in bull EBVs across birth years for production and conformation traits in Canada, to examine the impact of a standardization procedure applied to production traits on national evaluations, and to develop a procedure for Interbull to account for heterogeneous variances in bull proofs over time when calculating international evaluations.

Trends in Standard Deviation of Bull EBVs

Official evaluations in Canada for May 1999 were analysed by birth year for bulls born in the most recent complete 10-year period (1984-1993). The SD of bull EBVs for milk, fat and protein yields as well as overall conformation, capacity, feet & legs and mammary system were calculated for each year of birth and compared to determine the degree of trend (Tables 1 and 2). Standard deviation of bull EBVs for production traits decreased by 14.3% for milk, 10.1% for fat and 14.9% for protein. These are in the same direction but lower in magnitude compared to those reported in the Italian research (1) since the CTDM recently introduced in Canada has reduced this time trend.

Standardizing Variance in National System

In Canada, bull EBVs from the Canadian Test Day Model are available separately for first, second and third lactation yields. A process for standardizing the lactation EBVs to a common variance is used before they are averaged into a single published EBV for each trait. This standardization procedure forces the SD of the lactation EBVs for all bulls born in the most recent complete 10-year period to be equal.

In order to standardize the bull EBVs across birth years the current procedure was modified for production traits only such that the multiplicative factors used to standardize the lactation EBVs to the desired variance were specific to each trait and year of birth. In order to avoid large fluctuations in the multiplicative standardizing factors applied for consecutive birth years, the SD for each year of birth was estimated as the average of the SD for the two previous, the current and the two next years, weighted at 25:50:100:50:25, respectively, using only SD for bulls born from 1985 to 1992. For bulls born before 1985, the SD estimate for 1985 was kept constant while the same strategy was applied for bulls born after 1992. Table 3 provides the SD of bull EBVs, parent average (PA) and Mendelian sampling (EBV - PA) for each birth

year before and after the use of the standardization procedure. In general, the standardization process decreased the SD of bull EBVs for older bulls and increased the SD for younger bulls. As expected, the SD of bull PAs was less affected since the adjustment was only applied to bulls/sires and not to cows/dams. An important conclusion from Table 3 is that the standardization of heterogenous variances of bull EBVs across birth years has resulted in an increase in the variance of the Mendelian sampling terms for younger bulls, indicating that their national evaluations are less accurate relative to older bulls, after standardization.

International Evaluations

The current procedure used by Interbull to estimate sire variance (4) for each trait and country combination calculates an overall estimate based on the national evaluations for all bulls born in a 10-year time period for Holsteins. Standardization of variance in bull EBVs across birth years within a national evaluation system would have relatively little impact on the Interbull estimate of the sire variance. It would, however, improve the international ranking of top younger bulls since, as a group the variance of their national EBVs was increased relative to older bulls, by standardization.

In order to avoid this potential bias in international evaluations, a new procedure for estimating genetic (co)variances for models with genetic groups was developed by Sullivan (Appendix, 5). This REML procedure, which also allows for the estimation of sire variances within birth year, was compared to the current Interbull methodology using national evaluations for protein yield in Holsteins from Canada (before and after standardization), Germany, Italy, the Netherlands and the United States. Table 3 shows that the Sullivan method, when applied within birth year, properly accounts for the increased variance in Mendelian sampling of young sires after standardization and would therefore result in international evaluations that are unbiased by heterogeneous variances in bull EBVs over time.

When the Sullivan and Interbull methods are compared (Table 4), the ratio of overall sire variance estimates is very close to unity for all countries except Italy, which indicates that the Interbull method results in an upward bias due to genetic groupings for that country.

Table 4 also presents ratios of sire variance estimates, based on the Sullivan approach, comparing alternative methods to account for heterogeneous variance of bull EBVs over time. Alternatives A and B allow comparison of the current time editing approach to bulls born since 1982 versus those born since 1989, respectively. The ratios of resulting sire variance estimates (B/A) presented in Table 4 indicate that using bulls born since 1982, as currently at Interbull, underestimates the overall sire variance for Germany (ratio of 1.03) and overestimates for the other countries, particularly Italy (ratio of .94). Comparing these results to ratios of alternative C to A, shows that with the Sullivan procedure for estimating sire variances, no time editing is required as long as bulls included in the estimation analysis represent the main bulls of interest, which are those born in more recent years (ie: 5 years). In this way, breeding values for all male ancestors can be used in the sire variance estimation procedure rather than including breeding values for only male ancestors born within the time edit period.

Recommendation

Based on the results of this research, it is recommended that Interbull procedures be modified to incorporate the variance estimation method developed by Sullivan and its application within birth year will account for heterogeneity of variance in national bull proofs over time.

References

1 Cassandro, M., Miglior, F., Carnier, P., Bittante, G., Canavesi, F., Santus, E. & Banos, G. 1997. Effect of standardisation of within country-year sire variance of de-regressed proofs on international evaluations. Interbull Bulletin No. 16, 16.

2 Miglior, F. 1999. Personal Communication.

3 Miglior, F., Weigel, K.A. & Banos, G. 1998. Impact of heterogeneity of variance over time on international comparisons using a simulation approach. Interbull Bulletin No. 17, 40.

4 Sigurdsson, A. & Banos, G. 1995. Estimation of genetic correlations between countries. Interbull Bulletin No. 11, 1.

5 Sullivan, P.G. 1999. Estimating genetic variances and covariances for models with genetic groups. Handout at the Interbull Meeting, Zurich, Switzerland.

Table 1. Standard deviation [(1)] of Holstein bull estimated breeding values (EBV) for production traits, and conformation traits in the Lifetime Profit Index

Birth Year	Production Traits				Conformation Traits				
	No. Bulls	Milk Yield	Fat Yield	Protein Yield	No. Bulls	Overall Conformation	Frame & Capacity	Feet & Legs	Mammary System
1984	237	847	26.2	23.0	341	4.58	4.72	4.57	4.76
1985	274	846	28.6	23.8	308	4.89	5.25	4.57	4.89
1986	316	796	28.5	23.6	316	4.69	4.62	4.91	4.77
1987	390	788	27.7	23.2	374	4.85	5.05	5.06	4.72
1988	393	727	30.0	21.7	383	4.29	4.69	4.25	4.44
1989	401	808	29.2	23.3	391	4.42	4.77	4.80	4.43
1990	419	731	24.8	20.8	415	4.65	4.72	5.15	4.61
1991	449	664	25.9	19.0	443	4.37	4.82	4.77	4.40
1992	442	739	24.2	20.3	435	4.41	4.88	4.46	4.42
1993	447	612	28.6	17.3	446	4.51	4.47	4.60	4.82

(1) Standard deviations for bull born in 1993 are associated with bulls with an average Reliability of approximately 5 percentage points lower for production traits compared to other birth years whereas average Reliability for conformation traits was the same across all birth years.

Table 2. Average standard deviation (SD) of Holstein bull EBVs within 3-year periods and percentage change in SD from 1984-1986 birth years to 1990-1992 birth years

Birth Year (Period)	Milk Yield	Fat Yield	Protein Yield	Overall Conformation	Frame & Capacity	Feet & Legs	Mammary System
1984 - 1986 (1)	830	27.8	23.5	4.72	4.86	4.68	4.81
1987 - 1989 (2)	774	29.0	22.7	4.52	4.84	4.70	4.53
1990 - 1992 (3)	711	25.0	20.0	4.48	4.81	4.79	4.48
Difference in SD (3) - (1)	-119	-2.8	-3.5	-0.24	-0.05	+0.11	-0.33
Difference in SD as a % of (1)	-14.3	-10.1	-14.9	-5.1	-1.0	+2.4	-6.9

Table 3. Standard deviation (SD) of bull EBV, bull parent average (PA) and Mendelian sampling, as well as the REML estimate of sire standard deviation, before and after the standardization of the SD of bull EBV across birth years applied for protein yield in Holsteins

Birth Year	Bull EBV		Bull PA		Mendelian Sampling (EBV - PA)			REML Estimate of Sire Standard Deviation [(1)]		
	Before	After	Before	After	Before	After	Diff.	Before	After	Diff.
1984	23.0	21.2	14.3	13.2	13.9	13.0	-.92	11.8	11.1	-.72
1985	23.8	21.9	16.4	14.8	13.8	13.6	-.16	11.6	10.8	-.82
1986	23.6	22.2	17.6	16.7	13.4	12.8	-.65	11.5	10.7	-.78
1987	23.2	21.8	16.6	15.7	14.4	13.6	-.77	11.6	11.0	-.63
1988	21.7	20.8	15.7	15.0	14.1	13.7	-.38	11.3	10.9	-.43
1989	23.3	23.3	15.2	14.5	14.8	15.2	+.35	12.1	12.1	+.06
1990	20.8	21.3	13.4	13.1	14.6	15.1	+.45	12.1	12.4	+.28
1991	19.0	19.6	13.6	13.2	13.9	14.4	+.49	10.7	11.4	+.72
1992	20.3	21.6	13.5	13.1	13.7	14.9	+1.25	11.2	12.2	+.96
1993	17.3	18.5	11.4	11.2	13.0	13.9	+.87	10.4	11.8	+1.34

(1) Method of REML estimation described by Sullivan, 1999 (See Appendix).

Table 4. Ratio of REML estimates of sire standard deviation for protein yield in Holsteins based on the Sullivan [(1)] procedure, the Interbull [(2)] procedure and alternative [(3)] methods to account for heterogeneous variance of bull EBVs over time

Country of Evaluation	Ratio of Estimates by Sullivan versus Interbull	Ratio of Estimates by Sullivan Using Alternatives (B) versus (A)	Ratio of Estimates by Sullivan Using Alternatives (C) versus (A)
Canada	.99	.98	.99
Germany	.99	1.03	1.04
Italy	.97	.94	.96
Netherlands	.99	.97	.97
United States	1.00	.97	.98

(1) Method of REML estimation described by Sullivan, 1999 (See Appendix).
(2) Method of REML estimation described by Sigurdsson and Banos, 1995 and used by Interbull.
(3) Alternatives include:
(A) time editing including breeding values for all bulls born since 1982
(B) time editing including breeding values for all bulls born since 1989
(C) time editing including breeding values for all bulls born since 1982, and estimating sire variance specific to bulls born since 1989

- APPENDIX -
REML estimation of heterogeneous sire (co)variances for MACE
(extracted from Sullivan, 1999)

An animal model with genetic groups can be described as;

$$\mathbf{y} = \mathbf{X}\beta + \mathbf{ZQg} + \mathbf{Za} + \mathbf{e}$$

where

y is a vector of observations,
β and **g** are vectors of fixed effects,
a and **e** are vectors of random effects,
X and **Z** are design matrices linking observations to the effects in the model, and
Q is a matrix linking animals in **a** to group effects in **g**.

Each row in **Q** sums to 1, and row k of **Q** is equal to a weighted-average of rows in **Q** corresponding to the ancestors of individual k. For example;

$$\mathbf{Q}_{k.} = \tfrac{1}{2}\mathbf{Q}_{s.} + \tfrac{1}{2}\mathbf{Q}_{d.}$$
$$\mathbf{Q}_{k.} = \tfrac{1}{2}\mathbf{Q}_{s.} + \tfrac{1}{4}\mathbf{Q}_{d_s.} + \tfrac{1}{4}\mathbf{Q}_{d_d.}$$

where s is the sire of k, d is the dam of k, d_s and d_d are the sire and dam of d. Matrix **Q** can be augmented to consider genetic groups as follows;

$$\mathbf{Q}^* = \begin{bmatrix} \mathbf{I} \\ \mathbf{Q} \end{bmatrix}$$

The rows of $\mathbf{Q}^*$ follow the same pattern as the rows of **Q** with respect to the dependency among an animal's row and the rows of its ancestors. Ancestors in $\mathbf{Q}^*$ include known ancestors and genetic groups of unknown ancestors.

The model can be re-written by combining **(Qg+a)** into a new vector **u**;

$$\mathbf{y} = \mathbf{X}\beta + \mathbf{Zu} + \mathbf{e}$$

$$\begin{bmatrix} \mathbf{y} \\ \beta \\ \mathbf{u} \\ \mathbf{e} \end{bmatrix} \sim \mathbf{MVN} \left(\begin{bmatrix} \mathbf{X}\beta \\ \beta \\ \mathbf{Qg} \\ \mathbf{0} \end{bmatrix}, \begin{bmatrix} \mathbf{ZG}^*\mathbf{Z}'+\mathbf{R}^* & \mathbf{0} & \mathbf{G}^*\mathbf{Z}' & \mathbf{R}^* \\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} \\ \mathbf{ZG}^* & \mathbf{0} & \mathbf{G}^* & \mathbf{0} \\ \mathbf{R}^* & \mathbf{0} & \mathbf{0} & \mathbf{R}^* \end{bmatrix} \right)$$

For a multiple trait model, $\mathbf{G}^*=\mathbf{A}\otimes\mathbf{G}$, where **A** is the numerator relationship matrix among animals and **G** is the genetic covariance matrix among traits. Similarly, $\mathbf{R}^*=\mathbf{B}\otimes\mathbf{R}$, where **B** is an identity matrix with individual rows zeroed if trait observations are missing for some individuals and **R** is the residual covariance matrix among traits.

Mixed model equations (MME) can be set up, with all fixed effects except genetic groups absorbed, as;

$$\begin{bmatrix} \mathbf{T}^{gg} \otimes \mathbf{G}^{-1} & \mathbf{T}^{gu} \otimes \mathbf{G}^{-1} \\ \mathbf{T}^{ug} \otimes \mathbf{G}^{-1} & \mathbf{Z}'\mathbf{MZ} + \mathbf{T}^{uu} \otimes \mathbf{G}^{-1} \end{bmatrix} \begin{bmatrix} \mathbf{g} \\ \mathbf{u} \end{bmatrix} = \begin{bmatrix} \mathbf{0} \\ \mathbf{Z}'\mathbf{My} \end{bmatrix}$$

or

$$\mathbf{Cw}=\mathbf{r}.$$

Matrix $\mathbf{M} = \mathbf{R}^{*-1} - \mathbf{R}^{*-1}\mathbf{X}(\mathbf{X}'\mathbf{R}^{*-1}\mathbf{X})^{-1}\mathbf{X}'\mathbf{R}^{*-1}$ and matrix **T** is equivalent to matrix **W** of Westell et al (1988). From Sigurdsson and Banos (1995);

$$\begin{bmatrix} \mathbf{T}^{gg} & \mathbf{T}^{gu} \\ \mathbf{T}^{ug} & \mathbf{T}^{uu} \end{bmatrix} = \begin{bmatrix} \mathbf{Q}'\mathbf{A}^{-1}\mathbf{Q} & -\mathbf{Q}'\mathbf{A}^{-1} \\ -\mathbf{A}^{-1}\mathbf{Q} & \mathbf{A}^{-1} \end{bmatrix}$$

Solve the MME with;

$$\hat{\mathbf{w}} = \begin{bmatrix} \tilde{\mathbf{g}} \\ \hat{\mathbf{u}} \end{bmatrix} = \begin{bmatrix} \mathbf{C}^{gg} & \mathbf{C}^{gu} \\ \mathbf{C}^{ug} & \mathbf{C}^{uu} \end{bmatrix} \begin{bmatrix} \mathbf{0} \\ \mathbf{Z}'\mathbf{My} \end{bmatrix}$$

EM-REML equations

The equation to estimate the genetic covariance between trait *i* and *j*, when **A** is of order *q*, is:

$$\hat{\sigma}_{ij} = \{\hat{\mathbf{a}}_i'\mathbf{A}^{-1}\hat{\mathbf{a}}_j + tr(\mathbf{A}^{-1}\mathbf{C}^{\mathbf{aa}}_{ij})\}/q$$

Since the model is specified in terms of **u** instead of **a**, this equation cannot be directly applied. The equation of Sigurdsson and Banos (1995) presumably accounted for the difference in model specification, but it was not clear if their equation was equivalent or an approximation of the above. It turns out that their equation is equivalent to the above when genetic groups are treated as fixed effects, but not when groups are treated as random. The following, on the other hand, will be proven equivalent to the equation above for models with either fixed or random genetic groups;

$$s_{ij} = \{\hat{\mathbf{w}}_i'\mathbf{T}\hat{\mathbf{w}}_j + tr(\mathbf{T}\mathbf{C}^{-1}_{ij})\}/q$$

The matrix **T** can be decomposed in the same way that $\mathbf{A^{-1}}$ was decomposed to derive the simple rules of Henderson (1976) to form $\mathbf{A^{-1}}$;

$$\mathbf{T} = \mathbf{UDU}'$$

where column *k* of **U** is a zero vector for genetic group *k*, and for animal *k* it is a vector with 1 on the diagonal and fractions summing to -1 above the diagonal in the rows of the animal's sire (.5) and dam (.5) in an animal model, or sire (.5) and maternal grandsire (.25) and maternal granddam (.25) in the current MACE model. If any of these ancestors are missing, then the rows of the corresponding genetic groups are used. Elements of diagonal matrix **D**, ignoring inbreeding, are equal to 2, 4/3 or 1 for an animal model, 16/11, 16/12, 16/15, or 1 for the MACE model, depending on the number and type of missing parents. Now;

$$\hat{\mathbf{w}}_i'\mathbf{T}\hat{\mathbf{w}}_j = \hat{\mathbf{w}}_i'\mathbf{UDU}'\hat{\mathbf{w}}_j$$

$$\because \quad \mathbf{U} = \begin{bmatrix}\mathbf{0} & | & \mathbf{U}_{.\mathbf{u}}\end{bmatrix}$$

$$\therefore \quad \hat{\mathbf{w}}_i'\mathbf{U} = \tilde{\mathbf{g}}_i'\mathbf{Q}^{*\prime}\mathbf{U}_{.\mathbf{u}} + \hat{\mathbf{a}}_i'\mathbf{U}_{\mathbf{uu}}$$

$$\hat{\mathbf{w}}_i'\mathbf{U} = \tilde{\mathbf{g}}_i'\mathbf{P} + \hat{\mathbf{a}}_i'\mathbf{U}_{\mathbf{uu}}$$

Any element (*rk*) of matrix **P** is;

$$\mathbf{P}_{rk} = \mathbf{Q}^*_{kr} - \tfrac{1}{2}\mathbf{Q}^*_{sr} - \tfrac{1}{2}\mathbf{Q}^*_{dr} = 0$$

for an animal model, or;

$$\mathbf{P}_{rk} = \mathbf{Q}^*_{kr} - \tfrac{1}{2}\mathbf{Q}^*_{sr} - \tfrac{1}{4}\mathbf{Q}^*_{d_s r} - \tfrac{1}{4}\mathbf{Q}^*_{d_d r} = 0$$

for the MACE model. Therefore;

$$\hat{\mathbf{w}}_i'\mathbf{U} = \hat{\mathbf{a}}_i'\mathbf{U}_{\mathbf{uu}}$$

$$\hat{\mathbf{w}}_i'\mathbf{UDU}'\hat{\mathbf{w}}_j = \hat{\mathbf{a}}_i'\mathbf{U}_{\mathbf{uu}}\mathbf{D}_{\mathbf{uu}}\mathbf{U}'_{\mathbf{uu}}\hat{\mathbf{a}}_j$$

$$\hat{\mathbf{w}}_i'\mathbf{T}\hat{\mathbf{w}}_j = \hat{\mathbf{a}}_i'\mathbf{A}^{-1}\hat{\mathbf{a}}_j$$

$$E(\hat{\mathbf{w}}_i'\mathbf{T}\hat{\mathbf{w}}_j) = tr(\mathbf{T}\mathbf{C}^{-1}_{ij})$$

$$E(\hat{\mathbf{a}}_i'\mathbf{A}^{-1}\hat{\mathbf{a}}_j) = tr(\mathbf{A^{-1}}\mathbf{C}^{\mathbf{aa}}_{ij})$$

$$\therefore \quad tr(\mathbf{T}\mathbf{C}^{-1}_{ij}) = tr(\mathbf{A^{-1}}\mathbf{C}^{\mathbf{aa}}_{ij})$$

$$s_{ij} = \hat{\sigma}_{ij}$$

Random genetic group effects

The equation for s_{ij} is the same even if groups are treated as random effects, because the group solutions are cancelled in the bi-linear form involving **T**. It is important to remember that treating groups as random does not modify matrix **T**, although it is often programmed this way because it is logistically easy to do. A genetic group covariance matrix is inverted and added into the group equations of the MME, and the usual choice for the group covariance matrix is the animal genetic covariance matrix among traits for each group, with zero covariances between groups. Other choices of covariance matrices could also be used for groups. Covariances between groups are zero, so the EM-REML equation for the group covariance between traits *i* and *j*, when there are *r* groups, is as follows;

$$s_{g_{ij}} = \{\hat{\mathbf{g}}_i'\hat{\mathbf{g}}_j + tr(\mathbf{C}^{\mathbf{gg}}_{ij})\}/r$$

The REML covariances among group effects are not recommended for use in the MME if the purpose of having groups in the model is to reduce selection bias caused when data used for selection are not available for the evaluation. In this case, fixed or "nearly" fixed group effects are suggested.

Heterogeneous covariances

The equation for s_{ij} can be easily partitioned to estimate sire variances by sire birth year, or any other definable animal grouping. An estimate of the trait *i* Mendelian sampling effect for animal *k* can be written as;

$$\hat{m}_{ik} = \hat{\mathbf{w}}_i' \mathbf{U}_{.k}$$

which is a linear equation involving only 3 terms in an animal model, or 4 terms in the MACE model. Now;

$$\hat{\mathbf{w}}_i' \mathbf{T} \hat{\mathbf{w}}_j = \sum_{k=1}^{q} \hat{m}_{ik} \hat{m}_{jk} d_k$$

$$tr(\mathbf{T}\mathbf{C}_{ij}^{-1}) = tr(\mathbf{U}\mathbf{D}\mathbf{U}'\mathbf{C}_{ij}^{-1}) = tr(\mathbf{D}\mathbf{U}'\mathbf{C}_{ij}^{-1}\mathbf{U})$$

or

$$tr(\mathbf{T}\mathbf{C}_{ij}^{-1}) = \sum_{k=1}^{q} d_k Cov((\hat{m}_{ik} - m_{ik}),(\hat{m}_{jk} - m_{jk}))$$

which is a summation of bi-linear forms, each of order 3 in an animal model or 4 in the MACE model.

Animal genetic covariances can be estimated separately for sub-groups of interest by splitting up the two summations and q in the equation for s_{ij}. For sub-group *m*;

$$s_{ijm} = \frac{1}{q_m} \sum_{k=1}^{q_m} d_k [\hat{m}_{ik} \hat{m}_{jk} + Cov((\hat{m}_{ik} - m_{ik}),(\hat{m}_{jk} - m_{jk}))]$$

Sire variances can be estimated by sire year of birth using the above equation, and heterogeneous sire variances can be included in the MACE model using procedures outlined by Henderson (1984). An alternative to modeling heterogeneity of sire variances would be to estimate and use sire variance estimates for a subset of bulls that are most affected by those variances in MACE. A suitable subset could be bulls born in the most recent five years. This approach should be preferred over time editing of proofs because it targets variances appropriate for young bulls, but without the loss of information from exclusion of proofs on parents born prior to the defined period for time editing. The suggested approach would also be less affected by time editing than is the current procedure because the same set of Mendelian sampling estimates would be used regardless of the number of additional animals included in the evaluation.

Henderson, C.R. 1976. A simple method for computing the inverse of a numerator relationship matrix used in prediction of breeding values. Biometrics 32:69-79.

Henderson, C.R. 1984. Applications of linear models in animal breeding. Chapter 33. University of Guelph, Guelph, Canada.

Sigurdsson, A. and Banos, G. 1995. Estimation of genetic correlations between countries. Interbull bulletin 11.

Sullivan, P.G. 1999. Estimating genetic variances and covariances for models with genetic groups. Distributed at Interbull meeting, Zurich, Switzerland.

Westell, R.A., Quaas, R.L. and Van Vleck, L.D. 1988. Genetic groups in an animal model. J. Dairy Sci. 71:1310-1318.