Variance and covariance components for weaning weight for Herefords in three countries[1]

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ABSTRACT: Records from the Hereford Associations of the United States (USA), Canada, and Uruguay were used to estimate genetic and phenotypic variances and covariances for weaning weight. Estimation was done using a complete animal model, relatively large data sets, and the same methodology for the three countries in order to determine whether genetic parameters for weaning weight were homogeneous across environments. Data were composed of 2,322,722, 487,661, and 102,986 edited weaning weight records for USA, Canada, and Uruguay, respectively. Ten samples were obtained from each country by eliminating data from small herds with fewer than 500 records, selecting herds at random from the entire data set after removing the small herds, and then retaining the direct-sire-connected contemporary groups within each sample. The final sample sizes ranged from 9,832 to 46,377 records. An accelerated EM-REML algorithm was used in estimating the (co)variance components in each sample. The estimates were pooled by calculating the arithmetic mean of the 10 samples from within each country. Direct and maternal (in parentheses) heritability estimates were .24 (.16), .20 (.16), and .23 (.18) for USA, Canada, and Uruguay, respectively. Maternal heritabilities reported here are nearly 50% smaller than the values currently used in national genetic evaluation for the breed, which were estimated using sire-maternal grandsire models. Covariance between direct and maternal was negative in all countries, accounting for 6, 8, and 10% of the total phenotypic variation, and the total dam effect was 32.5, 37.0, and 34.0% in USA, Canada, and Uruguay, respectively. Total heritabilities were similar among the countries, with values of .19, .19, and .17 for the three respective countries. The similarity of genetic and environmental parameters across the three countries suggests that joint genetic evaluation is feasible across environments provided that the genotype × environment interaction is negligible and can be ignored.

Key Words: Beef Cattle, Genetic Parameters

Introduction

There has been increased interest for across-country genetic evaluation in beef cattle to increase accuracy of prediction and to enhance worldwide marketing of germ plasm. Models used to conduct international genetic evaluations and the ultimate usefulness of predicted breeding values will be determined by the similarity of genetic and environmental parameters across countries.

Even though estimates of genetic parameters for weaning weight in beef cattle are frequent in the literature from studies conducted in many countries and are summarized in several reviews (Mohiuddin, 1993; Koots et al., 1994a,b), it is difficult to use them to determine homogeneity of parameters across countries. Many studies report estimates obtained using either sire or sire-maternal grandsire models. Sire and sire-maternal grandsire models do not take into account different selection emphasis in males and females and selective mating. Most estimates derived using animal models were from analyses of small data files (Meyer, 1992b, 1993) or were from larger data sets with a restricted amount of pedigree information (Meyer, 1997).

To determine whether genetic parameters are homogeneous across countries for weaning weight, similar animal models and large data sets containing extended pedigree information must be used. Therefore, our objective was to estimate genetic and phenotypic variances and covariances for weaning weight in populations of Hereford beef cattle located in Canada, the

United States (USA), and Uruguay using a complete animal model, relatively large data sets, and similar methodology.

Materials and Methods

The data were composed of 2,322,722 edited weaning weight records from the American Hereford Association (**AHA**), 487,661 edited weaning weight records from the Canadian Hereford Association (**CHA**), and 102,986 edited weaning weight records from the Sociedad Criadores de Hereford del Uruguay. These three data sets were used in the genetic evaluation programs for the three breeds in 1997 and had been subjected to standard edits that included eliminating records of animals outside the range of three standard deviations from the overall mean and eliminating single-record contemporary groups. The basic definition of contemporary groups in all three within-country data sets was similar and was based on herd, sex, weaning management code (related to feeding regimen of calf), producer-assigned pasture code, and the date a group of calves were weighed at weaning. Weaning weight records within all three countries were preadjusted for age-of-calf and age-of-dam because the adjustments were derived from analyses involving the entire data set in each country; therefore, preadjusting the data would better correct for age-of-calf and age-of-dam effects than fitting these same effects in models used to analyze subsets of the data. The AHA and CHA combine their data to conduct genetic evaluation and use the same weaning weight age-of-calf and age-of-dam adjustments. These adjustments are contained in the Beef Improvement Federation (1996) guidelines. The age-of-dam and age-of-calf adjustments for the Uruguayan population were different from the ones used by AHA and CHA (J. K. Bertrand, personal communication). Meyer (1995) also reported that age-of-dam adjustments were different for beef data in Australia and New Zealand. Even though the age-of-dam adjustments between AHA-CHA and Uruguay were different in the present study, all countries used similar methodology that employed a fourth-degree polynomial based on dam age in days to adjust for differences in calf weaning weight due to the age of the dam of the calf. Research has shown that this method provides better adjustments than using age-of-dam year class adjustments, particulary for young females (Nelson, 1996).

In order to reduce the size of the data set, small herds with fewer than 500 weaning weight records were eliminated, then the data remaining for each country were sampled 10 times. To produce a sample, herds were selected at random with replacement from the data set available for each country. The selection of herds at each sampling was stopped due to computing considerations when the sample included between 25,000 and 50,000 records. The data were then checked for connectedness, and only contemporary groups with direct genetic connections through sires with progeny

in common were retained in each sample. Eliminating disconnected contemporary groups reduced the size of the final samples; however, only one of the final samples in one of the countries (Canada) had fewer than 10,000 records. Table 1 lists the descriptive statistics for the samples within each country.

A single-trait animal model was fit to the data in each sample including all the pedigree information available. The equation for the model in matrix notation was:

$$\mathbf{y} = \mathbf{X}\boldsymbol{\beta} + \mathbf{Z}\mathbf{a} + \mathbf{M}\mathbf{m} + \mathbf{W}\mathbf{pe} + \mathbf{e}$$

where $\mathbf{y}$ was the vector of observations; $\boldsymbol{\beta}$ was the vector of fixed effects (contemporary group); $\mathbf{a}$ was the vector of random additive direct genetic effects; $\mathbf{m}$ was the vector of random additive maternal genetic effects; $\mathbf{pe}$ was the vector of random permanent maternal environmental effects; $\mathbf{e}$ was the vector of random residual effects; and $\mathbf{X}$, $\mathbf{Z}$, $\mathbf{M}$, and $\mathbf{W}$ were known incidence matrices relating the observations to the respective fixed and random effects. The first and second moments for the model were assumed to be:

$$E\begin{bmatrix}\mathbf{a}\\\mathbf{m}\\\mathbf{pe}\\\mathbf{e}\end{bmatrix} = \begin{bmatrix}\mathbf{0}\\\mathbf{0}\\\mathbf{0}\\\mathbf{0}\end{bmatrix}$$

and

$$Var\begin{bmatrix}\mathbf{a}\\\mathbf{m}\\\mathbf{pe}\\\mathbf{e}\end{bmatrix} = \begin{bmatrix}\mathbf{A}\sigma_d^2 & \mathbf{A}\sigma_{d,m} & \mathbf{0} & \mathbf{0}\\\mathbf{A}\sigma_{d,m} & \mathbf{A}\sigma_m^2 & \mathbf{0} & \mathbf{0}\\\mathbf{0} & \mathbf{0} & \mathbf{I}\sigma_{pe}^2 & \mathbf{0}\\\mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{I}\sigma_e^2\end{bmatrix}$$

where σ_d^2 was the direct additive genetic variance; σ_m^2 was the maternal additive genetic variance; $\sigma_{d,m}$ was the covariance between additive direct and maternal genetic effects; σ_{pe}^2 was the permanent maternal environmental variance; σ_e^2 was the residual variance; and $\mathbf{A}$ was the additive numerator relationship matrix, ignoring inbreeding.

Estimation of (co)variance components were done with the program REMLF90 (Misztal, 1998), which uses an accelerated EM algorithm. The following populations parameters were derived from the variance components estimates: phenotypic variance (σ_p^2); total heritability (Willham, 1972: $h_T^2 = (\sigma_d^2 + 1.5\ \sigma_{d,m} + .5\ \sigma_m^2)/\sigma_P^2$) representing the regression of an animal's total genotype (direct and maternal) on its phenotype; direct heritability (h_d^2); maternal heritability (h_m^2); genetic correlation between direct and maternal effect ($r_{d,m}$); permanent maternal environmental variance as a proportion

Table 1. Summary of the data structure of 10 samples from USA, Canada, and Uruguay[a]

Item	USA			Canada			Uruguay		
	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max
No. of records	28,675	17,732	46,377	16,770	9,832	27,648	22,583	15,893	29,005
No. of animals	34,388	20,105	56,112	20,511	12,180	32,458	29,051	22,088	37,486
No. of sires	1,152	537	1,885	827	606	1,311	781	522	970
No. of dams	9,770	5,822	16,016	5,566	3,314	8,549	10,148	8,063	13,201
No. of herds	21	12	31	16	11	20	19	15	25
No. of contemporary groups	1,473	725	2,522	615	421	755	686	471	890

[a]Mean = arithmetic average of 10 samples; Min = minimum value; Max = maximum value.

of the total variance ($c^2 = \sigma^2_{pe}/\sigma^2_P$); percentage of total dam variation ($d_{d,m} = (\sigma^2_m + \sigma^2_{pe})/\sigma^2_P$); and proportion of the direct-maternal covariance to the total variance ($c_{d,m} = \sigma_{d,m}/\sigma^2_P$). The means and empirical SD of variances, covariances, and population parameter estimates from the 10 samples within each country were also computed.

Results and Discussion

Weaning weight (co)variance component estimates from the single-trait animal model for weaning weight are summarized in Table 2. Overall, the estimates were similar across countries; the mean of the pooled direct and maternal variances for each of the countries was always within the range of estimates for the remaining two countries. Furthermore, all the estimates for direct genetic variance, permanent maternal environmental variance, and direct-maternal covariance for the 10 samples in Canada and in Uruguay were within 2 SD of the mean estimates for USA, the country that had the largest across-sample SD for all the estimates. When considering the maternal genetic variance, 9 out of 10 samples for Canada and 8 out of 10 for Uruguay were within 2 SD of the mean estimate for USA. The direct variance estimate for Uruguay was 5% and 14% larger than for USA and Canada, respectively. However, the phenotypic variance was also larger in Uruguay, so the final heritability was similar for the three countries. The same trend was reflected in the maternal component; the estimate for Uruguay was 22 and 15% larger

than for USA and Canada; however, the proportion of the variation due to total dam effects (direct maternal plus permanent maternal environmental effects) was similar among countries. Total dam effect was 32.5, 37.0, and 34.0% for USA, Canada, and Uruguay, respectively. Similar results were reported by Waldron et al. (1993); the total variation due to maternal effects was from 24 to 35% of the total variation. Permanent maternal environmental variances were very similar among countries, accounting for 16 to 17% of the total phenotypic variance. These estimates were usually higher than previously reported from studies that used sire-maternal grandsire and sire-dam models (Bertrand and Benyshek, 1987; Johnston, 1992; de Mattos et al., 1996; Ferreira et al., 1999) but were in agreement with several other studies that used animal models (Snelling et al., 1996; Meyer, 1992b, 1993, 1995; Dodenhoff et al., 1998; Ferreira et al., 1999). Permanent maternal environmental variances were as important as the direct maternal variances, in agreement with Meyer (1992b, 1993), who reported similar results for the Hereford breed in Australia. Furthermore, Birchmeier and Cantet (1998, personal communication) found that 19% of the variation was due to maternal permanent maternal environmental effects for Hereford cattle in Argentina.

Heritabilities estimates and genetic correlations are summarized in Table 3. The results for direct heritability were somewhat smaller than some literature estimates (Pahnish et al., 1961; Blackwell et al., 1962; Cunningham and Henderson, 1965; Koch et al., 1973). More

Table 2. Means, SD, minimums, and maximums for the (co)variance estimates for weaning weight from the 10 samples within each country

(Co)variance[a]	USA				Canada				Uruguay			
	Mean	SD	Min	Max	Mean	SD	Min	Max	Mean	SD	Min	Max
σ^2_d	137.5	28.9	79.6	177.3	125.6	13.2	108.4	148.8	144.4	28.6	102.2	194.4
σ^2_m	93.4	14.8	74.7	126.7	99.5	16.5	77.5	129.8	114.9	14.3	91.3	145.1
$\sigma_{d,m}$	−48.0	18.8	−75.0	−19.9	−38.8	12.9	−66.0	−20.1	−65.0	13.1	−86.0	−45.9
σ^2_{pe}	94.9	19.5	48.5	120.1	128.9	14.1	101.0	147.8	99.5	5.8	90.4	108.7
σ^2_P	579.9	45.3	520.3	678.3	617.0	27.7	573.8	654.6	630.0	30.5	581.5	681.6
σ^2_e	302.1	40.1	253.7	393.7	301.8	12.7	282.8	333.0	336.2	21.4	283.9	364.6

[a]σ^2_d = direct additive genetic variance (kg^2), σ^2_m = maternal additive genetic variance (kg^2), $\sigma_{d,m}$ = direct and maternal covariance (kg^2), σ^2_{pe} = permanent maternal environmental variance (kg^2), σ^2_P = phenotypic variance (kg^2), and σ^2_e = error variance (kg^2).

Table 3. Means, SD, minimums, and maximums for the heritability
and other parameter estimates for weaning weight
from the 10 samples within each country

Parameter[a]	USA				Canada				Uruguay			
	Mean	SD	Min	Max	Mean	SD	Min	Max	Mean	SD	Min	Max
h^2_d	.24	.06	.15	.32	.20	.02	.19	.23	.23	.04	.17	.29
h^2_m	.16	.03	.13	.23	.16	.02	.13	.20	.18	.03	.15	.25
$r_{d,m}$	−.42	.13	−.60	−.22	−.35	.10	−.54	−.20	−.50	.05	−.57	−.41
c^2	.16	.03	.09	.20	.20	.02	.17	.23	.15	.01	.14	.17
$d_{d,m}$	.33	.03	.28	.38	.37	.03	.33	.42	.34	.03	.30	.41
$c_{d,m}$	−.08	.03	−.03	−.13	−.06	.02	−.03	−.11	−.10	.02	−.07	−.12
h^2_T	.19	.04	.15	.29	.19	.03	.14	.23	.17	.02	.12	.20

[a]h^2_d = Direct heritability for weaning weight, h^2_m = maternal heritability for weaning weight, $r_{d,m}$ = genetic correlation between direct and maternal additive genetic effects, c^2 = permanent maternal environmental variance as a proportion of the phenotypic variance, $d_{d,m}$ = total dam variation as a proportion of the phenotypic variance, $c_{d,m}$ = proportion of the direct-maternal covariance of the total variance, and h^2_T = total heritability = $(\sigma^2_d + 1.5\ \sigma_{d,m} + .5\ \sigma^2_m)/\sigma^2_P$.

recent articles using animal models reported similar estimates for direct heritability (Meyer, 1992b, 1997; Waldron et al., 1993; Koch et al., 1994; Dodenhoff et al., 1998). The estimates for USA, Canada, and Uruguay were .24, .20, and .23, respectively. The heritabilities were similar across countries. Similar results were reported for Angus cattle in Australia and New Zealand, with estimates of .23 and .20, respectively (Meyer, 1995).

Maternal heritabilities were also in agreement among countries, with estimates of .16, .16, and .18 for USA, Canada, and Uruguay, respectively. These estimates were in agreement with those previously reported by Meyer (1992b, 1993), Koch et al. (1994), and Snelling et al. (1996) but were slightly larger than the ones reported by Meyer (1995). The former citations used a complete animal model allowing covariances between direct and maternal, and the latter one fixed the covariance to be zero. Ferreira et al. (1999) reported that inflated estimates of maternal genetic variance and heritability were obtained using a sire-maternal grandsire model compared to an animal model. In a simulation study by Meyer (1992a), the author concluded that sizable data sets may be required to obtain accurate estimates and to provide adequate data structure to allow maternal components to be estimated. The maternal heritabilities obtained in the present study for Hereford cattle were nearly 50% smaller than the maternal heritabilites used in current genetic evaluation programs. The genetic parameters for North American and Uruguayan Herefords were previously estimated using sire-maternal grandsire models (Johnston, 1992 and J. K. Bertrand, personal communication).

Covariance between direct and maternal was negative in all countries with correlations of −.42, −.35, and −.50 for USA, Canada, and Uruguay, respectively. Similar results were reported by Meyer (1992b) for Australian Hereford cattle (h^2_d = .14, h^2_m = .13, $r_{d,m}$ = −.59), Waldron et al. (1993) (h^2_d = .15, h^2_m = .14, $r_{d,m}$ = −.35), and Koch et al. (1994) (h^2_d = .16, h^2_m = .17, $r_{d,m}$ = −.28).

The proportion of the total variance due to the direct-maternal correlation accounted for 6, 8, and 10% in USA, Canada, and Uruguay, respectively, which is very similar to the 8% reported by Meyer (1992b) for the Herefords in Australia. Substantial differences for direct-maternal covariances may exist among breeds. Meyer (1992b) found that the correlation in Angus was close to zero but was larger and more negative for Hereford, suggesting that milk was more limiting in the Herefords. In a simulation study, Robinson (1996) found that a large proportion of the negative correlation between direct and maternal for weaning weight could be caused × a sire by year interaction, which is especially important when a large proportion of sires are introduced into the population each year (i.e., imported animals). This was the case for Uruguay, where almost 18% of the progeny and grand-progeny in the database came from imported sires from North America, so the large negative value for the covariance (−.50) could be due, in part, to sire × year interactions. Another reason for the large negative correlation between direct and maternal genetic effects could be the negative direct-maternal environmental correlation, which affects the covariance between dam and offspring (fatty-udder syndrome). Results from Meyer (1997) suggested that fitting such an effect into the model reduced the negativity of the direct maternal correlation only for the Australian Hereford breed, although the correlation was still sizable and negative even after accounting for the dam-offspring covariance. Similar results were found by Dodenhoff et al. (1998), who concluded that the maternal heritability may be underestimated if grandmaternal effects are not included in the model. Total heritability (Willham, 1972) defined after Meyer (1992b), differed little among countries (.19, .19, and .17 for USA, Canada, and Uruguay, respectively).

Implications

The differences between the weaning weight maternal genetic and permanent maternal environmental

variances obtained in this study compared to past analyses that used sire-maternal grandsire and sire-dam models strongly suggest that genetic evaluation programs that use these previous estimates need to re-estimate them using animal models and large data sets. The similarity of genetic and environmental parameters across the three countries suggests that joint genetic evaluation is feasible, provided that no genotype × country interaction exists. Research needs to be conducted to investigate the importance of these interactions in international beef cattle evaluation.

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