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DIRECT AND MATERNAL GENETIC EFFECTS FOR GROWTH TRAITS IN INDUBRAZIL CATTLE

Efectos Genéticos Directos y Maternos para Características de Crecimiento de Bovinos Indubrasil

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ABSTRACT

The objective was to estimate (co)variance components and genetic parameters for birth weight, adjusted 205-day (d) weaning weight, and adjusted 365-d yearling weight of Mexican Indubrazil calves obtained from an experimental herd under tropical conditions. (Co)variance components and genetic parameters were estimated fitting single-trait animal models with the MTDFREML program. For birth weight, the model included the direct and maternal genetic effects as well as the (co)variance between these two effects. The model for adjusted 205-d weaning weight was similar to the one for birth weight, but also included the maternal permanent environmental effect. The animal model to analyze adjusted 365-d yearling weight included the direct genetic effect. For birth weight and adjusted 205-d weaning weight, direct genetic effects were more important than maternal genetic effects. Estimates of direct heritability were: 0.27, 0.11 and 0.13 for birth weight, adjusted 205-d weaning weight and adjusted 365-d yearling weight, respectively. Estimates of maternal heritability were: 0.10 and 0.09 for birth weight and adjusted 205-d weaning weight, respectively. The estimate of the correlation between direct and maternal effects for adjusted 205-d weaning weight was relatively low (-0.27). Estimates of direct heritability for weaning and yearling weights suggest that such traits could be increased by direct selection.

Key words: Genetic effects, growth traits, Indubrazil cattle, tropic.

RESUMEN

El objetivo fue estimar componentes de (co)varianza y parámetros genéticos para peso al nacimiento, peso al destete ajustado a 205 días (d) y peso al año ajustado a 365 d de edad de becerros Indubrasil mexicanos obtenidos en un hato experimental bajo condiciones tropicales. Los componentes de (co)varianza y parámetros genéticos se estimaron ajustando modelos animales para una sola característica con el programa MTDFREML. Para peso al nacimiento, el modelo incluyó los efectos genético directo, genético materno, así como la (co)varianza entre estos dos efectos. El modelo animal para peso al destete ajustado a 205 d fue similar al modelo para peso al nacimiento, pero además incluyó el efecto del ambiente materno permanente. El modelo animal para analizar el peso al año ajustado a 365 d de edad incluyó el efecto genético directo. Para peso al nacimiento y peso al destete ajustado a 205 d, el efecto genético directo fue más importante que el efecto genético materno. Los estimadores de heredabilidad directa fueron: 0,27; 0,11 y 0,13 para peso al nacimiento, peso al destete ajustado a 205 d y peso al año ajustado a 365 d de edad, respectivamente. Los estimadores de heredabilidad materna fueron: 0,10 y 0,09 para peso al nacimiento y peso al destete ajustado a 205 d, respectivamente. El estimador de la correlación entre efectos directos y maternos para peso al destete ajustado a 205 d fue relativamente bajo (-0,27). Los estimadores de heredabilidad directa para pesos al destete y al año sugieren que dichas características pueden incrementarse mediante selección.

Palabras clave: Efectos genéticos, características de crecimiento, ganado Indubrasil, trópico.

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INTRODUCTION

Many researchers around the world have shown that direct and maternal genetic effects significantly influence early (pre-weaning) and late (post-weaning) growth of cattle [33, 34] and other animal species, including sheep (*Ovis aries*) [26, 59]. During the last decade, there have been significant efforts in Mexico directed towards the estimation of genetic parameters of growth traits in various *Bos taurus* and *Bos indicus* beef breeds, such as: Tropicarne [10], Simmental [51], Nelore [31], Charolais [46], Sardo Negro [27], Brahman [38], Guzerat [28], Brangus/Salers [11], Limousin [48] and Charbray [49]. However, there is no information in the scientific literature related to the magnitude and importance of direct and maternal genetic effects (heritability) for growth traits of Indubrazil cattle raised in Mexico, although this breed, along with the Brahman, is one of the two major Zebu breeds in this country. Indubrazil is a beef cattle breed from Brazil and is the result from crosses between Gyr, Guzerat and Nelore cattle. It was introduced to Mexico (sires and cows) from 1945 to 1946. The breed was distributed from Yucatán, along the Gulf of Mexico coast, to Coahuila and Nuevo León, in Northern Mexico. This Zebu breed has shown good adaptability to a wide range of environmental conditions of Mexico. In the tropical areas, is well accepted by dual-purpose cattle producers because they use it to obtain Brown Swiss x Zebu and Holstein x Zebu crosses for milk and calf production. The "Asociación Mexicana de Criadores de Cebú" has an Indubrazil database with approximately 168,760 registered cattle [3].

One of the few studies conducted with Indubrazil cattle not done in Mexico is the work reported by Santos *et al*. [53], who evaluated the influence of direct and maternal genetic effects on weaning weight of animals reared in the State of Bahia, Brazil. However, it is necessary to know the direct and maternal heritability of other growth traits (e.g., birth and yearling weights) which also affect the efficiency of beef production systems, in order to establish successful breeding programs. In addition, genetic parameters are specific to each cattle population and heavily influenced by the environment. Hence, the objective of the present study was to estimate, fitting animal models, the variance components and genetic parameters for birth, weaning and yearling weights of Indubrazil cattle reared under tropical conditions of Mexico.

MATERIALS AND METHODS

Location and climate

The current study was conducted at Playa Vicente Research Station from the National Institute for Forestry, Agriculture and Livestock Research (INIFAP). The experimental site is located at 17° 19' NL and 95° 41' WL, at 95 meters above sea level, in the Municipality of Playa Vicente, in the State of Veracruz, Mexico. The climate is tropical wet [17], with mean annual temperature and precipitation of 26.8°C and 2200 mm, respectively [55].

Animals

Records of 598 Indubrazil calves born during a 27-year period (1980-2006) were analyzed. These calves were produced from 35 sires and 281 dams. Sires were mated to dams mainly through artificial insemination, but there was also some natural mating.

Feeding

From birth to weaning, calves were reared with restricted suckling, which lasted one hour (h) in the morning (07:00 to 08:00 h) and one h in the afternoon (17:00 to 18:00 h). The rest of the day (d) the calves were kept in rotational grazing on African Star grass (*Cynodon plectostachyus*). Weaning was performed at seven months of age, on average. Fifteen d before and 30 d after weaning, calves were supplemented with 1 kg/calf/d of a concentrate feed with 18% crude protein, 70% total digestible nutrients and 2.7 Mcal of metabolic energy/kg of dry mater. From weaning to yearling, the calves were still maintained in rotational grazing on African Star grass.

Traits

The evaluated traits were: birth weight, weaning weight adjusted to 205 d and yearling weight adjusted to 365 d. Weaning and yearling weights were linearly adjusted as recommended by the Guidelines for Uniform Beef Improvement Programs [5].

Statistical Analyses

Preliminary Analyses

Before estimating variance components and genetic parameters, preliminary statistical analyzes were performed for each trait, in order to determine which fixed effects were significant sources of variation. For this purpose, the Mixed procedure (PROC MIXED) was implemented in the SAS program [24]. PROC MIXED computations are based on likelihood principles [30] to obtain (restricted) maximum likelihood estimates of the variance component parameters. The DDFM=Satterth option of the Mixed procedure of SAS was used for computing the denominator degrees of freedom for the tests of fixed effects. The DDFM=Satterth option (a general Satterthwaite approximation) implemented here is intended to produce an accurate F approximation. The fixed effects included in the full model were: year of birth (1980, 1981,..., 2006), birth season (December to May; June to November), calf sex, first-order interactions derived from these three effects, and cow age at calving in d as a linear and quadratic covariable. In addition, the preliminary full model included sire as a random effect. To determine the final models, sequential analyzes were performed by removing from the full model not significant interactions and covariates (P> 0.05).

The final model for birth weight resulting from these preliminary analyzes included year of birth, birth season, calf sex, year of birth x birth season interaction, and the age of dam at calving, as well as sire as a random effect. The final model to analyze weaning weight was similar to the model for birth weight, but instead of year of birth x birth season interaction it included year of birth x calf sex interaction. For yearling weight, the final model was similar to the model to analyze birth weight, but it did not include year of birth x birth season interaction.

Animal models in matrix notation

After a series of preliminary analyzes with different variants of the animal model, the following models were assumed: $\mathbf{y = Xb + Z_1a + Z_2m + e}$, with cov($\mathbf{a}$,$\mathbf{m}$)= $\mathbf{A}\sigma_{am}$, $\mathbf{y = Xb + Z_1a + Z_2m + Z_3c + e}$, with cov($\mathbf{a}$,$\mathbf{m}$)=$\mathbf{A}\sigma_{am}$, and $\mathbf{y = Xb + Z_1a + e}$, for birth weight, weaning weight and yearling weight, respectively. In these models, $\mathbf{y}$ is a vector of observations for each one of the different traits, $\mathbf{b}$ is a vector of fixed effects, $\mathbf{a}$ is an unknown random vector of direct additive genetic effects, $\mathbf{m}$ is an unknown random vector of maternal additive genetic effects, **C** is an unknown random vector of maternal permanent environmental effects, $\mathbf{e}$ is an unknown random vector of temporary environmental effects, and $\mathbf{X}$, $\mathbf{Z_1}$, $\mathbf{Z_2}$ and $\mathbf{Z_3}$ are known incidence matrices relating records to $\mathbf{b}$, $\mathbf{a}$, $\mathbf{m}$, and $\mathbf{c}$, respectively. It was assumed that direct additive genetic, maternal additive genetic, maternal permanent environmental and residual effects were normally distributed with mean 0.

The variance-covariance structure ($\mathbf{V}$) assumed in the weaning weight analysis was:

$$V\begin{bmatrix} a \\ m \\ c \\ e \end{bmatrix} = \begin{bmatrix} A\sigma_a^2 & A\sigma_{am} & 0 & 0 \\ A\sigma_{am} & A\sigma_m^2 & 0 & 0 \\ 0 & 0 & I_c\sigma_c^2 & 0 \\ 0 & 0 & 0 & I_n\sigma_e^2 \end{bmatrix}$$

where $\mathbf{A}$ is the Wright's additive relationship matrix [60] 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_c^2 is the maternal permanent environmental variance, σ_e^2 is the residual variance and I_c and I_n are identity matrices of size equal to the number of dams and the number of observations, respectively.

Estimation of variance components

Variances and (co)variances were estimated with Derivative-Free REML [56], using the MTDFREML program [6]. It was assumed that convergence was reached when the variance of minus twice the logarithm of the likelihood in the simplex was less than 10^{-12}. After the program converged for the first time, several restarts were performed to ensure a global rather than a local maximum had been reached. In each new analysis, parameter estimates obtained in the previous analysis were used as initial values. Solutions of random effects were obtained from the last iteration cycle where a global maximum was reached.

Estimates of genetic parameters

Estimates were obtained for phenotypic variance $\left(\sigma_p^2 = \sigma_a^2 + \sigma_m^2 + \sigma_{am} + \sigma_c^2 + \sigma_e^2\right)$, heritability for direct additive genetic effects $\left(h_a^2 = \sigma_a^2 / \sigma_p^2\right)$, heritability for maternal additive genetic effects $\left(h_m^2 = \sigma_m^2 / \sigma_p^2\right)$, correlation between direct and maternal additive genetic effects $\left(r_{am} = \sigma_{am} / \left(\sigma_a^2\sigma_m^2\right)^{1/2}\right)$, fraction of phenotypic variance due to maternal permanent environmental effects $\left(c^2 = \sigma_c^2 / \sigma_p^2\right)$, and residual variance as proportion of phenotypic variance $\left(e^2 = \sigma_e^2 / \sigma_p^2\right)$. Standard errors for estimates of genetic parameters were approximated and were calculated using the average information matrix [20] and the Delta Method [9]. Additionally, total heritability estimates (h_t^2) were calculated using the following equation: $h_t^2 = \left(\sigma_a^2 + 0.5\sigma_m^2 + 1.5\sigma_{am}\right) / \sigma_p^2$.

RESULTS AND DISCUSSION

Descriptive statistics and data structure are shown in TABLE I. Means and standard deviations of weights at birth, weaning and yearling were: 32.3 ± 5.27, 182.5 ± 30.00 and 220.7 ± 43.00 kg, respectively. The coefficients of variation for weaning weight and yearling weight were greater than the coefficient of variation for birth weight, as expected. The number of calves, sires and dams was 598, 35, and 281, respectively. The pedigree file consisted of 796 animals. TABLE II presents estimates of variance components and genetic parameters for each of the analyzed growth traits.

Birth weight

Direct heritability

The direct genetic effect for birth weight was found to be moderately heritable, with a heritability estimate of 27%, which suggests that birth weight can be modified through selection. Present estimate of direct heritability is within the range of direct heritability estimates of 0.37, 0.33, 0.33, 0.28, 0.32, 0.28 and 0.31 reported for American [22], Venezuelan [42, 43], South African [40] and Mexican [39] Brahman cattle, as well as for Brazilian Nelore [1] and Gyr [21] cattle. Ríos-Utrera [47] in a review of estimates of genetic parameters reported that unweighted means obtained from estimates of direct heritability for birth weight were 0.32 for Brahman and 0.34 for Nelore cattle. Mercadante *et al*. [32] and Lira *et al*. [23] reported average estimates of direct heritability for birth weight with values of 0.33 (weighted mean) and 0.34 (unweighted mean), respectively, for different *Bos indicus* beef breeds. In contrast, Estrada-León *et al*. [15] for Mexican Brahman, and Martínez-González *et al*. [29] for Mexican Nelore cattle reported estimates of direct heritability for birth weight with values of 0.56 and 0.59, respectively. However, according to Meyer [34], these heritability values could be overestimated because corre-

TABLE I
DESCRIPTIVE STATISTICS AND DATA STRUCTURE FOR BIRTH WEIGHT (BW), WEANING WEIGHT (WW) AND YEARLING WEIGHT (YW) OF INDUBRAZIL CATTLE REARED IN MEXICO

	Trait		
	BW, kg	WW, kg	YW, kg
Descriptive statistics			
Mean	32.30	182.53	220.73
Minimum value	19	101	93
Maximum value	50	317	397
Standard deviation	5.27	30.0	43.0
Coefficient of variation, %	16.32	16.45	19.49
Data structure			
Calves, number	598	598	598
Sires, number	35	35	35
Dams, number	281	281	281
Animals in the pedigree, number	796	796	796

lations between direct and maternal effects for birth weight obtained by these authors were considerably high and negative (-0.55 and -0.90, respectively), inflating the estimate of the direct additive genetic variance.

Maternal heritability

The maternal genetic effect was less heritable than the direct genetic effect, having a low heritability estimate. The estimate of maternal heritability for birth weight obtained in the present study is within the range of estimates reported in the literature, but most of literature estimates are lower than the one reported here. Albuquerque and Meyer [1], Arnason and Kassa-Mersha [2], Diop *et al.* [8] and Salces *et al.* [52] reported estimates of maternal heritability for birth weight with values of 0.01, 0.02, 0.03 and 0.02 for Nelore, Boran, Gobra and Brahman cattle. On the other hand, several authors [12, 13, 15, 22, 29, 39, 40] have obtained estimates of maternal heritability for birth weight similar to the one reported in the present investigation, with values ranging from 0.11 to 0.18. The unweighted means of maternal heritability estimates reported by Ríos-Utrera [47] for Brahman (0.10) and Nelore cattle (0.09) and by Lira *et al.* [23] for different *Bos indicus* breeds (0.09) were also similar to the corresponding estimate obtained in the present study.

The estimate of the genetic covariance between direct and maternal effects was practically zero, with a value of -0.00039 kg^2. Together, direct and maternal genetic effects explained 37% of the phenotypic variance of birth weight, so that about 63% of the total variation was due to unknown environmental and genetic effects. The estimate of total heritability for birth weight was moderate (0.32).

Weaning weight

Direct heritability

In contrast to the findings for birth weight, maternal heritability (0.09) for weaning weight was similar to the corresponding direct heritability (0.11). The low direct heritability for weaning weight estimated in the present paper suggests that selection to improve this trait would be lowly effective for the Indubrazil herd under study. Several authors have also reported low estimates of direct heritability (0.11 to 0.17) for weaning weight of Nelore, Guzerat, Tabapua, Brahman and Indubrazil cattle [12, 16, 25, 36, 40, 44, 45, 53, 54, 57]. Some other researches obtained estimates of direct heritability for weaning weight close to zero in different Zebu breeds [4, 14, 37, 42, 43]. In Mexico, by contrast, for Guzerat [28] and Nelore cattle [31] were reported higher estimates of direct heritability for weaning weight (0.53 and 0.43, respectively). The difference between these two estimates and the estimate of the current study may be due, in addition to the difference in the breeds tested, to the type of animal model used, since it has been shown that when the model does not include maternal effects (genetic and permanent environmental), as with the animal model adjusted for Martínez-González *et al*. [28] and Medina-Zaldivar *et al.* [31], direct heritability is overestimated (biased).

Maternal heritability

The magnitude of the maternal genetic effect for weaning weight suggests that Indubrazil cows in the experimental herd under study had low maternal (milking) ability, but there is enough maternal genetic variation (54.6 kg2; TABLE II) to increase milk yield of cows, though genetic progress probably would be slow. For other Zebu breeds, as well as for the experimental Indubrazil herd evaluated, it has been found that maternal genetic effects for weaning weight are lowly heritable, since scientific literature reports heritability values of 0.05, 0.03, 0.01, 0.10, 0.03, 0.04, 0.06, 0.10 for Indubrazil [53], Gyr [21], Guzerat [36], Tabapua [16], Bermejo Zebu [4], Brahman [50], Boran [19] and Nelore [7] cattle, respectively.

Maternal permanent environmental variance as a proportion of the total variance

The maternal permanent environmental effect was a minor source of variation for weaning weight. This result suggests that the loss or bad condition of molars and/or permanent inju-

TABLE II
ESTIMATES OF VARIANCE COMPONENTS AND GENETIC PARAMETERS[a] FOR BIRTH WEIGHT (BW), WEANING WEIGHT (WW) AND YEARLING WEIGHT (YW) OF INDUBRAZIL CATTLE REARED IN MEXICO

	BW	WW	YW
Variance components, kg^2			
σ_a^2	5.98	65.73	132.73
σ_m^2	2.16	54.60	–
σ_{am}	-0.00039	-16.069	–
σ_c^2	–	0.02	–
σ_e^2	14.43	482.15	881.53
σ_p^2	22.58	586.44	1.014.25
Genetic parameters			
h_a^2	0.27 ± 0.19	0.11 ± 0.11	0.13 ± 0.08
h_m^2	0.10 ± 0.08	0.09 ± 0.09	–
r_{am}	0.00 ± 0.63	-0.27 ± 0.86	–
c^2	–	0.00 ± 0.06	–
e^2	0.64 ± 0.14	0.82 ± 0.10	0.87 ± 0.08
h_t^2	0.32	0.11	0.13

[a] σ_a^2= direct additive genetic variance, σ_m^2= maternal additive genetic variance, σ_c^2= maternal permanent environmental variance, σ_e^2= residual variance, σ_p^2= phenotypic variance, h_a^2= direct heritability, h_m^2= maternal heritability, c^2= maternal permanent environmental variance as a proportion of phenotypic variance, e^2= residual variance as a proportion of phenotypic variance, h_t^2= total heritability.

ries due to accidents or diseases were minimal in dams, or if these problems occurred, they were harmless and did not affect the weaning weight of their calves. Unlike the findings of the present study, in which the maternal permanent environmental effect was practically zero for weaning weight (corresponding variance= 0.02 kg2; TABLE II), other researchers [7, 16] have reported values ranging from 0.04 to 0.17.

Correlation between direct and maternal genetic effects

The estimate of the correlation between direct and maternal effects for weaning weight was relatively low (-0.27). This estimate is similar to the weighted value (-0.23) reported in a published review of genetic parameters for Zebu cattle [32], as well as to the estimates obtained in studies by Cabrera *et al.* [7] (-0.20), Elzo and Wakeman [13] (-0.22) and Gunski *et al.* [18] (-0.24). Conversely, other researchers [8, 15, 19, 29, 41, 45] found more intense genetic correlations, with values of -0.46, -0.90, -0.58, -0.70, -0.57 and -0.68. However, Meyer [35] 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. The moderate antagonism between direct and maternal effects found in present study may be related to adaptive mechanisms of Zebu cattle to tropical conditions. In extreme environments, preserving animal size within certain limits may have adaptive advantages from a genetic viewpoint [58].

The genetic effects (direct and maternal) for weaning weight explained 20% of the total variation, so weaning weight depended on a higher proportion of unknown genetic and environmental effects. The estimate of total heritability for weaning weight was 11%.

Yearling weight

Direct heritability

The direct genetic effect for yearling weight proved to be a lowly heritable component, with a value of 13%. Compared with weights at birth and at weaning, yearling weight was mainly determined by unknown environmental and genetic effects. The direct heritability estimate for yearling weight found in the current research suggests that this trait can be improved by applying selection. Moreover, comparison with other estimates reveals that present estimate of direct heritability is within the range of corresponding estimates (0.08 to 0.17) reported in the literature for Tabapua [16], Guzerat [36], Brahman [40] and Nelore [57] cattle, although some other studies have reported little higher estimates for other *Bos indicus* breeds [8, 27]. Estimates of direct heritability for yearling weight of Indubrazil cattle were not found in the scientific literature, suggesting that such estimates are rare or that there have not been previously reported values.

CONCLUSIONS

For birth weight and weaning weight, the direct genetic effect was of greater importance than the maternal genetic effect. Also, there was no maternal permanent environmental effect on weaning weight. In general, estimates of direct and maternal heritability for Indubrazil cattle found in the present study are within the range of estimates reported for different Zebu breeds reared in Mexico and other countries. The magnitude of the estimates of direct heritability for weaning weight and yearling weight suggests that implementation of a selection program to improve these characteristics in our experimental herd would be feasible.

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