



COMPARISON OF MODELS FOR THE ESTIMATION OF VARIANCE COMPONENTS FOR GROWTH TRAITS OF REGISTERED LIMOUSIN CATTLE

[COMPARACIÓN DE MODELOS PARA LA ESTIMACIÓN DE COMPONENTES DE VARIANZA DE CARACTERÍSTICAS DE CRECIMIENTO DE BOVINOS LIMOUSIN DE REGISTRO]

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SUMMARY

Six models to estimate genetic parameters for birth weight (BW), weaning weight adjusted to 205 days (W205), and yearling weight adjusted to 365 days (W365) were compared. Model A included direct genetic effects. Model AP allowed for direct genetic and permanent environmental effect of the dam. Model AM included direct genetic and maternal genetic effects. Models AMC and AMP were the same as Model AM but they also allowed for the covariance between direct and maternal genetic effects, and the common environmental effect due to the dam, respectively; and Model AMCP was fitted for all three random effects plus the covariance between direct and maternal effects. Models were compared using the likelihood ratio test. The AMC model was selected to be the most appropriate for BW and W205, whereas Model A was chosen for W365. When maternal effects were included, direct genetic variance and direct heritability estimates were reduced for BW and W205. Direct heritability estimates with appropriate models were: 0.13, 0.21 and 0.20 for BW, W205 and W365. Heritability of maternal effects with appropriate models was: 0.15 and 0.32 for BW and W205, and direct-maternal genetic correlations with appropriate models were: -0.67 and -0.69 for BW and W205, respectively.

Key Words: Maternal Effects; Birth weight; Weaning weight; Animal Model; Limousin

INTRODUCTION

The magnitude of estimates of genetic parameters for growth traits of beef cattle may vary depending on

RESUMEN

Se compararon seis modelos para estimar parámetros genéticos para peso al nacimiento (PN), peso ajustado a 205 días (P205) y peso ajustado a 365 días (P365). El Modelo A incluyó el efecto genético directo (A); el Modelo AP incluyó, además del efecto genético directo, el efecto materno ambiental permanente (P); el Modelo AM incluyó el efecto genético materno (M), además de A; los Modelos AMC y AMP fueron iguales al Modelo AM, pero además incluyeron la covarianza entre A y M, y P, respectivamente; y el Modelo AMCP incluyó todos los efectos aleatorios, más la covarianza A-M. Los modelos fueron comparados utilizando la prueba de razón de verosimilitudes. El Modelo AMC fue el más apropiado para PN y P205, mientras que el A lo fue para P365. Cuando se incluyeron efectos maternos, los estimadores de la varianza genética y heredabilidad directas disminuyeron para PN y P205. Los estimadores de heredabilidad directa obtenidos con los modelos seleccionados fueron: 0.13, 0.21 y 0.20 para PN, P205 y P365. La heredabilidad materna obtenida con los modelos seleccionados fue: 0.15 y 0.32 para PN y P205, y la correlación genética entre A y M fue: -0.67 y -0.69 para PN y P205, respectivamente.

Palabras clave: Efectos maternos; Peso al nacer; Peso al destete; Modelo animal; Limousin.

breed group and genetic effects included in the statistical model, among other factors (Meyer, 1992; Ríos-Utrera, 2008). It has been reported that exclusion of maternal effects (maternal genetic and permanent

environment) from the statistical model results in overestimation of variance and heritability of direct additive genetic effects for weight at weaning (Khombe *et al.*, 1995; Robinson, 1996). Therefore, before performing the genetic evaluation of any economically important trait, selection of proper statistical model should be of primary interest for geneticists and producers, in order to formulate optimum breeding programs and to evaluate the genetic progress of ongoing programs.

For Simmental (Rosales-Alday *et al.*, 2004), Charolais (Ríos-Utrera *et al.*, 2007) and Brahman registered cattle (Parra-Bracamonte *et al.*, 2007) under Mexican production conditions, estimates of genetic parameters for growth traits have been reported. Limousin is a beef cattle breed from France; however, the Mexican Limousin originated from multiple importations of Limousin germplasm (semen and cows) from Canada and U.S.A. In the North American Limousin population, a positive genetic trend for several traits (e.g., weaning and yearling weight) has been found (NALF, 2011). In contrast, in spite of Limousin is one of the most important breeds (after Simmental and Charolais) in beef production systems of Mexico, estimates of genetic parameters for this breed have not been reported. Knowledge of the size of the variances, as well as of the sign and size of the covariances, is necessary to improve beef productivity through selection of Mexican Limousin cattle.

The likelihood ratio test has been extensively used to compare the suitability of different statistical models for the estimation of genetic parameters of beef cattle. In a study carried out in Canada with crossbred bulls (Mwansa *et al.*, 2000), the effect of including concomitant body weight and(or) a random dam effect in genetic evaluation models on variance components estimates for scrotal circumference was evaluated using likelihood ratio tests.

Hoque *et al.* (2007) reported a comparison of different animal models with direct and including or excluding associated maternal effects for feed intake, feed-conversion ratio, residual feed intake and metabolic body weight in Japanese Black cattle using also such test. In Mexico, the likelihood ratio test has been applied to define proper statistical models for the national genetic evaluations of Salers and Brangus cattle (Domínguez-Viveros *et al.*, 2009). Sometimes, however, it is difficult to make a good choice of the proper model (Swalve, 1993), while some other times researchers have failed to separate direct and maternal additive genetic effects for birth and other weights appropriately due to structure of data, complicating selection of appropriate model (Pelicioni *et al.*, 2003). Based on the aforementioned, the aim of this study was to identify the most suitable model to estimate

genetic parameters for weights at birth, weaning and yearling of Mexican registered Limousin cattle.

MATERIALS AND METHODS

Description of data

Field data for birth weight, weaning weight, and yearling weight, as well as pedigree information were supplied by the Mexican Limousin Breeders Association for the period from 1991 to 2006. All weaning and yearling weight records were adjusted to a 205- and 365-d basis, according to the Guidelines for Uniform Beef Improvement Programs (BIF, 2002). Adjusted weaning and yearling weights should be calculated for calves within an age range of 160 to 250 and of 320 to 410 days of age. Records on calves outside these ranges were eliminated from the analysis but not from the pedigree file. After basic edits, 8,910 animals with birth weight, 5,192 animals with weaning weight adjusted to 205 d, and 2,836 animals with yearling weight adjusted to 365 d records were used in the analysis. The number of sires with progeny in the data was 645, 488 and 315 for birth weight, weaning weight adjusted to 205 d and yearling weight adjusted to 365 d, respectively. The pedigree file, which incorporated all pedigree information available, was the same for these traits and consisted of 12,736 animals, including parents without records. Connectivity among different Limousin herds has been established to some extent through the use of common semen of Limousin sires from U.S.A., France and Mexico, and through auction of bulls and heifers among Mexican Limousin breeders. Numbers of records and sires for each trait and further details of the data structure are summarized in Table 1.

Table 1. Descriptive statistics and data structure for growth traits^a of Mexican registered Limousin cattle

	BW	WW205	YW365
Number of records	8,910	5,192	2,836
Minimum	23.00	95.15	171.21
Maximum	49.00	389.97	564.66
Mean	36.06	215.73	355.28
Standard deviation	4.35	40.13	61.65
Coefficient of variation	12.06	18.60	17.35
Number of sires	645	488	315
Number of dams	4,558	3,325	2,030
Number of de herds	107	87	70
Number of contemporary groups	2,083	1,145	662
Number of animals in the pedigree	12,736	12,736	12,736

^aBW= birth weight; WW205= weaning weight adjusted to 205 days of age; YW365= yearling weight adjusted to 365 days of age.

Definition of models

Each growth trait was analyzed with six different single trait animal models, like those described by Meyer (1992), to assess the importance of different maternal effects. The first model, Model A, was the basic animal model fitting the animal’s direct genetic effect as the only random effect. Model AP included the direct genetic plus the common environmental effect due to the dam, fitted as an additional random effect. In contrast, Model AM attributed all the maternal effects to the genotype, fitting maternal additive genetic effects as a second random effect for each animal. Models AMC and AMP were the same as Model AM but they also allowed for a covariance between direct and maternal genetic effects, and a common environmental effect due to the dam (uncorrelated with the genotype of the dam), respectively. Finally, the most complete model, Model AMCP, was adjusted for all three random effects plus the covariance between direct and maternal genetic effects. All animal models included the same fixed effects, contemporary group and age of dam. Contemporary groups were constructed using herd, year, season, and sex of calf information, while dam age was taken into account by fitting it as a linear covariable.

In matrix notation, the AMCP model was: $\mathbf{y} = \mathbf{X}\boldsymbol{\beta} + \mathbf{Z}_1\mathbf{a} + \mathbf{Z}_2\mathbf{m} + \mathbf{W}_1\mathbf{p} + \mathbf{e}$, where \mathbf{y} is the vector of records, $\boldsymbol{\beta}$ is a vector of fixed effects, \mathbf{a} is an unknown vector of random direct additive genetic effects, \mathbf{m} is an unknown vector of random maternal additive genetic effects, \mathbf{p} is an unknown vector of random maternal permanent environmental effects, \mathbf{e} is an unknown vector of random temporary environmental effects, and \mathbf{X} , \mathbf{Z}_1 , \mathbf{Z}_2 , and \mathbf{W}_1 are known incidence matrices relating records to $\boldsymbol{\beta}$, \mathbf{a} , \mathbf{m} , and \mathbf{p} , respectively. The (co)variance matrix for random effects in the AMCP model was:

$$V \begin{bmatrix} a \\ m \\ p \\ e \end{bmatrix} = \begin{bmatrix} A\sigma_a^2 & A\sigma_{am} & 0 & 0 \\ A\sigma_{am} & A\sigma_m^2 & 0 & 0 \\ 0 & 0 & I_{N_d}\sigma_p^2 & 0 \\ 0 & 0 & 0 & I_N\sigma_e^2 \end{bmatrix},$$

where A is the matrix of Wright’s additive numerator relationships among all animals in the pedigree, σ_a^2 is the direct additive genetic variance, σ_m^2 is the maternal additive genetic variance, σ_{am} is the direct-maternal genetic covariance, σ_{pe}^2 is the maternal permanent environmental variance, σ_e^2 is the temporary environmental variance, and I_{N_d} and I_N are identity

matrices with orders the number of dams and the number of observations, respectively.

Estimates of genetic parameters

Variance and covariance components were estimated by Derivative-Free Restricted Maximum Likelihood, using the MTDFREML set of programs developed by Boldman *et al.* (1995). Convergence was assumed to have been reached if the variance of minus twice the logarithm of the likelihood (-2[log likelihood]) in the simplex was less than 10^{-8} . After first convergence, restarts were performed to verify that it was not at a local minimum. Estimates of fraction of total phenotypic variance (σ_p^2) due to maternal permanent environmental effects ($c^2 = \sigma_{pe}^2 / \sigma_p^2$), direct heritability ($h_a^2 = \sigma_a^2 / \sigma_p^2$), maternal heritability ($h_m^2 = \sigma_m^2 / \sigma_p^2$) and genetic correlation between direct and maternal additive genetic effects ($r_{am} = \sigma_{am} / (\sigma_a^2 \sigma_m^2)^{1/2}$) were derived from estimates of variance and covariance components.

Comparisons between models

Suitability of one model over another to fit significantly better birth, weaning and yearling weight data was determined via the likelihood ratio test (Dobson, 1990) for maternal permanent environmental effects, maternal genetic effects or covariance between direct and maternal genetic effects. Likelihood ratio tests were carried out subtracting the value of -2[log likelihood] for the model with more parameters from that value corresponding to the model with fewer parameters. After that, the probability of rejecting the null hypothesis (e.g., maternal additive genetic variance is equal to zero) was calculated using the probchi function of SAS (SAS, 2001) with one degree of freedom (number of different parameters estimated for two models), since all comparisons were made for models that differed in only one random factor.

RESULTS AND DISCUSSION

Estimates of (co)variance components and genetic parameters obtained with the six different animal models for birth weight, weaning weight adjusted to 205 days, and yearling weight adjusted to 365 days, together with values for -2[log likelihood] are summarized in Table 2, while likelihood ratio test statistics for maternal permanent environmental effects, maternal additive genetic effects and direct-maternal genetic covariance for the same traits are in Table 3.

Table 2. Estimates of (co)variance components (kg^2) and genetic parameters^a obtained with six different animal models^b for birth weight (BW), weaning weight adjusted to 205 days (WW205), and yearling weight adjusted to 365 days (YW365) of Mexican registered Limousin cattle

Model	σ_a^2	σ_m^2	σ_{am}	σ_{pe}^2	σ_e^2	h_a^2	h_m^2	r_{am}	c^2	-2 log L ^c
BW										
A	1.920				8.299	0.19 ± 0.03				24,540.117
AP	1.191			0.697	8.220	0.12 ± 0.02			0.07 ± 0.01	24,521.172
AM	1.089	0.678			8.335	0.11 ± 0.02	0.07 ± 0.01			24,519.009
AMP	1.088	0.678		0.661	7.675	0.11 ± 0.02	0.07 ± 0.01		0.07 ± 0.01	24,519.009
AMC	1.353	1.512	-0.96		8.195	0.13 ± 0.03	0.15 ± 0.03	-0.67 ± 0.35		24,505.893
AMCP	1.338	1.159	-0.91	0.388	8.122	0.13 ± 0.03	0.11 ± 0.04	-0.73 ± 0.42	0.04 ± 0.03	24,503.888
WW205										
A	209.3				432.2	0.33 ± 0.04				31,897.616
AP	116.2			97.6	414.8	0.18 ± 0.04			0.16 ± 0.02	31,868.975
AM	106.6	96.6			426.3	0.17 ± 0.04	0.15 ± 0.02			31,867.649
AMP	106.3	96.7		78.9	347.7	0.17 ± 0.04	0.15 ± 0.02		0.13 ± 0.02	31,867.649
AMC	133.6	199.8	-113.5		410.6	0.21 ± 0.05	0.32 ± 0.06	-0.69 ± 0.34		31,856.149
AMCP	133.5	167.1	-107.7	30.3	406.5	0.21 ± 0.05	0.27 ± 0.08	-0.72 ± 0.40	0.05 ± 0.05	31,855.579
YW365										
A	192.4				780.5	0.20 ± 0.06				17,717.321
AP	170.9			34.2	765.1	0.18 ± 0.06			0.04 ± 0.04	17,716.775
AM	178.2	17.7			775.4	0.18 ± 0.06	0.02 ± 0.04			17,717.122
AMP	178.1	17.7		179.3	596.2	0.18 ± 0.06	0.02 ± 0.04		0.18 ± 0.01	17,717.122
AMC	276.6	235.3	-239.2		711.0	0.28 ± 0.09	0.24 ± 0.09	-0.94 ± 0.65		17,709.356
AMCP	273.8	200.2	-231.5	40.4	700.0	0.28 ± 0.09	0.20 ± 0.11	-0.99 ± 0.75	0.04 ± 0.07	17,709.054

^a σ_a^2 = direct additive genetic variance; σ_m^2 = maternal additive genetic variance; σ_{am} = covariance between additive direct and additive maternal genetic effects; σ_{pe}^2 = maternal permanent environmental variance; σ_e^2 = residual variance; h_a^2 = direct heritability; h_m^2 = maternal heritability; r_{am} = correlation between direct and maternal genetic effects; c^2 = fraction of total variance due to maternal permanent environmental effects.

^b Effects included in the statistical models: A= direct additive genetic effects; P= maternal permanent environmental effects; M= maternal additive genetic effects; C= covariance between direct and maternal genetic effects.

^c -2 log L = -2(logarithm of the likelihood).

Birth weight

Estimates of direct additive genetic variance and direct heritability for birth weight were substantially reduced when maternal additive genetic effects and (or) maternal permanent environmental effects were added to the basic animal model. In particular, comparison of estimates of direct heritability for Model A and Model AM indicates that there was a decrease from 0.19 to 0.11 (Table 2). It seems that estimates of direct additive genetic variance included at least part of the maternal variance. Therefore, direct heritability estimates decreased when maternal effects were considered in the model. Including maternal additive genetic effects and (or) maternal permanent environmental effects gave similar estimates of direct heritability.

Likelihood ratio tests (Table 3) for maternal additive genetic variance (e.g., when comparing Model AM vs Model A) and direct-maternal genetic covariance (e.g., when contrasting Model AMC vs Model AM or Model AMCP vs Model AMP) indicates that maternal additive genetic effects and the covariance between direct and maternal additive genetic effects contributed to a better adjustment ($P < 0.01$) of birth weight data. Therefore, using estimates of genetic parameters from Models A and AM, would result in biased estimated breeding values. The maternal permanent environmental variance was only important ($P < 0.01$) when the permanent environment was fitted as the only maternal effect (Model AP) besides the residual. In addition, the value of $-2[\log \text{likelihood}]$ for Model AMCP (24,503.9) was not considerably smaller ($P > 0.05$) than the value of $-2[\log \text{likelihood}]$ for Model AMC (24,505.9). Therefore, Model AMC was considered the best animal model for birth weight. Estimates of direct and maternal heritability with the AMC animal model were similar.

For Simmental, Boran, Tropicarne, mixed breeds and crosses, and Salers cattle, Swalve (1993), Haile-Mariam and Kassa-Mersha (1995), Domínguez-Viveros *et al.* (2003), Demeke *et al.* (2003) and Domínguez-Viveros *et al.* (2009), assessing a comparable series of six different animal models (Models A, AP, AM, AMC, AMP and AMCP), concluded also that birth weight data were best described by an animal model including both direct and maternal genetic effects and the covariance between them, i.e., the AMC model was the most suitable animal model to analyze birth weight data. The estimates of direct heritability for birth weight (0.12 and 0.14) reported by Domínguez-Viveros *et al.* (2003) and Demeke *et al.* (2003) were similar to the current estimate reported here. However, estimates of direct heritability for birth weight by Swalve (1993) and Haile-Mariam and Kassa-Mersha (1995) were larger than corresponding estimate obtained in the

present study with the AMC model (0.33 and 0.24 vs 0.13). On the other hand, current estimate of maternal heritability for birth weight was greater than corresponding estimates (0.15 vs 0.10, 0.07, 0.08 and 0.07) obtained by those authors with a model equivalent to Model AMC from our study. In contrast to the present result, Meyer (1992) for Angus, Hereford and Zebu crosses, Meyer (1993) for Polled Hereford, and Maiwashe *et al.* (2002) for Bonsmara cattle, concluded that the best animal model to fit their birth weight data included effects due to permanent environment of the dam along with direct and maternal additive genetic effects and their covariance, i.e., the best model was a model comparable to the AMCP model from our study. In a previous study (Meyer *et al.*, 1993) conducted in Australia with Polled Hereford and Wokalup cattle, a model that included direct and maternal additive genetic effects, as well as permanent environmental effects of the dam, was chosen as the best animal model to fit birth weight data, contrasting also with our findings.

Weaning weight

As with estimates of direct additive genetic variance and direct heritability for birth weight, corresponding estimates for weaning weight were substantially inflated when ignoring maternal effects. Estimates of direct additive genetic variance for weaning weight ranged from 106 kg² with Model AM to 209 kg² with Model A, while estimates of direct heritability ranged from 0.17 to 0.33 with these two different animal models. In a previous study (Waldron *et al.*, 1993) carried out in New Zealand with Angus and Hereford cattle, it was concluded that animal models which ignored maternal effects tended to overestimate direct heritability. In contrast, estimates of direct heritability were similar for each of the five different animal models including maternal effects (Table 2).

Maternal additive genetic effects and the covariance between direct and maternal additive genetic effects contributed to a better adjustment ($P < 0.01$) of weaning weight data as indicated by likelihood ratio tests. Like the estimate of maternal additive genetic variance for birth weight, the estimate of maternal additive genetic variance for weaning weight remained practically constant after adding maternal permanent environmental effects to the AM model. The estimate of maternal additive genetic variance for Model AM was 96.6 kg², and the corresponding estimate for Model AMP was 96.7 kg². With Model AMCP, the value of $-2[\log \text{likelihood}]$ (31,855.6) did not substantially decrease compared to the corresponding value with Model AMC (31,856.1). Hence, Model AMC fitted weaning weight data better than any other animal model. When fitting the “best” animal model, estimates of maternal heritability were greater than estimates of direct heritability (0.32 vs 0.21),

indicating that maternal additive genetic effects are more important than direct additive genetic effects for weaning weight in Mexican Limousin cattle.

In agreement with present results, Spanish researchers (Gutierrez *et al.*, 1997), working with Asturiana de los Valles cattle, found that a model fitting direct and maternal additive genetic effects and their covariance was the “best” animal model for weaning weight. For, Nelore, Boran, Bonsmara, Tabapua, Angus, Polled Hereford, Simmental and Limousin cattle, researchers from other countries (Ferraz Filho *et al.*, 2004; Haile-Mariam and Kassa-Mersha, 1995; Maiwashe *et al.*, 2002; Mercadante and Lôbo, 1997; Meyer, 1992; Meyer, 1993; Swalve, 1993; Van Niekerk and Naser, 2006) concluded that the most suitable model to analyze weaning weight data was a comprehensive model, equal to the AMCP model from our study. The estimate of direct heritability for weaning weight from the present study is within the range (0.16 to 0.35) of corresponding estimates reported for those eight breeds of cattle. Current estimate of maternal heritability, however, was greater than corresponding estimates (0.18, 0.14, 0.22, 0.06, 0.18, 0.12, 0.13, 0.10) for such breeds in those studies. In other previous studies (Ap Dewi *et al.*, 1998; Demeke *et al.*, 2003; Meyer *et al.*, 1993), Models AMP, AM and AP were considered the best models to analyze weaning

weight records. Estimates of direct heritability for weaning weight obtained with these three models were also low, in agreement with present estimate of direct heritability; however, the estimate of maternal heritability for weaning weight reported here is greater than corresponding estimates obtained in those previous studies with these three models.

Yearling weight

For yearling weight, fitting maternal permanent environmental effects or maternal additive genetic effects along with direct additive genetic effects in the model (Models AP and AM, respectively) did not significantly improved the $-2[\log \text{likelihood}]$, as indicated by likelihood ratio tests, i.e., estimates of maternal permanent environmental variance and maternal additive genetic variance were not different ($P > 0.10$) from zero. Therefore, the simplest animal model, Model A, was considered the most appropriate model for genetic evaluation of yearling weight records of Mexican Limousin cattle. Like estimates of heritability for birth and weaning weight, estimates of heritability for yearling weight were low, indicating that response to selection for these traits would be slow.

Table 3. Likelihood ratio test statistics for maternal permanent environmental effects (σ_{pe}^2), maternal genetic effects (σ_m^2) and direct-maternal genetic covariance (σ_{am}) for birth weight (BW), weaning weight adjusted to 205 days (WW205) and yearling weight adjusted to 365 days (YW365) of Mexican registered Limousin cattle

Comparisons between models ^a	Growth trait			Hypothesis tested
	BW	WW205	YW365	
Model AP vs Model A	-18.95**	-28.64**	-0.55	$\sigma_{pe}^2 = 0$
Model AM vs Model A	-21.11**	-29.97**	-0.20	$\sigma_m^2 = 0$
Model AMP vs Model AP	-2.16	-1.33	-0.35	$\sigma_m^2 = 0$
Model AMP vs Model AM	-0.00	-0.00	-0.00	$\sigma_{pe}^2 = 0$
Model AMC vs Model AM	-13.12**	-11.50**	-7.77**	$\sigma_{am} = 0$
Model AMCP vs Model AMP	-15.12**	-12.07**	-8.07**	$\sigma_{am} = 0$
Model AMCP vs Model AMC	-2.00	-0.57	-0.30	$\sigma_{pe}^2 = 0$

^aEffects included in the statistical models: A= direct additive genetic effects; P= maternal permanent environmental effects; M= maternal additive genetic effects; C= covariance between direct and maternal genetic effects.

**($P < 0.01$).

For Boran, Barca and Horro and their crosses with Holstein Friesian, Jersey and Simmental breeds of cattle in Ethiopia, Demeke *et al.* (2003) concluded also that an animal model that involved only the animal's

direct additive genetic effect was a better fit for yearling weight data. However, the estimate of direct heritability for yearling weight reported by these authors was smaller than the corresponding estimate

reported in the present study for Limousin cattle (0.13 vs 0.20). In preceding studies carried out in Australia (Robinson, 1996; Swalve, 1993), Brazil (Ferraz Filho *et al.*, 2004; Mercadante and Lôbo, 1997) and Addis Ababa (Haile-Mariam and Kassa-Mersha, 1995), in which similar models to those used in the present study were compared, researchers concluded that maternal effects were important for yearling weight, and indicated that such effects should be considered in genetic evaluations of this trait. On the contrary, for Charolais and Angus cattle in Germany, Grotheer *et al.* (1997) found that fitting maternal permanent environmental effects along with direct additive genetic effects in the model led to robust estimation of genetic variances for yearling weight, concluding that this form of the animal model is appropriate for the estimation of breeding values.

CONCLUSIONS AND IMPLICATIONS

In general, estimates of direct and maternal heritability obtained in the present study for weights of Mexican Limousin cattle at birth, weaning and yearling were low, suggesting that expected genetic progress by single trait selection would not to be high, mainly for birth weight. For birth weight and weaning weight adjusted to 205 d, the AMC model showed better adjustment for (co)variance components of registered Limousin data. When maternal effects were not included in the animal model, estimates of direct heritability were overestimated for birth and weaning weights, and consequently expected progeny differences will be biased, affecting selection efficiency. Maternal effects, genetic as well as permanent environmental, were not important for yearling weight, indicating absence of carry-over effects in Mexican Limousin cattle after weaning. Hence, a simple animal model, including only direct additive genetic effects of the animal as a random effect, besides the residual, is appropriate to analyze yearling weight data.

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*Submitted December 20, 2010 – Accepted February 02, 2011
Revised received February 15, 2011*