

## Estimation of segregation variance for birth weight in beef cattle

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### Abstract

Genetic evaluation using multibreed covariance theory requires estimating the segregation variance. The segregation variance is the amount by which the additive variance in the F2 exceeds that in F1. The goal of this research was to obtain REML estimates of the additive variances plus segregation variance, assuming equal environmental variances for all genetic groups. The data were originated in two experimental herds of beef cattle from New Zealand (NZ) and Argentina (AR). Records were birth weights of 4082 Angus–Hereford (NZ) and 6963 Nellore–Hereford (AR) cross calves, including purebreds, F1, backcrosses, F2, and advanced generations (F3, F4, F5). Variance components were estimated using an additive animal model by REML, with a first-derivative algorithm. The asymptotic standard errors of the REML estimates were calculated using the inverse of the information matrix. After 400 iterations, estimates of the additive variances (in kg<sup>2</sup>) were  $7.77 \pm 0.91$  (Angus) and  $10.02 \pm 1.11$  (Hereford), and estimate of the segregation variance was  $1.14 \pm 0.85$ , in NZ data. Whereas in AR data, estimates of the additive variances were  $6.59 \pm 0.71$  (Nellore) and  $8.97 \pm 0.75$  (Hereford), and estimate of the segregation variance was  $1.48 \pm 0.74$ . The error variances were estimated to be  $7.92 \pm 0.06$  in NZ and  $6.86 \pm 0.06$  in AR. Asymptotic tests (Likelihood Ratio and Lagrange Multiplier) of the hypothesis of null segregation variance suggested that this was not the case in these data.

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### 1. Introduction

Developing genetic evaluation procedures for breed crosses and composite populations is a neces-

sary follow up of current evaluation procedures. Genetic evaluation by Best Linear Unbiased Prediction (Henderson, 1984) requires computing the variance-covariance matrix for genetic merit. Lo et al. (1993) developed the theory of the covariance between relatives when two or more breeds are combined to form a composite population, using an additive model. The parameterization includes the

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additive variance for each purebreed and an extra component for each type of F1 crosses. This component is called segregation variance and is due to the difference in allelic frequencies between the two breeds. It is equal to the difference in additive variances between the F2 and F1 breed groups (Lande, 1981). The presence of segregation variance in the additive covariance matrix of composite populations is the main difference between the parameterization of Lo et al. (1993) and the one given by Elzo (1990). To obtain accurate estimates of segregation variance, records of F2 animals or advanced generations of inter se matings (F3, F4, F5 and so on) are needed. Backcross data are half as informative as F2 records.

Cantet and Fernando (1995) implemented the theory of Lo et al. (1993) to predict breeding values of crosses originated in two breeds. They discussed the consequences of not accounting for segregation variance while calculating prediction error variance of breeding value. There are no estimates of segregation variance using the animal model of Cantet and Fernando (1995). The objective of this research was to estimate additive variances and segregation variance in two experimental composite herds of Angus  $\times$  Hereford and Nelore  $\times$  Hereford cattle, using Restricted Maximum Likelihood (REML, Patterson and Thompson, 1971). The trait under study was birth weight.

## 2. Materials and methods

Birth weights from two experimental beef herds were used in this research. The first data set was developed by personnel of AgResearch, Ruakura Agriculture Centre, Hamilton New Zealand. The second data set was from a herd belonging to the National Institute of Agricultural Technology (INTA) at Leales Experimental Station, Tucumán, Argentina.

### 2.1. New Zealand (NZ) data

A heterosis retention experiment was carried out on a property of Landcorp Farming, Goudies Station, 60 km southeast of Rotorua, a typical temperate region. The experiment was designed to measure the

relative performances of advanced generations of rotation crosses and inter se matings with Angus and Hereford cattle. Previous analyses of the same data, as well as the description of the mating design and the herd management were given by Morris et al. (1994). Data used for the present analysis were 4082 birth weights from 27 different genotypes or breed types, including advanced generations such as F2, F3, F4 and F5. Records for the present study were collected between 1973 and 1990. Parents without records were added to the pedigree file so that the total number of animals for the analysis was 4939.

### 2.2. Argentinian (AR) data

Data were recorded from a rotational cross experiment at Leales Experimental Station, near San Miguel de Tucumán, province of Tucumán, in northern Argentina. The climate is subtropical with a rainy summer and a dry winter and spring. The birth weights of 6963 animals from 17 cross types of a rotational cross experiment between Hereford and Nelore cattle, were collected from 1960 to 1993. The genotypes were both purebreds, F1, F2, F3, first and second backcrosses and different rotation crosses. All cattle were kept in pastures without any supplemental feeding. Except for a few years in which artificial insemination was used, all matings were natural single-sire matings. In all years purebred matings to Hereford and Nelore allowed disentangling effects of genotype and year. Heifers were first bred to calve as 3 year olds. Calves were born mostly during spring. A total of 7357 animals were included in the pedigree file, including 90 bulls and 1725 cows.

### 2.3. Model of analysis

Each data set was analyzed separately with the following single-trait additive animal model (Cantet and Fernando, 1995):

$$y = X_1\beta_1 + X_2\beta_2 + Za + e \quad [1]$$

where  $y$ ,  $\beta_1$ ,  $\beta_2$ ,  $a$ , and  $e$  are the vectors of records, fixed environmental effects, mean genetic parameters, random breeding values (BV) and errors, respectively. The incidence matrices  $X_1$ ,  $X_2$  and  $Z$

relate records to fixed effects, genetic parameters and BV, respectively. For data set NZ, the effects included in  $\beta_i$  were sex of calf, age of dam (2, 3, 4, >4), year of birth (1,...,18), and date of birth (covariate), as in Morris et al. (1994). Corresponding effects for the AR data were sex of calf, age of dam (3, 4, 5–8, >8), and contemporary groups (1,..., 49). Following Hill (1982), two mean genetic parameters were included in  $\beta_2$  for both data sets: additive effects ( $A$ ) and dominance effects ( $D$ ). Let  $p_{Fi}$  and  $p_{Mi}$  be the breed composition of the sire and of the dam of individual  $i$ , where  $p_{Fi}$  ( $p_{Mi}$ ) is equal to 1 if the father (mother) of  $i$  is a purebred Angus or equal to 0 if a purebred Hereford, in the NZ data. For the AR data,  $p_{Fi} = 0$  for Hereford or  $p_{Fi} = 1$  for Nellore. Then, coefficients of  $A$  and  $D$  for animal  $i$  were calculated using the following algebraic modification of the formulae given by Lynch and Walsh (1998, p. 207):

$$A_i = p_{Fi} + p_{Mi} - 1$$

$$D_i = 2[p_{Fi}(1 - p_{Mi}) + p_{Mi}(1 - p_{Fi})] - 1$$

To complete the specification of the fixed effects, we parameterize  $\beta' = [\beta'_1 \beta'_2]$  so that  $X = [X_1 | X_2]$  be a full rank matrix.

The vector  $a$  was assumed to follow the multivariate Normal density with mean  $\theta$  and covariance matrix  $G$ . Diagonal element of  $G$  for animal  $i$  was calculated following Lo et al. (1993) and Cantet and Fernando (1995), as:

$$G_{ii} = f_{i1}\sigma_{A1}^2 + f_{i2}\sigma_{A2}^2 + 1/2 \text{cov}(a_S, a_D) + 2(f_{S1}f_{S2} + f_{D1}f_{D2})\sigma_{AS}^2$$

where  $f_{ij}$  is the expected fraction of genes in individual  $i$  that originates in parental breed  $j$ . The parameter  $\sigma_{A1}^2$  is the additive variance of Angus in NZ, or Nellore in data set AR, whereas  $\sigma_{A2}^2$  represents the additive variance of the Hereford breed in both data sets. The segregation variance  $\sigma_{AS}^2$  (Wright, 1968; Lande, 1981; Lo et al., 1993; Cantet and Fernando, 1995) is due to differences in gene frequencies between the two parental breeds. Once diagonal elements of  $G$  are calculated, Lo et al. (1993) suggested calculating off-diagonal elements by means of the following formula:

$$G_{ij} = \frac{1}{2}[\text{cov}(a_i, a_k) + \text{cov}(a_i, a_l)]$$

where  $a_i$  is the BV of  $i$  and  $k$  and  $l$  are the parents of animal  $j$ . Lo et al. (1993) further observed that  $G$  can be inverted as  $A$  in the animal model for one breed (Henderson, 1984), so that by inverting back  $G^{-1}$  in expression (36) of Lo et al. (1993),  $G$  is equal to:

$$G = (I - P_Q)^{-1}(D_1\sigma_{A1}^2 + D_2\sigma_{A2}^2 + D_S\sigma_{AS}^2) \times (I - P'_Q)^{-1}$$

$P_Q$  being the matrix that relates BV of progeny to BV of parents (Quaas, 1988). The diagonal matrices  $D_1$ ,  $D_2$  and  $D_S$  contain the fractions of either  $\sigma_{A1}^2$ ,  $\sigma_{A2}^2$  or  $\sigma_{AS}^2$ , that are present in the Mendelian sampling residuals of each individual, so that  $G_\epsilon = D_1\sigma_{A1}^2 + D_2\sigma_{A2}^2 + D_S\sigma_{AS}^2$  is the diagonal variance matrix of Mendelian residuals. The vector of errors is assumed to be distributed  $e \sim \text{MVN}(\mathbf{0}, I\sigma_e^2)$  and independent of  $a$ , meaning that all genetic groups have the same environmental variance. Finally, the distribution of the data vector  $y$  is  $\text{MVN}(X\beta, V)$  with  $V = ZGZ' + I\sigma_e^2$

#### 2.4. REML estimation of the variance components

Let  $\theta' = [\sigma_{A1}^2 \sigma_{A2}^2 \sigma_{AS}^2 \sigma_e^2]$  the vector of dispersion parameters to be estimated. The REML estimators of  $\theta$  were obtained by maximizing the logarithm of the restricted likelihood ( $L$ ) in model [1]. After Searle (1979, p. 91), the first derivatives with respect to the scalar variance components in  $\theta$  are equal to:

$$\frac{\partial L}{\partial \theta_i} = \text{tr}\left(\frac{\partial V}{\partial \theta_i} P\right) + y' P \frac{\partial V}{\partial \theta_i} P y$$

where  $P = V^{-1} - V^{-1}X(X'V^{-1}X)^{-1}X'V^{-1}$ . It is shown in Appendix A that the expression for the first derivative with respect to any of the additive variances ( $\theta_i$  with  $i = 1, 2, 3$ ), is as follows:

$$\frac{\partial L}{\partial \theta_i} = \text{tr}(D_i G_\epsilon^{-1}) - \text{tr}(C^{aa} H_i) - \hat{a}' H_i \hat{a}$$

where  $C^{aa}$  is the partition of the inverse of the coefficient matrix of the mixed model equations (MME) corresponding to  $a$ ,  $\hat{a}$  is BLUP( $a$ ), and matrix  $H_i$  is equal to:

$$\mathbf{H}_i = (\mathbf{I} - \mathbf{P}'_Q) \mathbf{G}_\varepsilon^{-1} \mathbf{D}_i \mathbf{G}_\varepsilon^{-1} (\mathbf{I} - \mathbf{P}_Q)$$

The expression for the first derivative with respect to the error variance  $\sigma_\varepsilon^2$  is derived in Appendix A, and it is as follows

$$\frac{\partial L}{\partial \sigma_\varepsilon^2} = \frac{n - r[\mathbf{X}] - q + \text{tr}(\mathbf{C}^{\text{aa}} \mathbf{G}^{-1})}{\sigma_\varepsilon^2} - \frac{\hat{\boldsymbol{\varepsilon}}' \hat{\boldsymbol{\varepsilon}}}{(\sigma_\varepsilon^2)^2}$$

where  $n$  is the number of animals with birth weight recorded (4082 for NZ and 6963 for AR),  $r[\mathbf{X}]$  is the rank of  $\mathbf{X}$  (24 for NZ, and 54 for AR),  $q$  is the number of animals in the pedigree file (4939 for NZ and 7357 for AR) and  $\hat{\boldsymbol{\varepsilon}} = \mathbf{y} - \mathbf{X}\hat{\boldsymbol{\beta}} - \mathbf{Z}\hat{\boldsymbol{\alpha}}$ .

The formulae for the REML estimates of the variance components are obtained by setting (A.5) and (A.9) to zero and solving for them. The REML estimate in iteration  $[r + 1]$  for any additive variance component ( $i = 1, 2, 3$ ) is equal to:

$$\sigma_{A_i}^{2[r+1]} = \frac{\hat{\boldsymbol{\alpha}}^{[r+1]'} \mathbf{H}_i^{[r]} \hat{\boldsymbol{\alpha}}^{[r+1]} + \text{tr}(\mathbf{C}^{\text{aa}[r+1]} \mathbf{H}_i^{[r]}) - \text{tr}[(\mathbf{D}_j \sigma_{A_j}^2 + \mathbf{D}_k \sigma_{A_k}^2) \mathbf{G}_\varepsilon^{-1} \mathbf{D}_i \mathbf{G}_\varepsilon^{-1}]^{[r]}}{\text{tr}(\mathbf{D}_i \mathbf{G}_\varepsilon^{-1} \mathbf{D}_i \mathbf{G}_\varepsilon^{-1})^{[r]}}$$

and for the error term is:

$$\sigma_\varepsilon^{2[r+1]} = \frac{[\hat{\boldsymbol{\varepsilon}}' \hat{\boldsymbol{\varepsilon}}]^{[r+1]}}{n - r[\mathbf{X}] - q + \text{tr}(\mathbf{C}^{\text{aa}[r+1]} \mathbf{G}^{-1[r]})}$$

These expressions were computed by a program written in FORTRAN and the use of sparse matrix techniques. Traces involving  $\mathbf{C}^{\text{aa}}$  were calculated using the factorization of Takahashi (Duff et al., 1992, pp. 273–275). Elements in the diagonals of the  $\mathbf{D}$ -matrices were calculated by an extension of the algorithm of Quaas (1976) for calculating diagonals of the additive relationship matrix.

The fraction of total additive variance that is present in different genotypes (see Table 1, p. 427 in Lo et al., 1993) was expressed as a  $h^2$  value. The difference in  $h^2$  for the F2 with respect to the F1 is due to  $\sigma_{\text{AS}}^2$ , and is a measure of the relative magnitude of the parameter.

### 2.5. Asymptotic covariance matrix of REML estimates

The asymptotic variance matrix of the REML estimates was calculated as the inverse of the

information matrix (Jiang, 1996):  $\text{Var}(\hat{\boldsymbol{\theta}}) = [\mathbf{I}(\boldsymbol{\theta})]^{-1}$ . The information matrix is minus the expectation of the second derivatives of the restricted likelihood, with element  $i, j$  being equal to (Harville, 1977):

$$\mathbf{I}_{ij}(\boldsymbol{\theta}) = \frac{1}{2} \text{tr} \left( \mathbf{P} \frac{\partial \mathbf{V}}{\partial \theta_i} \mathbf{P} \frac{\partial \mathbf{V}}{\partial \theta_j} \right)$$

In order to calculate the information matrix, its elements were expressed in terms of matrices previously defined, as follows:

$$\begin{aligned} \mathbf{I}_{ij}(\boldsymbol{\theta}) &= \text{tr}[\mathbf{D}_i \mathbf{G}_\varepsilon^{-1} \mathbf{D}_j \mathbf{G}_\varepsilon^{-1}] \\ &\quad - 2 \text{tr}[(\mathbf{I} - \mathbf{P}'_Q) \mathbf{G}_\varepsilon^{-1} \mathbf{D}_i \mathbf{G}_\varepsilon^{-1} \mathbf{D}_j \mathbf{G}_\varepsilon^{-1} (\mathbf{I} - \mathbf{P}_Q) \mathbf{C}^{\text{aa}}] \\ &\quad + \text{tr}[(\mathbf{I} - \mathbf{P}'_Q) \mathbf{G}_\varepsilon^{-1} \mathbf{D}_i \mathbf{G}_\varepsilon^{-1} (\mathbf{I} - \mathbf{P}_Q) \mathbf{C}^{\text{aa}} (\mathbf{I} - \mathbf{P}'_Q) \\ &\quad \times \mathbf{G}_\varepsilon^{-1} \mathbf{D}_j \mathbf{G}_\varepsilon^{-1} (\mathbf{I} - \mathbf{P}_Q) \mathbf{C}^{\text{aa}}] \quad i, j = 1, 2, 3 \end{aligned}$$

$$\begin{aligned} \mathbf{I}_{i4}(\boldsymbol{\theta}) &= \text{tr}[(\mathbf{I} - \mathbf{P}'_Q) \mathbf{G}_\varepsilon^{-1} \mathbf{D}_i \mathbf{G}_\varepsilon^{-1} (\mathbf{I} - \mathbf{P}_Q) \\ &\quad \times (\mathbf{C}^{\text{aa}} - \mathbf{C}^{\text{aa}} \mathbf{G}^{-1} \mathbf{C}^{\text{aa}})] \quad i = 1, 2, 3 \end{aligned}$$

$$\mathbf{I}_{44}(\boldsymbol{\theta}) = n - r(\mathbf{X}) - q + \text{tr}[\mathbf{C}^{\text{aa}} \mathbf{G}^{-1} \mathbf{C}^{\text{aa}} \mathbf{G}^{-1}]$$

2.6. Tests of the hypothesis  $H_0: \sigma_{\text{AS}}^2 = 0$  vs.  $H_a: \sigma_{\text{AS}}^2 > 0$

Asymptotic tests were employed as the sampling distributions of statistics which are functions of the REML estimate of  $\sigma_{\text{AS}}^2$  are unknown. The two tests used are based on the restricted likelihood, rather than in the full likelihood. The first one was the Likelihood Ratio (LR). Discussion of the distribution and properties of this statistic can be found in Verbeke and Molenberghs (1997). Let  $\boldsymbol{\theta}$  be the vector of dispersion parameters including  $\sigma_{\text{AS}}^2$ , and let  $\boldsymbol{\theta}_-$  be the respective vector without segregation variance. Then, the statistics  $\text{LR} = 2[L(\boldsymbol{\theta}) - L(\boldsymbol{\theta}_-)]$  asymptotically follows a mixture of  $0.5(\chi_0^2 + \chi_1^2)$ , under  $H_0$  (Self and Liang, 1996). The values of the two log-likelihoods were calculated as in Harville (1977):

$$\begin{aligned} L(\boldsymbol{\theta}) &= -\frac{1}{2} [\ln(\det(\mathbf{R})) - \ln(\det(\mathbf{C})) \\ &\quad - \mathbf{y}' \mathbf{R}^{-1} (\mathbf{y} - \mathbf{X}\hat{\boldsymbol{\beta}} - \mathbf{Z}\hat{\boldsymbol{\alpha}})] \end{aligned}$$

$C$  being the inverse of the coefficient matrix of the MME.

The Lagrange Multiplier test (LM), as implemented by Rahman and King (1997) was also used. Let  $s$  be the score (i.e. the first derivative of the REML likelihood function with respect to the segregation variance), and let  $I(\theta)$  be the information matrix, being both statistics evaluated under  $H_0$ . Then, the LM statistics  $LM=s/(I^{33})^{1/2}$  follows a standard normal density under  $H_0$  (Rahman and King, 1997). The scalar  $I^{33}$  is the diagonal element in the inverse of  $I(\theta)$  corresponding to  $\sigma_{AS}^2$ .

### 3. Results

#### 3.1. Genetic fixed effects

Besides  $A$  and  $D$ , the parameterization of Hill (1982) for two breeds includes the epistatic components  $A \times A$ ,  $A \times D$  and  $D \times D$ . An attempt to fit all five parameters in  $\beta_2$  ended with estimates of the epistatic components almost perfectly correlated to  $A$  and  $D$ , for both data sets. Therefore, as multicollinearity precluded the individual estimation of all five parameters, only  $A$  and  $D$  were included in  $\beta_2$ , and these estimates are shown in Table 1.

The estimate of  $A$  in NZ was not significant

( $P>0.05$ ), but was highly significant ( $P=0.000002$ ) in AR. None of the estimates of  $D$  were significantly different ( $P>0.05$ ) from zero. These results do not support the hypothesis of the presence of dominance effects for birth weight in both data sets.

#### 3.2. Estimates of the variance components

The REML estimates of variance components in both populations, with their asymptotic standard errors, under the models of Elzo (1990) and of Cantet and Fernando (1995), are shown in Table 2. Convergence was attained when  $\sigma_{AS}^2$  changed to the fourth decimal place, which happened at about iteration 400 in both data sets. The estimated additive variance of the Hereford breeds ( $\hat{\sigma}_{A2}^2$ ) was 29% larger than that of the Angus breed ( $\hat{\sigma}_{A1}^2$  in NZ), and 36% larger than that of the Nellore breed ( $\hat{\sigma}_{A1}^2$  in AR). The estimates of segregation variance ( $\hat{\sigma}_{AS}^2$ ) were equal to 1.14 kg<sup>2</sup> in NZ, and 1.48 kg<sup>2</sup> in AR.

Estimates of  $h^2$  for birth weight are presented in Table 3. Similar estimates of  $h^2$  were found in both populations. Estimated segregation variance represented 11.4 and 16% of the total additive variance in F2 animals for the NZ and AR data sets, respectively. The F2 is used as the reference population in Hill (1982) and Lo et al. (1993).

Table 1  
Estimates of mean additive ( $A$ ) and dominance ( $D$ ) effects (kg)

Data base	$A$	$D$
NZ	$-0.582 \pm 0.179$ , $P=0.132$	$-0.699 \pm 0.205$ , $P=0.113$
AR	$2.216 \pm 0.222$ , $P<0.001$	$0.202 \pm 0.220$ , $P=0.631$

Table 2  
Estimates of the variance components (in kg<sup>2</sup>)

Model	$\sigma_{A1}^2$	$\sigma_{A2}^2$	$\sigma_{AS}^2$	$\sigma_e^2$
Data base NZ				
Cantet and Fernando (1995)	$7.77 \pm 0.91$	$10.02 \pm 1.11$	$1.14 \pm 0.85$	$7.92 \pm 0.06$
Elzo (1990)	$7.85 \pm 0.91$	$10.39 \pm 1.13$	–	$8.12 \pm 0.06$
Data base AR				
Cantet and Fernando (1995)	$6.59 \pm 0.71$	$8.97 \pm 0.75$	$1.48 \pm 0.74$	$6.86 \pm 0.06$
Elzo (1990)	$7.23 \pm 0.72$	$9.22 \pm 0.75$	–	$6.99 \pm 0.05$

$\sigma_{A1}^2$ , additive variance of Angus for NZ or Nellore for AR;  $\sigma_{A2}^2$ , additive variance for Hereford;  $\sigma_{AS}^2$ , segregation variance;  $\sigma_e^2$ , error variance.

Table 3  
Heritabilities of different genotypes

Genotype	Cantet and Fernando (1995)	Elzo (1990)
NZ Data base		
Angus	0.495	0.492
Hereford	0.559	0.561
F1	0.529	0.529
F2	0.559	0.529
AR Data base		
Nellore	0.49	0.508
Hereford	0.567	0.569
F1	0.531	0.541
F2	0.574	0.541

### 3.3. Asymptotic (co)variances among REML estimates of the variance components

The asymptotic covariances among REML estimates of the variance components (expressed as correlations), are shown in Table 4. Correlations varied between 0.17, for  $r(\hat{\sigma}_{A1}^2, \hat{\sigma}_{A2}^2)$  in AR, to  $-0.54$  for  $r(\hat{\sigma}_{A1}^2, \hat{\sigma}_e^2)$  in both data sets. The correlations with the greatest values were  $r(\hat{\sigma}_{A1}^2, \hat{\sigma}_e^2)$  and  $r(\hat{\sigma}_{A2}^2, \hat{\sigma}_e^2)$ . In the NZ data,  $r(\hat{\sigma}_{AS}^2, \hat{\sigma}_{A2}^2)$  had a larger magnitude ( $-0.23$ ) than  $r(\hat{\sigma}_{AS}^2, \hat{\sigma}_{A1}^2)$  ( $-0.09$ ). Whereas in the AR data,  $r(\hat{\sigma}_{AS}^2, \hat{\sigma}_{A2}^2)$  and  $r(\hat{\sigma}_{AS}^2, \hat{\sigma}_{A1}^2)$  were similar:  $-0.27$  and  $-0.29$ , respectively.

### 3.4. Test of the hypothesis $H_0: \sigma_{AS}^2 = 0$

The  $P$  values of the LR test were smaller than 0.00001 for both NZ and AR, whereas the  $P$  values of the LM test were 0.093 and 0.063, for NZ and AR, respectively.

## 4. Discussion

The REML estimates of  $\sigma_{AS}^2$  were  $1.14 \text{ kg}^2$  for NZ and  $1.48 \text{ kg}^2$  for AR. For both populations the LR statistics strongly supported the rejection of the hypothesis that  $\sigma_{AS}^2$  was null. However, the LM statistics did not reach a significance level of 0.05, although the  $P$  values were  $<0.10$ . A major difference between the LR and the LM test is that the latter statistic involves the asymptotic variance of REML estimates, whereas the former does not. Note

Table 4  
Asymptotic covariances among REML estimates of the variance components (expressed as correlations)

	$\hat{\sigma}_{A1}^2$	$\hat{\sigma}_{A2}^2$	$\hat{\sigma}_{AS}^2$	$\hat{\sigma}_e^2$
NZ				
AR				
$\hat{\sigma}_{A1}^2$	1	0.09	$-0.09$	$-0.54$
$\hat{\sigma}_{A2}^2$	0.17	1	$-0.23$	$-0.45$
$\hat{\sigma}_{AS}^2$	$-0.29$	$-0.27$	1	$-0.28$
$\hat{\sigma}_e^2$	$-0.54$	$-0.52$	$-0.18$	1

that the coefficients of variation of REML estimates of  $\sigma_{AS}^2$  in Table 2 are of sizeable value (75% for NZ and 50% for AR), which may explain the different significance levels attained by both tests.

Overall, the results support the existence of segregation variance for birth weight in beef cattle. Using a two-trait sire-maternal grandsire model, Elzo and Wakeman (1998) obtained an estimate of segregation variance ('interbreed additive variance') for birth weight of  $0.21 \text{ kg}^2$ , in an Angus–Brahman composite population. This estimate is smaller than the two estimates of segregation variance obtained in the present research. Segregation variance is related to the size of the difference in gene frequencies between the two parental breeds (Lande, 1981; Lo et al., 1993). In the present study,  $\sigma_{AS}^2$  accounted for 11.4 and 16.0% of the total additive variance in the F2 animals, for the NZ and AR data, respectively. Whether these differences may be due to selection or drift, or a combination of both (Falconer and MacKay, 1996), is difficult to ascertain. The number of records of animals that provides most of the information for estimating  $\sigma_{AS}^2$  (F2, F3, F4, F5), in other non-maternally affected traits of data sets NZ and AR, precluded estimating the parameter with a reasonable level of precision. Alternatively, a model considering heterogeneous additive variance for a maternally influenced trait requires nine parameters to estimate (Cantet and Fernando, 1995), which in turn requires informative records on the dams from advanced generations, such as F2, F3, F4, and this makes it difficult to obtain accurate estimates of all parameters. Extension of the theory presented here to accommodate dominance effects was accomplished by Lo et al. (1995), but the number of parameters needed to fit a model with two breeds (25) poses a difficult problem of estimation, so that except for simple terminal schemes (Lo et al., 1997), wide

application of the additive plus dominance model in most experimental or field data sets is unlikely. The model used for the estimation of additive variances included the assumption of equal environmental variance among the purebreds and all crosses (F1, F2, F3, F4, F5, and all backcrosses). To test this assumption, estimates from a sire model with different environmental variances for 1) the purebreds, the F1, and all other genetic groups, using PROC MIXED of SAS, were obtained. The results showed quite similar estimates of the environmental variances in both data sets, specially for those associated with the purebreds and the F1 generation, which are non informative genotypes for segregation variance. This evidences the fact that all cows were managed in one herd for both data sets. Also, purebred and F1 animals were kept as controls during most years of the data collection.

Implementation of the standard version of the EM algorithm of Dempster et al. (1977) to estimate the variance components by REML (Searle et al., 1992, p. 302–303), in the model of Cantet and Fernando (1995), is not possible as  $\sigma_{A1}^2$ ,  $\sigma_{A2}^2$ , and  $\sigma_{AS}^2$  cannot be factored from the sufficient statistics (see expression (A.4) in Appendix A). Therefore, REML was implemented as suggested by Foulley (1993), and later used by Foulley and Quaas (1995) to estimate dispersion parameters in a mixed model with heterogeneous variance components.

We failed to obtain reliable estimates of the mean genetic parameters ( $A$ ,  $D$ ,  $A \times A$ ,  $A \times D$  and  $D \times D$ ) in the two-breed model of Hill (1982), due to almost perfect (close to 1 or  $-1$ ) correlations among most of the estimates. A similar situation occurred when the parameterization of Dickerson (1969,1973) was used (data not reported). This may indicate that estimates of mean genetic parameters to differentiate between additive and dominance, on one side, and epistatic effects, on the other side, may be difficult to obtain in most field data sets used for genetic evaluation purposes. Regardless of the mechanism of genetic determination that affects differences in mean cross value (additive, dominance, additive  $\times$  additive, etc.), a feasible solution is to fit the genetic means using the parameterizations of Dickerson (1969, 1973) or Hill (1982), and write down an additive variance-covariance matrix for the breeding values.

## 5. Conclusion

The REML estimates of segregation variance for birth weight, explained 11.4–16.0% of total additive variance in F2 animals from two composite populations of beef cattle. Asymptotic tests suggested that segregation variance was not null in these data.

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## Appendix A

*First derivatives of the logarithm of the restricted likelihood function with respect to the additive variances  $\sigma_{Ai}^2$  ( $i = 1,2,3$ )*

Using Searle (1979, p. 91), the first derivative of the logarithm of the REML likelihood with respect to any additive variance is equal to:

$$\frac{\partial L}{\partial \sigma_{Ai}^2} = -\frac{1}{2} \text{tr} \left( \frac{\partial \mathbf{V}}{\partial \sigma_{Ai}^2} \mathbf{P} \right) + \frac{1}{2} \mathbf{y}' \mathbf{P} \frac{\partial \mathbf{V}}{\partial \sigma_{Ai}^2} \mathbf{P} \mathbf{y} \quad (\text{A.1})$$

The first term on the right of (A.1) is:

$$\begin{aligned} \text{tr} \left( \frac{\partial \mathbf{V}}{\partial \sigma_{Ai}^2} \mathbf{P} \right) &= \text{tr} \left( \mathbf{Z} \frac{\partial \mathbf{G}}{\partial \sigma_{Ai}^2} \mathbf{Z}' \mathbf{P} \right) \\ &= \text{tr} [(\mathbf{Z}' \mathbf{P} \mathbf{Z})(\mathbf{I} - \mathbf{P}_Q)^{-1} \mathbf{D}_i (\mathbf{I} - \mathbf{P}_Q)^{-1}] \end{aligned} \quad (\text{A.2})$$

On using the equality  $\mathbf{Z}' \mathbf{P} \mathbf{Z} = \mathbf{G}^{-1} - \mathbf{G}^{-1} \mathbf{C}^{aa} \mathbf{G}^{-1}$  in (A.2), the trace is equal to:

$$\begin{aligned} &\text{tr} [(\mathbf{G}^{-1} - \mathbf{G}^{-1} \mathbf{C}^{aa} \mathbf{G}^{-1})(\mathbf{I} - \mathbf{P}_Q)^{-1} \mathbf{D}_i (\mathbf{I} - \mathbf{P}'_Q)^{-1}] \\ &= \text{tr} [(\mathbf{I} - \mathbf{P}'_Q) \mathbf{G}_\varepsilon^{-1} (\mathbf{I} - \mathbf{P}_Q)(\mathbf{I} - \mathbf{P}_Q)^{-1} \mathbf{D}_i (\mathbf{I} - \mathbf{P}'_Q)^{-1}] \\ &\quad - \text{tr} [(\mathbf{G}^{-1} \mathbf{C}^{aa} \mathbf{G}^{-1})(\mathbf{I} - \mathbf{P}_Q)^{-1} \mathbf{D}_i (\mathbf{I} - \mathbf{P}'_Q)^{-1}] \\ &= \text{tr} (\mathbf{D}_i \mathbf{G}_\varepsilon^{-1}) - \text{tr} [\mathbf{C}^{aa} (\mathbf{I} - \mathbf{P}'_Q) \mathbf{G}_\varepsilon^{-1} (\mathbf{I} - \mathbf{P}_Q) \\ &\quad (\mathbf{I} - \mathbf{P}_Q)^{-1} \mathbf{D}_i (\mathbf{I} - \mathbf{P}'_Q)^{-1} \mathbf{G}^{-1}] \\ &= \text{tr} (\mathbf{D}_i \mathbf{G}_\varepsilon^{-1}) - \text{tr} [\mathbf{C}^{aa} (\mathbf{I} - \mathbf{P}'_Q) \mathbf{G}_\varepsilon^{-1} \mathbf{D}_i (\mathbf{I} - \mathbf{P}'_Q)^{-1} \\ &\quad (\mathbf{I} - \mathbf{P}'_Q) \mathbf{G}_\varepsilon^{-1} (\mathbf{I} - \mathbf{P}_Q)] \\ &= \text{tr} (\mathbf{D}_i \mathbf{G}_\varepsilon^{-1}) - \text{tr} [\mathbf{C}^{aa} (\mathbf{I} - \mathbf{P}'_Q) \mathbf{G}_\varepsilon^{-1} \mathbf{D}_i \mathbf{G}_\varepsilon^{-1} (\mathbf{I} - \mathbf{P}_Q)] \end{aligned} \quad (\text{A.3})$$

The second term on the right of (A.1) is as:

$$\begin{aligned} & \mathbf{y}'\mathbf{P}\mathbf{Z}\frac{\partial\mathbf{G}}{\partial\sigma_{\text{Ai}}^2}\mathbf{Z}'\mathbf{P}'\mathbf{y} \\ &= (\mathbf{y}'\mathbf{P}\mathbf{Z})(\mathbf{I}-\mathbf{P}_{\text{Q}})^{-1}\mathbf{D}_i(\mathbf{I}-\mathbf{P}'_{\text{Q}})^{-1}(\mathbf{Z}'\mathbf{P}\mathbf{y}) \\ &= \hat{\mathbf{a}}'\mathbf{G}^{-1}[(\mathbf{I}-\mathbf{P}_{\text{Q}})^{-1}\mathbf{D}_i(\mathbf{I}-\mathbf{P}'_{\text{Q}})^{-1}]\mathbf{G}^{-1}\hat{\mathbf{a}} \\ &= \hat{\mathbf{a}}'[(\mathbf{I}-\mathbf{P}'_{\text{Q}})\mathbf{G}_{\varepsilon}^{-1}\mathbf{D}_i\mathbf{G}_{\varepsilon}^{-1}(\mathbf{I}-\mathbf{P}_{\text{Q}})]\hat{\mathbf{a}} \end{aligned} \quad (\text{A.4})$$

To simplify notation, let  $\mathbf{H}_i$  be equal to:

$$\mathbf{H}_i = [(\mathbf{I}-\mathbf{P}'_{\text{Q}})\mathbf{G}_{\varepsilon}^{-1}\mathbf{D}_i\mathbf{G}_{\varepsilon}^{-1}(\mathbf{I}-\mathbf{P}_{\text{Q}})]$$

Then, the derivative of the REML likelihood is obtained by replacing with (A.3) and (A.4) in (A.1) and using  $\mathbf{H}_i$ , as follows:

$$\frac{\partial L}{\partial\sigma_{\text{Ai}}^2} = \text{tr}(\mathbf{D}_i\mathbf{G}_{\varepsilon}^{-1}) - \text{tr}[\mathbf{C}^{\text{aa}}\mathbf{H}_i] - \hat{\mathbf{a}}'\mathbf{H}_i\hat{\mathbf{a}} \quad (\text{A.5})$$

*First derivatives of the logarithm of the restricted likelihood function with respect to the error variance  $\sigma_{\varepsilon}^2$*

Proceeding as in the previous section, the first derivative of the REML likelihood is:

$$\begin{aligned} \frac{\partial L}{\partial\sigma_{\varepsilon}^2} &= -\frac{1}{2}\text{tr}\left(\frac{\partial\mathbf{V}}{\partial\sigma_{\varepsilon}^2}\mathbf{P}\right) + \frac{1}{2}\mathbf{y}'\mathbf{P}\frac{\partial\mathbf{V}}{\partial\sigma_{\varepsilon}^2}\mathbf{P}\mathbf{y} \\ &= -\frac{1}{2}\text{tr}\left(\frac{\partial(\mathbf{I}\sigma_{\varepsilon}^2)}{\partial\sigma_{\varepsilon}^2}\mathbf{P}\right) + \frac{1}{2}\mathbf{y}'\mathbf{P}\frac{\partial(\mathbf{I}\sigma_{\varepsilon}^2)}{\partial\sigma_{\varepsilon}^2}\mathbf{P}\mathbf{y} \\ &= -\frac{1}{2}\text{tr}(\mathbf{P}) + \frac{1}{2}\mathbf{y}'\mathbf{P}\mathbf{P}\mathbf{y} \end{aligned} \quad (\text{A.6})$$

Let the matrix  $\mathbf{S}$  be equal to:

$$\begin{aligned} \mathbf{S} &= \mathbf{R}^{-1} - \mathbf{R}^{-1}\mathbf{X}(\mathbf{X}'\mathbf{R}^{-1}\mathbf{X})^{-1}\mathbf{X}'\mathbf{R}^{-1} \\ &= \frac{1}{\sigma_{\varepsilon}^2}(\mathbf{I} - \mathbf{X}(\mathbf{X}'\mathbf{X})^{-1}\mathbf{X}') \end{aligned}$$

Then, on using expression (A.3) in Johnson and Thompson (1994), the trace in the first term on the right of (A.6) can be written as:

$$\begin{aligned} \text{tr}(\mathbf{P}) &= \text{tr}(\mathbf{S}) - \text{tr}[(\mathbf{Z}'\mathbf{S}\mathbf{Z} + \mathbf{G}^{-1})^{-1}\mathbf{Z}'\mathbf{S}\mathbf{S}\mathbf{Z}] \\ &= \text{tr}(\mathbf{S}) - 1/\sigma_{\varepsilon}^2\text{tr}[(\mathbf{Z}'\mathbf{S}\mathbf{Z} + \mathbf{G}^{-1})^{-1} \\ &\quad ((\mathbf{Z}'\mathbf{S}\mathbf{Z} + \mathbf{G}^{-1}) - \mathbf{G}^{-1})] \\ &= \text{tr}(\mathbf{S}) - 1/\sigma_{\varepsilon}^2\text{tr}[\mathbf{I}_{\text{q}} - (\mathbf{Z}'\mathbf{S}\mathbf{Z} + \mathbf{G}^{-1})^{-1}\mathbf{G}^{-1}] \end{aligned}$$

$$= \frac{n-r(\mathbf{X})}{\sigma_{\varepsilon}^2} - \frac{q - \text{tr}[\mathbf{C}^{\text{aa}}\mathbf{G}^{-1}]}{\sigma_{\varepsilon}^2} \quad (\text{A.7})$$

Now, the second term on the right of (A.6) is:

$$\mathbf{y}'\mathbf{P}\mathbf{P}\mathbf{y} = \frac{\hat{\boldsymbol{\varepsilon}}'\hat{\boldsymbol{\varepsilon}}}{(\sigma_{\varepsilon}^2)^2} \quad (\text{A.8})$$

as:

$$\mathbf{P}\mathbf{y} = \mathbf{S}\mathbf{y} - \mathbf{S}\mathbf{Z}\hat{\mathbf{u}} = \mathbf{S}(\mathbf{y} - \mathbf{X}\hat{\boldsymbol{\beta}} - \mathbf{Z}\hat{\mathbf{u}}) = \mathbf{R}^{-1}\hat{\boldsymbol{\varepsilon}} = \frac{\hat{\boldsymbol{\varepsilon}}}{\sigma_{\varepsilon}^2}$$

After replacing with (A.7) and (A.8) in (A.6), we obtain:

$$\frac{\partial L}{\partial\sigma_{\varepsilon}^2} = -\frac{n-r(\mathbf{X}) - q + \text{tr}[\mathbf{C}^{\text{aa}}\mathbf{G}^{-1}]}{2\sigma_{\varepsilon}^2} + \frac{\hat{\boldsymbol{\varepsilon}}'\hat{\boldsymbol{\varepsilon}}}{2(\sigma_{\varepsilon}^2)^2} \quad (\text{A.9})$$

The next step is to set (A.5) and (A.9) to 0. For the additive variances we have that

$$\text{tr}(\mathbf{D}_i\mathbf{G}_{\varepsilon}^{-1}) = \text{tr}(\mathbf{C}^{\text{aa}}\mathbf{H}_i) + \hat{\mathbf{a}}'\mathbf{H}_i\hat{\mathbf{a}} \quad (\text{A.10})$$

The first term on the right of (A.10) is equal to:

$$\begin{aligned} \text{tr}(\mathbf{D}_i\mathbf{G}_{\varepsilon}^{-1}) &= \text{tr}(\mathbf{G}_{\varepsilon}^{-1}\mathbf{D}_i\mathbf{G}_{\varepsilon}^{-1}\mathbf{G}_{\varepsilon}) \\ &= \text{tr}[(\mathbf{G}_{\varepsilon}^{-1}\mathbf{D}_i\mathbf{G}_{\varepsilon}^{-1})(\mathbf{D}_i\sigma_{\text{Ai}}^2 + \mathbf{D}_j\sigma_{\text{Aj}}^2 + \mathbf{D}_k\sigma_{\text{Ak}}^2)] \\ &= \text{tr}(\mathbf{G}_{\varepsilon}^{-1}\mathbf{D}_i\mathbf{G}_{\varepsilon}^{-1}\mathbf{D}_i\sigma_{\text{Ai}}^2) \\ &\quad + \text{tr}[(\mathbf{G}_{\varepsilon}^{-1}\mathbf{D}_i\mathbf{G}_{\varepsilon}^{-1})(\mathbf{D}_j\sigma_{\text{Aj}}^2 + \mathbf{D}_k\sigma_{\text{Ak}}^2)] \\ &= \sigma_{\text{Ai}}^2\text{tr}(\mathbf{G}_{\varepsilon}^{-1}\mathbf{D}_i\mathbf{G}_{\varepsilon}^{-1}\mathbf{D}_i) \\ &\quad + \text{tr}[(\mathbf{G}_{\varepsilon}^{-1}\mathbf{D}_i\mathbf{G}_{\varepsilon}^{-1})(\mathbf{D}_j\sigma_{\text{Aj}}^2 + \mathbf{D}_k\sigma_{\text{Ak}}^2)] \end{aligned} \quad (\text{A.11})$$

To obtain the REML estimating equations in iteration  $[r]$ , the additive variance components  $\sigma^2 A_i$  ( $i = 1, 2, 3$ ) are factored out from (A.11), so that the resulting expressions are equal to:

$$\sigma_{\text{Ai}}^{2[r]} = \frac{\hat{\mathbf{a}}'\mathbf{H}_i\hat{\mathbf{a}}^{[r+1]} + \text{tr}(\mathbf{C}^{\text{aa}}\mathbf{H}_i)^{[r+1]} - \text{tr}[(\mathbf{D}_j\sigma_{\text{Aj}}^2 + \mathbf{D}_k\sigma_{\text{Ak}}^2\mathbf{G}_{\varepsilon}^{-1}\mathbf{D}_i\mathbf{G}_{\varepsilon}^{-1})^{[r+1]}]}{\text{tr}(\mathbf{D}_i\mathbf{G}_{\varepsilon}^{-1}\mathbf{D}_i\mathbf{G}_{\varepsilon}^{-1})^{[r+1]}} \quad (\text{A.12})$$

Factoring out  $\sigma_{\varepsilon}^2$  from (A.9), produces the following estimating equation for the error component:

$$\sigma_{\varepsilon}^{2[r]} = \frac{\hat{\boldsymbol{\varepsilon}}'\hat{\boldsymbol{\varepsilon}}^{[r+1]}}{n-r(\mathbf{X}) - q + \text{tr}(\mathbf{C}^{\text{aa}}\mathbf{G}^{-1})^{[r+1]}} \quad (\text{A.13})$$



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