Tropical and Subtropical Agroecosystems, 15 (2012): 403 - 414

MULTIPLE-BREED GENETIC EVALUATION OF GROWTH TRAITS IN SIMMENTAL AND SIMBRAH CATTLE

[EVALUACIÓN GENÉTICA MULTIRRACIAL DE CARACTERÍSTICAS DE CRECIMIENTO EN BOVINOS SIMMENTAL Y SIMBRAH]

Vicente Eliezer Vega-Murillo[1], Ángel Ríos-Utrera[2*],
Moisés Montaño-Bermúdez[3] and Guillermo Martínez-Velázquez[4]

[1]Centro de Investigación Regional Golfo-Centro, INIFAP, km 22.5 carretera Veracruz-Córdoba, Paso del Toro, Medellín de Bravo, Veracruz, México, 94277, e-mail vega.vicente@inifap.gob.mx.
[2]Campo Experimental La Posta, INIFAP, km 22.5 carretera Veracruz-Córdoba, Paso del Toro, Medellín de Bravo, Veracruz, México, 94277, Tel. (229) 2622222, e-mail rios.angel@inifap.gob.mx.
[3]CENID Fisiología y Mejoramiento Animal, INIFAP, km 1 carretera a Colón, Ajuchitlán, Querétaro, México. 76280. e-mail montano.moises@inifap.gob.mx.
[4]Sitio Experimental El Verdineño, INIFAP, km 7.5 carretera Navarrete-Sauta, Santiago Ixcuintla, Nayarit, México, 63570.
e-mail martinez.guillermo@inifap.gob.mx.
[*]Corresponding author.

SUMMARY

Covariance components and genetic parameters were estimated in Simmental, Simbrah and Simmental x Zebu calves fitting six alternative models to birth weight (BW; n=105,297), 205-day weight (WW; n=82,752) and 365-day weight data (YW; n=49,450) provided by Asociación Mexicana de Criadores de Ganado Simmental Simbrah, A.C. Models ranged from a model which included direct additive genetic effects (Model 1) to a model which included direct and maternal additive genetic effects, their covariance and maternal permanent environmental effects (Model 6). Fixed effects were: contemporary group, age of dam, proportion of Simmental genes, heterozygosity and recombination losses. Estimates of direct and maternal heritability varied between alternative models. Due to the problems associated with the estimation of the direct-maternal correlation, which was extremely high (absolute value), Model 4, which included both dams' genetic and permanent environmental effects in addition to direct additive genetic effects, was considered to be the most appropriate for all traits. Application of any of the other models would result in inaccurate expected progeny differences, affecting selection efficiency. Model-4 estimates of direct heritability, maternal heritability and of the ratio of maternal permanent environmental variance to the total phenotypic variance were: 0.17, 0.01 and 0.03; 0.14, 0.02 and 0.04; and 0.15, 0.01 and 0.01 for BW, WW and YW, respectively.

Key words: Beef cattle, growth, maternal effects, genetic parameters

RESUMEN

Se estimaron componentes de varianza y parámetros genéticos en becerros Simmental, Simbrah y Simmental x Cebú ajustando seis diferentes modelos en datos de peso al nacimiento (PN; n=105,297) y pesos ajustados a 205 (PD; n=82,752) y 365 días de edad (PA; n=49,450) proporcionados por la Asociación Mexicana de Criadores de Ganado Simmental Simbrah, A.C. Los modelos variaron de un modelo que incluyó efectos genéticos directos (Modelo 1) a uno que incluyó efectos genéticos directos y maternos, su covarianza y efectos del ambiente permanente (Modelo 6). Los efectos fijos fueron: grupo contemporáneo, edad de la madre, proporción de genes Simmental, heterocigosis y pérdidas por recombinación. Los estimadores de heredabilidad directa y materna variaron entre modelos. Debido a problemas en la estimación de la correlación directa-materna, la cual fue extremadamente alta (valor absoluto), el Modelo 4, que incluyó efectos genéticos directos y maternos y del ambiente permanente, se consideró el más apropiado para las tres características. El uso de cualquiera de los otros modelos resultaría en diferencias esperadas en la progenie poco confiables, afectando la eficiencia de la selección. Con el Modelo 4, los estimadores de heredabilidad directa y materna y proporción de la varianza fenotípica debida al ambiente permanente fueron: 0.17, 0.01 y 0.03; 0.14, 0.02 y 0.04; y 0.15, 0.01 y 0.01 para PN, PD y PA, respectivamente.

Palabras clave: Ganado de carne, crecimiento, efectos maternos, parámetros genéticos.

INTRODUCTION

According to CONARGEN (2010), high quality beef produced in Mexico is based on the use of breeds originated in France (Charolais, Limousin, Salers), England (Angus, Hereford), Switzerland (Braunvieh, Simmental) and the United States of America (Brangus, Charbay, Santa Gertrudis, Simbrah). Among such beef cattle breeds Simmental is predominant. Rosales-Alday *et al*. (2004) mentioned that "purebred and crossbred Simmental animals are well accepted by Mexican producers because their beef is well accepted by both local and international markets, and have good adaptability to a wide range of environmental conditions." The profitability of a beef enterprise depends on two major components: calf growth and female reproduction. Under Mexican seedstock production systems, however, farmers place much importance on calf growth, since genetic evaluations are mainly based on birth, weaning and yearling weights (CONARGEN, 2010). The potential for change in calf growth is largely dependent on its genetic variation for direct and maternal effects, as well as the magnitude and sign of the correlation between these effects. Accurate estimates of these variances and corresponding heritabilities depend on application of the most suitable model for growth traits (Robison, 1981). When datasets include purebred and crossbred animals, a multibreed approach is recommended (Pollak and Quaas, 1998).

Multiple-breed genetic evaluation has been found to be important to the beef industry for several reasons: 1) do a better job of evaluating breeding values of individuals with two or more breeds in their pedigree; 2) allows to evaluate more animals; 3) provides information that more closely matches the potential genetics in current and future beef production systems; 4) beef producers want to alternate breeds to take advantage of crossbreeding and biological type complementarity; 5) the beef industry wants to utilize composite seedstock that benefit from seedstock production heterosis and provide heterosis in commercial production systems; and 6) allows to rank and evaluate the potential genetic value of any animal regardless of breed composition (Lipsey, 1999).

The present investigation had the purpose of evaluating the influence of maternal effects on estimates of (co)variance components and genetic parameters from birth, weaning and yearling weight records in the Mexican Simmental and Simbrah beef cattle populations.

MATERIAL AND METHODS

Data

Pedigree information and growth performance records for birth weight, weaning weight and yearling weight of Simmental, Simbrah and Simmental x Zebu calves born from 1984 to 2009 in 562 ranches across Mexico, were provided by Asociación Mexicana de Criadores de Ganado Simmental Simbrah, A.C. Simmental x Zebu crossbred calves were produced during the process of grading up to Simmental (backcrosses to Simmental sires) and during the process to produce the Simbrah synthetic breed, which has a genetic composition of 5/8 Simmental and 3/8 Brahman. Dam ages ranged from 2 to 13 or more years. Weaning and yearling weight records were adjusted to 205 and 365 days of age as recommended by the Beef Improvement Federation (BIF, 2002). Ranges allowed for age at weighing were 160 to 250 days for weaning weight, and 320 to 410 days for yearling weight. Records on calves outside these ranges were eliminated from the analysis but not from the pedigree file. Productive data was edited to eliminate unreliable dates and weights (± 3 Standard Deviations from the mean), and the pedigree file was checked to make sure all parents were born before their progeny. After editing the raw dataset, the final dataset consisted of 105,297 birth weight, 82,752 weaning weight and 49,450 yearling weight records. The number of sires with progeny in the dataset was 5,627, 4,757 and 3,552 for birth weight, 205-day weight and 365-day weight, respectively.

Table 1. Structure of the edited dataset.

	Growth trait[a]		
	BW	WW	YW
Number of records	105,297	82,752	49,450
Number of sires	5,627	4,757	3,552
Number of dams	49,092	40,909	28,714
Number of herds	562	468	389
Number of contemporary groups	17,875	13,368	8,552
Number of animals in the pedigree	136,676	136,676	136,676

[a] BW= birth weight; WW= 205-day weight; YW=365-day weight.

For all traits, the pedigree file contained 136,676 animals, including dams and sires without records. Table 1 shows additional details of the data (numbers of dams, herds and contemporary groups) for each trait. Breed composition of animals in the performance file is provided in Table 2.

Table 2. Breed composition of animals in data file.

Breed composition	No. of animals
Simmental	51,310
Simbrah[a]	39,397
1/4 Simmental	821
3/8 Simmental	303
1/2 Simmental	6,688
3/4 Simmental	6,327
7/8 Simmental	451

[a] Simbrah= 5/8 Simmental x 3/8 Brahman

Models for analyses

Genetic, environmental and phenotypic parameters were estimated using univariate analyses. Different animal models were used for data analyses, depending on the parameters being estimated. The alternative models were:

Model 1: $\boldsymbol{y} = \boldsymbol{X\beta} + \boldsymbol{Z_a a} + \boldsymbol{e}$
Model 2: $\boldsymbol{y} = \boldsymbol{X\beta} + \boldsymbol{Z_a a} + \boldsymbol{Z_c c} + \boldsymbol{e}$
Model 3: $\boldsymbol{y} = \boldsymbol{X\beta} + \boldsymbol{Z_a a} + \boldsymbol{Z_m m} + \boldsymbol{e}$ with cov(a,m)= 0
Model 4: $\boldsymbol{y} = \boldsymbol{X\beta} + \boldsymbol{Z_a a} + \boldsymbol{Z_m m} + \boldsymbol{Z_c c} + \boldsymbol{e}$ with cov(a,m)= 0
Model 5: $\boldsymbol{y} = \boldsymbol{X\beta} + \boldsymbol{Z_a a} + \boldsymbol{Z_m m} + \boldsymbol{e}$ with cov(a,m)= A σ_{am}
Model 6: $\boldsymbol{y} = \boldsymbol{X\beta}+\boldsymbol{Z_a a}+\boldsymbol{Z_m m}+\boldsymbol{Z_c c}+\boldsymbol{e}$ with cov(a,m)=A σ_{am}

Where:
$\boldsymbol{y}$ is a vector of observations, $\boldsymbol{\beta}$ is a vector of fixed effects with incidence matrix $\boldsymbol{X}$, $\boldsymbol{a}\sim N(0, \boldsymbol{A}\sigma^2_a)$ and $\boldsymbol{m}\sim N(0, \boldsymbol{A}\sigma^2_m)$ are vectors of random direct and maternal additive genetic effects with incidence matrices $\boldsymbol{Z_a}$ and $\boldsymbol{Z_m}$, respectively, $\boldsymbol{c}\sim N(0, \boldsymbol{I}_c\sigma^2_c)$ is a vector of random maternal permanent environmental effects with incidence matrix $\boldsymbol{Z_c}$, and $\boldsymbol{e}\sim N(0, \boldsymbol{I}_n\sigma^2_e)$ is a vector of random residual effects. It was also assumed that $\mathrm{cov}(\boldsymbol{a},\boldsymbol{c}') = \mathrm{cov}(\boldsymbol{a},\boldsymbol{e}') = \mathrm{cov}(\boldsymbol{c},\boldsymbol{e}') = \boldsymbol{0}$. In addition, $\boldsymbol{A}$ is the matrix of Wright's additive numerator relationships among all animals (10 generation pedigree), $\boldsymbol{I_c}$ and $\boldsymbol{I_n}$ are identity matrices of order equal to the number of dams and the number of records, respectively, σ^2_a is the additive genetic variance for direct effects, σ^2_m is the additive genetic variance for maternal effects, σ_{am} is the covariance between direct and maternal effects, σ^2_c is the variance due to maternal permanent environmental effects, and σ^2_e is the residual error variance. Contemporary group and the age of the dam at calving, in days, were included in the animal models as fixed environmental effects. Contemporary groups were groups of calves of the same sex, born in the same ranch, year and season, and weighed on the same day. In addition, all the models included fixed genetic effects of proportion of Simmental genes, heterozygosity and recombination loss as covariates. The coefficients of heterosis and recombination loss in the cow were calculated using the following formulas proposed by Akbas *et al*. (1993):

Heterosis = $P_s(1 - P_d) + P_d(1 - P_s)$
Recombination loss = $P_s(1 - P_s) + P_d(1 - P_d)$

Where:
P_s and P_d are the proportion of Simmental in the sire and dam, respectively. The coefficient of recombination loss describes the average fraction of independently segregating pairs of loci in gametes from both parents which are expected to be

nonparental combinations (Dickerson, 1973). Demeke *et al*. (2003) concluded that ignoring heterosis and recombination loss effects on individual animals results in overestimation of both direct and maternal genetic variances and direct heritability for early growth traits in a mixed population of purebred *Bos indicus* and crossbred *Bos taurus* x *Bos indicus* cattle.

Estimated (co)variance components

Restricted maximum likelihood (REML) estimates of covariance components with the different models were obtained using the MTDFREML program (Boldman *et al*., 1995). For all of the analyses, if the variance of likelihood values in the simplex method was less than 10^{-8}, it was assumed that convergence had been achieved.

Estimated genetic, environmental and phenotypic parameters

Estimates were obtained for total phenotypic variance ($\sigma_p^2 = \sigma_a^2 + \sigma_m^2 + \sigma_{am} + \sigma_c^2 + \sigma_e^2$), heritability for direct additive genetic effects ($h_a^2 = \sigma_a^2 / \sigma_p^2$), heritability for maternal additive genetic effects ($h_m^2 = \sigma_m^2 / \sigma_p^2$), genetic covariance between direct and maternal effects as a proportion of phenotypic variance ($c_{am} = \sigma_{am} / \sigma_p^2$), genetic correlation between direct and maternal additive genetic effects ($r_{am} = \sigma_{am} / (\sigma_a^2\ \sigma_m^2)^{1/2}$) , fraction of phenotypic variance due to maternal permanent environmental effects ($c^2 = \sigma_c^2 / \sigma_p^2$), and residual variance as a proportion of phenotypic variance ($e^2 = \sigma_e^2 / \sigma_p^2$). Standard errors for estimates of genetic parameters were approximated and were calculated using the Average Information matrix (Johnson and Thompson, 1995) and the Delta Method (Dodenhoff *et al*., 1998). All fractions of phenotypic variance and their standard errors were calculated by the MTDFREML program, except the fraction of the genetic covariance, which was calculated by hand. Standard error for the estimate of this genetic parameter is not provided. Estimates of total heritability (h_t^2) were also calculated, using the equation ($h_t^2 = [\sigma_a^2 + 0.5\,\sigma_m^2 + 1.5\,\sigma_{am}] / \sigma_p^2$) proposed by Willham (1972). This equation represents the regression of the entire genotype (direct and maternal) of an animal on its phenotype.

Model comparison

Selection of the most appropriate model for each trait was based on likelihood ratio tests (Dobson, 1990) to compare the significance of additional variances and covariances (maternal genetic variance, permanent environmental variance, direct-maternal covariance). The likelihood ratio tests were conducted by comparing minus twice the difference between the log likelihood values with the tabulated Chi-squared statistic with degrees of freedom taken as the difference in the number of parameters (one for all comparisons) fitted in two models. The Probchi function implemented in the SAS package (SAS, 2001) was used to carry out the Chi-square test.

RESULTS AND DISCUSSION

Phenotypic means, standard deviations and coefficients of variation for birth weight, 205-day weight and 365-day weight are presented in Table 3. Phenotypic means (± standard deviations) were: 37.4 ± 5.5, 226 ± 43, and 332 ± 62 kg, respectively. Estimates of (co)variance components, along with values for minus twice the logarithm of the likelihood (-2[log likelihood]), and estimates of genetic parameters for growth traits evaluated are shown in Tables 4 and 5, respectively. Likelihood ratio test statistics for maternal permanent environmental effects, maternal genetic effects and direct-maternal genetic covariance by growth trait are in Table 6.

Table 3. Summary statistics of the edited dataset.

	Growth trait[a]		
	BW, kg	WW, kg	YW, kg
Mean	37.4	226	332
Minimum	20	91	117
Maximum	56	470	653
Standard deviation	5.5	43.0	62.0
Coef. variation, %	14.7	19.0	18.6

[a]BW= birth weight; WW= 205-day weight; YW=365-day weight.

Comparisons between models

Likelihood ratio tests (Table 5) within each trait showed that maternal permanent environmental effects, maternal genetic effects and direct-maternal genetic covariance included in alternative models were significant. Fitting permanent environmental effects in Model 2 or maternal genetic effects in Model 3 in addition to direct genetic effects resulted in smaller estimates of direct heritability for birth weight, 205-day weight and 365-day weight, compared with corresponding estimates of direct heritability for Model 1. Similarly, inclusion of permanent environmental effects together with maternal genetic effects in Model 4 reduced estimates of direct heritability for birth weight, 205-day weight and 365-day weight by 3 (0.17 *vs* 0.20), 4 (0.14 *vs* 0.18) and 2 percent units (0.15 *vs* 0.17), respectively, compared to corresponding estimates of direct heritability obtained with Model 1. In Mexican genetic evaluations of Brangus and Salers (Domínguez-Viveros *et al*., 2009), Limousin (Ríos-Utrera *et al*., 2011) and Charolais and Charbray beef cattle (Ríos-Utrera *et al*., 2012) a similar trend has been found with equivalent models, in agreement with our results. In contrast, inclusion of the direct-maternal covariance in Models 5 and 6 within trait resulted in larger estimates of direct heritability and in large and negative estimates of the corresponding genetic correlation (Table 4), suggesting bias in the estimation of this parameter. The same phenomenon has occurred in many other beef cattle studies with comparable models (Meyer, 1993; Berweger Baschnagel *et al*., 1999; Schoeman and Jordaan, 1999; Domínguez-Viveros *et al*., 2009; Ríos-Utrera *et al*., 2011, 2012). According to Robinson (1996), strongly negative estimates of the direct-maternal correlation could be partially due to large variation between sires, due either to larger genetic variance or confounding environmental effects such as paddock with sire. On the other hand, Meyer (1997) reported that strongly negative estimates of the direct-maternal correlation can be partially explained by unaccounted ranch practices, such as inappropriate identification of management groups, increasing the covariance between paternal sibs in contemporary groups. Therefore, strongly negative estimates of the direct-maternal correlation do not always are a true sign of genetic antagonism between growth and maternal ability. Contrasted to Model 3, addition of maternal permanent environmental effects to Model 4 decreased the estimate of maternal heritability from 0.03 to 0.01, 0.05 to 0.02, and 0.02 to 0.01 for birth weight, 205-day weight and 365-day weight, respectively. Thus, if permanent environmental effects of the dam are not included in the model, estimates of maternal heritability are also overestimated. Based on all of the above mentioned and assuming that direct-maternal correlations are biased estimates, Model 4, which allowed for direct genetic, maternal genetic and permanent environmental effects, could be considered the most appropriate model to analyze birth, weaning and yearling weight data. In contrast, if the assumption was to consider the estimated direct-maternal correlations as reliable estimates of genetic antagonism, then Model 6 could be a suitable model to analyze our dataset. Hence, is important to clarify the origin of the direct-maternal correlation to avoid the application of inappropriate models that would affect the accuracy of the predicted breeding values and the expected genetic progress. In the present study, Model 4 was considered to be the most appropriate model to analyze all traits.

Birth-weight estimates

The estimate of direct heritability for birth weight (0.17) obtained with the selected model (Model 4) is similar to corresponding estimates (0.16, 0.18, 0.19) reported by Quaas *et al*. (1985) and Dong *et al*. (1991) for American, and by Kemp *et al*. (1988) for Canadian Simmental beef cattle. However, most Simmental estimates of direct heritability for birth weight found in the literature (Trus and Wilton, 1988; Garrick *et al*., 1989; Woodward *et al*., 1992; Swalve, 1993; Rust *et al*., 1998; Eriksson *et al*., 2002) are greater than the corresponding estimate reported in the present study (0.34, 0.44, 0.28, 0.33, 0.30 and 0.28 *vs* 0.17). From 17 genetic studies examining the Simmental beef breed, Ríos-Utrera (2008) obtained an unweighted mean of direct heritability of 0.36, which is also greater than present corresponding estimate. One of the main reasons for the small direct heritability reported in the present study could be the lower standard of calf management followed under Mexican production conditions. Animal management levels and environmental (nutrition, temperature, parasitic) stress highly affect the magnitude of additive genetic variance for different traits. For instance, it has been reported a higher additive genetic variance and hence a higher heritability for milk production in the United Kingdom (0.45 ± 0.02) compared to that estimated under Kenyan conditions (0.26 ± 0.06) for Holstein cows that were progeny of bulls commonly used in both countries (Ojango and Pollott, 2002). In regard to maternal genetic effects, most studies have reported larger estimates of maternal heritability for birth weight than the present corresponding estimate (0.01). Trus and Wilton (1988), Garrick *et al*. (1989), Rust *et al*. (1998), Marques *et al*. (1999) and Eriksson *et al*. (2002) obtained estimates of maternal heritability for birth weight of 0.20, 0.12, 0.14, 0.10 and 0.12 for Canadian, American, South African, Brazilian and Swedish Simmental beef cattle, respectively. Maternal permanent environmental effects were a little important factor determining birth weight, explaining only 3% of the respective phenotypic variance. This result is, to some extent, in contrast to the findings by Marques *et al*. (2000) and Eriksson *et al*. (2002), who reported that permanent environmental effects explained 7% of the phenotypic variance for birth weight. Estimates of heritability and of permanent environmental effects fraction for birth weight obtained in our study revealed that direct genetic effects were more important than both genetic and permanent environmental effects of the dam.

Table 4. Estimates of (co)variance components[a] for birth weight (BW), 205-day weight (WW), and 365-day weight (YW) obtained with six alternative models

	Model					
	1	2	3	4	5	6
BW, kg^2						
σ^2_a	3.53501	3.00719	2.97017	2.94231	4.84601	4.84741
σ^2_m	-	-	0.50491	0.13049	2.01724	1.33888
σ_{am}	-	-	0	0	-2.08381	-1.89822
σ^2_c	-	0.704959	-	0.604897	-	0.678761
σ^2_e	13.80937	13.54720	13.79716	13.57564	12.73746	12.52965
σ^2_p	17.34439	17.25934	17.27225	17.25334	17.51690	17.49649
-2[log(L)]	354928	354805	354853	354801	354638	354586
WW, kg^2						
σ^2_a	106.25131	86.00022	80.49286	80.59276	180.18633	166.03736
σ^2_m	-	-	26.48509	11.25232	107.53042	79.90532
σ_{am}	-	-	0	0	-108.52419	-90.40223
σ^2_c	-	33.2669	-	24.5497	-	21.6002
σ^2_e	468.74562	452.89823	465.21795	455.32728	407.55685	406.98085
σ^2_p	574.99693	572.16533	572.19590	571.72205	586.74941	584.12151
-2[log(L)]	522985	522828	522860	522811	522587	524235
YW, kg^2						
σ^2_a	131.84961	121.48326	120.06515	119.31338	210.27264	217.80917
σ^2_m	-	-	12.40595	4.52923	110.94284	102.5357
σ_{am}	-	-	0	0	-125.33135	-122.06128
σ^2_c	-	17.2394	-	13.7200	-	13.3127
σ^2_e	639.32939	633.49077	639.86171	634.47238	588.88266	585.51759
σ^2_p	771.17900	772.21345	772.33280	772.03496	784.76680	797.11387
-2[log(L)]	321826	320080	320082	320079	320000	321458

[a] σ^2_a = direct additive genetic variance, σ^2_m = maternal additive genetic variance, σ_{am} = covariance between direct and maternal additive genetic effects, σ^2_c = maternal permanent environmental variance, σ^2_e = residual variance, σ^2_p = phenotypic variance, -2[log(L)]= variance of minus twice the logarithm of the likelihood.

Table 5. Estimates of genetic parameters[a] for birth weight (BW), 205-day weight (WW) and 365-day weight (YW) obtained with six alternative models.

	Model					
	1	2	3	4	5	6
BW						
h^2_a	0.20 ± 0.007	0.17 ± 0.008	0.17 ± 0.008	0.17 ± 0.008	0.28 ± 0.014	0.28 ± 0.014
h^2_m	-	-	0.03 ± 0.004	0.01 ± 0.004	0.12 ± 0.008	0.08 ± 0.009
c_{am}	-	-	0	0	-0.12	-0.11
r_{am}	-	-	0	0	-0.67 ± 0.090	-0.75 ± 0.115
c^2	-	0.04 ± 0.004	-	0.03 ± 0.005	-	0.04 ± 0.006
e^2	0.80 ± 0.007	0.78 ± 0.007	0.80 ± 0.007	0.79 ± 0.007	0.73 ± 0.011	0.72 ± 0.011
h^2_t	0.20	0.17	0.19	0.17	0.16	0.15
WW						
h^2_a	0.18 ± 0.008	0.15 ± 0.008	0.14 ± 0.009	0.14 ± 0.009	0.31 ± 0.017	0.28 ± 0.016
h^2_m	-	-	0.05 ± 0.005	0.02 ± 0.006	0.18 ± 0.011	0.14 ± 0.012
c_{am}	-	-	0	0	-0.18	-0.15
r_{am}	-	-	0	0	-0.78 ± 0.095	-0.78 ± 0.111
c^2	-	0.06 ± 0.005	-	0.04 ± 0.006	-	0.04 ± 0.007
e^2	0.82 ± 0.008	0.79 ± 0.008	0.81 ± 0.008	0.80 ± 0.008	0.69 ± 0.013	0.70 ± 0.012
h^2_t	0.18	0.15	0.16	0.15	0.12	0.12
YW						
h^2_a	0.17 ± 0.012	0.16 ± 0.013	0.16 ± 0.013	0.15 ± 0.013	0.27 ± 0.021	0.27 ± 0.021
h^2_m	-	-	0.02 ± 0.006	0.01 ± 0.008	0.14 ± 0.016	0.13 ± 0.018
c_{am}	-	-	0	0	-0.16	-0.15
r_{am}	-	-	0	0	-0.82 ± 0.161	-0.82 ± 0.171
c^2	-	0.02 ± 0.007	-	0.01 ± 0.010	-	0.02 ± 0.011
e^2	0.83 ± 0.012	0.82 ± 0.012	0.83 ± 0.012	0.82 ± 0.012	0.75 ± 0.016	0.73 ± 0.017
h^2_t	0.17	0.16	0.16	0.16	0.10	0.11

[a] h^2_a = direct heritability, h^2_m = maternal heritability, c_{am} = genetic covariance between direct and maternal effects as a proportion of phenotypic variance, r_{am} = genetic correlation between direct and maternal effects, c^2 = maternal permanent environmental variance as a proportion of phenotypic variance, e^2 = residual variance as a proportion of phenotypic variance, h^2_t = total heritability.

Table 6. Likelihood ratio test statistics for maternal permanent environmental effects (σ_c^2), maternal genetic effects (σ_m^2) and direct-maternal genetic covariance (σ_{am}).

Comparisons between models	Growth trait[a] BW	WW	YW	Hypothesis tested
Model 2 *vs* Model 1	-122.71**	-157.01**	-1746.68**	$\sigma_c^2 = 0$
Model 3 *vs* Model 1	-74.77**	-125.41**	-1744.06**	$\sigma_m^2 = 0$
Model 4 *vs* Model 2	-3.81*	-17.08**	-0.53	$\sigma_m^2 = 0$
Model 4 *vs* Model 3	-51.75**	-48.69**	-3.15†	$\sigma_c^2 = 0$
Model 5 *vs* Model 3	-215.51**	-273.33**	-82.18**	$\sigma_{am} = 0$
Model 6 *vs* Model 4	-215.25**	-1423.68**	-1378.55**	$\sigma_{am} = 0$
Model 6 *vs* Model 5	-51.49**	-1648.32**	-1457.57**	$\sigma_c^2 = 0$

[a] BW= birth weight; WW= 205-day weight; YW=365-day weight.
†(P < 0.10); *(P < 0.05); **(P < 0.01).

Weaning-weight estimates

For 205-day weight, Model-4 estimate of direct heritability (0.14) indicates that this trait may be changed by direct selection; however, response to selection would be slow. Present Model-4 estimate of direct heritability for 205-day weight is comparable with estimates of 0.10, 0.12, 0.13 and 0.17 reported by Graser and Hammond (1985), Quaas *et al*. (1985), Boldman *et al*. (1991) and Marques *et al*. (2000) for Simmental beef cattle. However, most of previous research with Simmental beef cattle found in the literature (Schaeffer and Wilton, 1981; Garrick *et al*., 1989; Redman and Brinks, 1991; Swalve, 1993; Marques, 1994; Lee *et al*., 1997; Rust *et al*., 1998; Rosales-Alday *et al*., 2004) suggest that estimates of direct heritability for weaning weight are moderate (0.31, 0.36, 0.48, 0.34, 0.39, 0.25, 0.26, 0.33). The unweighted mean of direct heritability for Simmental beef cattle (0.26) reported in the review by Ríos-Utrera (2008) is also greater than present corresponding estimate. Appropriate estimate of maternal heritability for 205-day weight from Model 4 was very small (0.02), in disagreement with corresponding estimates for Simmental and Simbrah cattle found in other studies (Wright *et al*., 1987; Lee *et al*., 1997; Rust *et al*., 1998; Marques *et al*., 1999; Rosales-Alday *et al*., 2004; Smith, 2010). The proportion of phenotypic variance due to permanent environmental effects associated with the dam accounted for only 4% (Model 4) of the phenotypic variance for 205-day weight. For Simmental cattle, Mrode and Thompson (1990), in a study carried out in the United Kingdom, and Swalve (1993), in a similar study carried out in Australia, found that proportion of phenotypic variance due to permanent environmental effects was two-fold greater than current corresponding estimate. In the present study, 205-day weight was mainly determined by direct genetic effects than by both genetic and permanent environmental effects of the dam, as occurred with birth weight, in accordance with results of previous research with Zebu and Charolais beef cattle (Parra-Bracamonte *et al*., 2007; Palacios-Espinosa *et al*., 2010; Ríos-Utrera *et al*., 2012). In contrast, Boldman *et al*. (1991), evaluating the Simmental beef cattle breed, found that direct genetic, maternal genetic and permanent environmental effects were practically of the same magnitude with estimates of direct heritability, maternal heritability and maternal permanent environmental effects portion being 0.17, 0.20 and 0.18, respectively.

Yearling-weight estimates

Like Model-4 estimates of direct heritability for birth weight and 205-day weight, Model-4 estimate of direct heritability for 365-day weight was low (0.15), indicating that genetic progress from direct selection on 365-day weight might be slow. Model-4 estimate of direct heritability for 365-day weight is similar to corresponding animal-model estimates (0.13, 0.19) reported by Rust *et al*. (1998) and Marques *et al*. (2000), but is much smaller than those corresponding animal-model estimates (0.27, 0.37, 0.41) reported for Simmental cattle in other studies (Mrode and Thompson, 1990; Swalve, 1993; Bennett and Gregory, 1996). For Simbrah cattle reared in South

Africa, Smith (2010) estimated even a higher direct heritability (0.70) for yearling weight measured at 400 days of age. Maternal heritability estimated with Model 4 (0.01) in the current study is six to ten times smaller than corresponding estimates reported for Simmental cattle by Rust *et al*. (1998) and Marques *et al*. (2000). With Model 4, maternal permanent environmental effects explained only a small fraction of the total phenotypic variance (1%) for 365-day weight. Mrode and Thompson (1990) and Marques *et al*. (2000) found that permanent environmental effects of the dam explained a little more (3 and 5%, respectively) of the total variation. Similar to the findings for birth weight and 205-day weight, direct genetic effects had greater influence on 365-day weight than maternal genetic effects and maternal permanent environmental effects.

CONCLUSIONS AND IMPLICATIONS

Estimates of direct, maternal and total heritability exhibited quite a variation between alternative models. Exclusion of maternal effects from the basic animal model resulted in inflated estimates of direct heritability as previously reported by other authors. Due to the problems associated with the estimation of the direct-maternal correlation, which was extremely high (absolute value), Model 4, which included direct, maternal and permanent environmental effects, was the model of choice for multiple-breed genetic evaluation for growth traits of the Simmental and Simbrah beef cattle breeds in Mexico. Hence, selection efficiency would be affected if inappropriate models were applied. Estimates of direct and maternal heritabilities in the present study tended to be smaller than corresponding estimates reported for Simmental cattle in other studies (countries). In general, genetic and permanent environmental effects of the dam were small with estimates near zero. Across traits, estimates of direct heritability were similar for birth, weaning and yearling weights, as were estimates of maternal heritability and of proportion of total phenotypic variance due to maternal permanent environmental effects. However, direct heritability estimates were substantially greater than estimates of maternal heritability and maternal permanent environmental effects within each trait, revealing that direct genetic effects had greater influence on growth traits than both genetic and permanent environmental effects of the dam. Low estimates of heritability found in the present study are indicative that single-trait selection for 205-day weight or 365-day weight would result in little genetic progress per year.

REFERENCES

Akbas, Y., Brotherstone, S., Hill, W.G. 1993. Animal model estimation of non-additive genetic parameters in dairy cattle, and their effect on heritability estimation and breeding value prediction. Journal of Animal Breeding and Genetics. 110:105-113.

Bennett, G.L., Gregory, K.E. 1996. Genetic (co)variances among birth weight, 200-day weight, and postweaning gain in composites and parental breeds of beef cattle. Journal of Animal Science. 74:2598-2611.

Berweger Baschnagel, M., Moll, J., Künzi, N. 1999. Comparison of models to estimate maternal effects for weaning weight of Swiss Angus cattle fitting a sire x herd interaction as an additional random effect. Livestock Production Science. 60:203-208.

BIF. Beef Improvement Federation. 2002. Guidelines for uniform beef improvement programs. 8th ed. The University of Georgia, Athens.

Boldman, K.G., Kriese, L.A., Van Vleck, L.D., Van Tassell, C.P., Kachman, S.D. 1995. A manual for use of MTDFREML. A set of programs to obtain estimates of variances and covariances (DRAFT). USDA, ARS, Washington, DC. 114 p.

Boldman, K.G., Van Vleck, L.D., Gregory, K.E., Cundiff, L.V. 1991. Estimates of direct and maternal parameters for 200 d weight in purebred and composite lines of beef cattle [abstract]. Journal of Animal Science. 69(Suppl 1):203.

CONARGEN. Consejo Nacional de los Recursos Genéticos Pecuarios, A.C. 2010. Guía técnica de programas de control de producción y mejoramiento genético de bovinos carne.

Demeke, S., Neser, F.W.C., Schoeman, S.J. 2003. Variance components and genetic parameters for early growth traits in a mixed population of purebred *Bos indicus* and crossbred cattle. Livestock Production Science. 84:11-21.

Dickerson, G.E. 1973. Inbreeding and heterosis in animals. In: Proceedings of animal breeding and genetics symposium in honor of Dr. Jay L. Lush. Champaign, IL, American Society of Animal Science. Pp. 54-77.

Dobson, A.J. 1990. An introduction to Generalized Linear Models. Chapman and Hall, New York. p. 57.

Dodenhoff, J., Van Vleck, L.D., Kachman, S.D., Koch, R.M. 1998. Parameter estimates for direct, maternal, and grandmaternal genetic effects for birth weight and weaning weight in Hereford cattle. Journal of Animal Science. 76:2521-2527.

Domínguez-Viveros, J., Rodríguez-Almeida, F.A., Ortega-Gutiérrez, J.A., Flores-Mariñelarena, A. 2009. Selección de modelos, parámetros genéticos y tendencias genéticas en las evaluaciones genéticas nacionales de bovinos Brangus y Salers. Agrociencia. 43:107-117.

Dong, M.C., Quaas, R.L., Pollak, E.J. 1991. Estimation of genetic parameters of calving ease and birth weight by a threshold model [abstract]. Journal of Animal Science. 69(Suppl 1):204.

Eriksson, S., Näsholm, A., Johansson, K., Philipsson, J. 2002. Sex-especific genetic parameters for field recorded birth weight of beef calves. In: Proceedings of the 7th World Congress on Genetics Applied to Livestock Production. Montpellier, France [CD-ROM]. Session 02, Breeding ruminants for meat production, Communication No. 02-25.

Garrick, D.J., Pollak, E.J., Quaas, R.L., Van Vleck, L.D. 1989. Variance heterogeneity in direct and maternal weight traits by sex and percent purebred for Simmental-sired calves. Journal of Animal Science. 67:2515-2528.

Graser, H.U., Hammond, K. 1985. Mixed model procedures for the Australian beef industry. I. Multiple-trait model for estimation of breeding values for 200-day and final weights of cattle. Australian Journal of Agricultural Research. 36:527-535.

Johnson, D.L., Thompson, R. 1995. Restricted maximum likelihood estimation of variance components for univariate animal models using sparse matrix techniques and average information. Journal Dairy Science.78:449-456.

Kemp, R.A., Wilton, J.W., Schaeffer, L.R. 1988. Phenotypic and genetic parameter estimates for gestation length, calving ease and birth weight in Simmental cattle. Canadian Journal of Animal Science. 68:291-294.

Lee, C., Van Tassell, C.P., Pollak, E.J. 1997. Estimation of genetic variance and covariance components for weaning weight in Simmental cattle. Journal of Animal Science. 75:325-330.

Lipsey, J. 1999. Development of multibreed genetic evaluation. Proceedings of The Range Beef Cow Symposium XVI, December 14-16, Greeley, CO. http://digitalcommons.unl.edu/rangebeefcowsymp/126. Consulted November 30, 2011.

Marques, L.F.A. 1994. Variação genética aditiva do crescimento da raça Simental no Brasil, em dois períodos. Revista Sociedade Brasileira de Zootecnia. 23:1021-1029.

Marques, L.F.A., Pereira, J.C.C., Oliveira, H.N., Pereira, C.S., Bergmann, J.A.G. 1999. Componentes de (co)variância e parâmetros genéticos de características de crescimento da raça Simental no Brasil. Arquivo Brasileiro de Medicina Veterinária e Zootecnia. 51:363-370.

Marques, L.F.A., Pereira, J.C.C., Oliveira, H.N., Silva, M.A., Bergmann, J.A.G. 2000. Análise de características de crescimento da raça Simental. Arquivo Brasileiro de Medicina Veterinária e Zootecnia. 52(5). http:// www.scielo.br/scielo.php?script=sci_arttext&pid=S0102- 09352000000500020 &lng=en&nrm=iso. Consulted September 24, 2011.

Meyer, K. 1993. Estimates of covariance components for growth traits of Australian Charolais cattle. Australian Journal of Agricultural Research. 44:1501-1508.

Meyer, K. 1997. Estimates of genetic parameters for weaning weight of beef cattle accounting for direct-maternal environmental covariances. Livestock Production Science. 52:187-199.

Mrode, R.A., Thompson, R. 1990. Genetic parameters for body weight in beef cattle in Britain. In: Proceedings of the 4th World Congress on Genetics Applied to Livestock Production. Edinburgh. 15:271-274.

Ojango, J.M.K., Pollott, G.E. 2002. The relationship between Holstein bull breeding values for milk derived in both the UK and Kenya. Livestock Production Science. 74: 1-12.

Palacios-Espinosa, A., Espinoza-Villavicencio, J.L., Guerra-Iglesias, D., González-Peña F.D., de Luna P.R. 2010. Efectos genéticos directos y maternos del peso al destete en una población de ganado Cebú de Cuba. Técnica Pecuaria en México. 48:1-11.

Parra-Bracamonte, G.M., Martínez-González, J.C., Cienfuegos-Rivas, E.G., García-Esquivel, F.J., Ortega-Rivas, E. 2007. Parámetros genéticos de variables de crecimiento de ganado Brahman de registro en México. Veterinaria México. 38:217-229.

Pollak, E.J., Quaas, R.L. 1998. Multibreed genetic evaluations of beef cattle. In: Proceedings of the 6th World Congress on Genetics Applied to Livestock Production. Armidale, NSW, Australia. 23:81-88.

Quaas, R.L., Elzo, M.A., Pollak, E.J. 1985. Analysis of Simmental data: estimation of direct and maternal genetic (co)variances [abstract]. Journal of Animal Science. 61(Suppl 1):221.

Redman, K.J., Brinks, J.S. 1991. Genetic parameters for linear and performance measures in Simmental cattle [abstract]. Journal of Animal Science. 69(Suppl 1):207.

Ríos-Utrera, A. 2008. Estimadores de parámetros genéticos para características de crecimiento predestete de bovinos. Revisión. Técnica Pecuaria en México. 46:37-67.

Ríos-Utrera, A., Martínez-Velázquez, G., Vega-Murillo, V.E., Montaño-Bermúdez, M. 2012. Genetic effects for growth traits of Mexican Charolais and Charbray cattle estimated with alternative models. Revista Mexicana de Ciencias Pecuarias. (In Press).

Ríos-Utrera, A., Vega-Murillo, V.E., Martínez-Velázquez, G., Montaño-Bermúdez, M. 2011. Comparison of models for the estimation of variance components for growth traits of registered Limousin cattle. Tropical and Subtropical Agroecosystems. 14:667-674.

Robison, O.W. 1981. The influence of maternal effects on the efficiency of selection: a review. Livestock Production Science. 8:121-137.

Robinson, D.L. 1996. Models which might explain negative correlations between direct and maternal genetic effects. Livestock Production Science. 45:111-122.

Rosales-Alday, J., Elzo, M.A., Montaño-Bermúdez, M., Vega-Murillo, V.E. 2004. Genetic parameters and trends for preweaning growth traits in the Mexican Simmental population. Técnica Pecuaria en México. 42:171-180.

Rust, T., Groeneveld, E., Mostert, B.E. 1998. A comparison between multivariate direct and maternal (co)variance components for growth traits in Southern African Simmentaler beef cattle and those estimated on other continents. In: Proceedings of the 6th World Congress on Genetics Applied to Livestock Production. Armidale, NSW, Australia. 23:125-128.

SAS. SAS/STAT User´s Guide (Release 8.20). Cary, NC, USA. SAS Inst. Inc. 2001.

Schaeffer, L.R., Wilton, J.W. 1981. Estimation of variances and covariances for use in a multiple trait beef sire evaluation model. Canadian Journal Animal Science. 61:531-538.

Schoeman, S.J., Jordaan, G.F. 1999. Multitrait estimation of direct and maternal (co)variances for growth and efficiency traits in a multibreed beef cattle herd. South African Journal of Animal Science. 29:124-136.

Smith, A.M.J. 2010. Genetic analyses of growth traits for the Simbra composite breed. Master thesis. University of Stellenbosch, Republic of South Africa.

Swalve, H.H. 1993. Estimation of direct and maternal (co)variance components for growth traits in Australian Simmental beef cattle. Journal of Animal Breeding and Genetics. 110:241-252.

Trus, D., Wilton, J.W. 1988. Genetic parameters for maternal traits in beef cattle. Canadian Journal of Animal Science. 68:119-128.

Willham, R.L. 1972. The role of maternal effects in animal breeding: III. Biometrical aspects of maternal effects in animals. Journal of Animal Science. 35:1288-1293.

Woodward, B.W., Pollak, E.J., Quaas, R.L. 1992. Parameter estimation for carcass traits including growth information of Simmental beef cattle using restricted maximum likelihood with a multiple-trait model. Journal of Animal Science. 70:1098-1109.

Wright, H.B., Pollak, E.J., Quaas, R.L. 1987. Estimation of variance and covariance components to determine heritabilities and repeatability of weaning weight in American Simmental cattle. Journal of Animal Science. 65:975-981.

Submitted August 08, 2011– Accepted September 10, 2011
Revised received September 22, 2011