

Alternative animal models to estimate heritabilities and genetic correlations between direct and maternal effects of Pre and Post-Weaning weights of Tabapuã cattle¹

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ABSTRACT. The Tabapuã is a Zebu polled breed used for beef production, with white or gray hair coat and pigmented skin. Weaning (W205, 30,746 observations), twelve-month (W365, 27,701 observations) and 18-month (W550, 18,493 observations) weights of Tabapuã cattle, raised on pastures in several regions of Brazil, from 1975 to 1995, were analyzed with four different single trait animal models (including or not the maternal genetic and/or the permanent environmental effects with the direct genetic effect). Genetic parameters and covariance components were estimated by restricted maximum likelihood method. For all three traits the most complete model that included all three random effects was the best. The model that included only direct genetic effects overestimated the additive genetic variance and heritability (0.27, 0.24 and 0.15 for W205, W365 and W550, respectively). When the permanent environmental effect was included in the model, the portion of the total variance due to it was 0.09, 0.06 and 0.02 for W205, W365 and W550, respectively, and the estimate of the additive genetic variance decreased. The inclusion of the additive maternal effect instead of the permanent environmental effect did not change the estimate of the additive direct variance. Heritability estimates, obtained with the most complete model, were low: 0.16, 0.17 and 0.13 for direct genetic effects, and 0.10, 0.03 and 0.03 for maternal genetic effects, for W205, W365 and W550, respectively. Estimates of genetic correlation between direct and maternal effects were negative, showing an antagonism between such effects. Maternal effects still remained evident after weaning, though they became less important.

Keywords: genetic parameters, direct and maternal genetic effects, genetic correlation.

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Arch. Latinoam. Prod. Anim. 2004. 12(3): 119-125

Modelos animais alternativos para estimar heredabilidade e correlações genéticas entre efeitos diretos e maternal de pesosas pre e post desmamedado gado Tabaqua

RESUMO. Dados de pesos ao desmame (P205), ao ano (P365) e ao sobreano (P550) de bovinos da raça Tabapuã, criados em regime de pastagens em diversas regiões do Brasil, no período de 1975 a 1995, foram estudados em análise univariadas, sob quatro diferentes modelos de análises (incluindo ou não os efeitos genético materno e de ambiente permanente, além do efeito aditivo direto). Os componentes de (co)variância e parâmetros genéticos foram estimados pelo método da máxima verossimilhança restrita (REML), usando o aplicativo MTDFREML. Para as três características, o modelo mais completo forneceu o melhor ajuste dos dados. O modelo que incluiu somente o efeito genético direto do animal superestimou a variância genética aditiva, inflacionando o valor de herdabilidade (0,27, 0,24 e 0,15 para P205, P365 e P550, respectivamente). Quando o efeito de ambiente permanente foi incluído no modelo, a variância genética aditiva decresceu e a porção da variância total em função deste efeito reduziu com o aumento da idade (0,09; 0,06 e 0,02 para P205, P365 e P550, respectivamente). A inclusão do efeito genético materno em vez do efeito de ambiente permanente, praticamente não alterou o valor da variância genética aditiva direta. As estimativas de herdabilidade,

Recibido Mayo 05, 2003. Aceptado Septiembre 10, 2004

¹The authors thank CAPES for financing this study.

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obtidas sob o modelo mais completo, foram baixas: 0,16; 0,17 e 0,13 para os efeitos direto e 0,10; 0,03 e 0,03 para os efeitos maternos, para P205, P365 e P550, respectivamente e as estimativas de correlações genéticas entre os efeitos direto e materno foram negativas, evidenciando antagonismo entre estes efeitos. Efeitos maternos permaneceram ainda evidentes após a desmama, porém menos importantes.

Palavras-chave: parâmetros genéticos, efeitos genéticos direto e materno, correlação genética

Introduction

In mammals, the dam's contribution to the phenotype of her progeny is greater than the sire's, since besides the transmission of the additive genetic effect to the progeny, the dam provides her progeny with the maternal environment. Maternal effects can be defined as any contribution, influence or impact upon the individual's phenotype, directly attributed to the dam, which can be caused by genetic or environmental effects or by a combination of both. Maternal effects can be manifested in fertilization, during pregnancy or lactation, and can be transitory or persist throughout the entire life of the animal (Hohenboken, 1985). According to Murphey (1998), it is necessary to consider the maternal effects in the intrauterine environment during pregnancy and postnatally. These effects include the quality and quantity of protection provided by the dam through her behavior, and the passive immunity that she passes on to her offspring, as well as the genetic ability for adapting to the environment.

Meyer *et al.* (1994) considered the quantity and quality of colostrum and milk that are directly provided by the dam as the most important maternal effect. According to Fries and Albuquerque (1998), besides nursing, the dam is very effective in determining the macro and microenvironments in which she raises her progeny. Therefore her decisions when choosing these environments will directly affect her progeny. The dam also teaches her progeny to defend itself and to search for water and food. However, as time goes by this dependency decreases and terminates at weaning, as maternal bonds with the offspring are broken.

Thus, besides being influenced by its own genetic code (direct genetic effect), the initial stages of an animal's development (mainly until weaning), are influenced by the dam's genotype for maternal genetic effects and also by the environment, which acts upon both genotypes (Hohenboken ad Brinks, 1971).

It is important to quantify maternal influence and the magnitude of the correlation between the direct and the maternal genetic effects on the offspring's body weight in beef cattle in order to develop effective breeding programs, including unbiased estimation of heritability for this trait. If the correlation were positive or null, selection based on

weight at weaning normally would not be a problem. However if the correlation is negative, genetic progress will be compromised. Part of the gain obtained by increasing the animal's growth rate would be accompanied by a reduction of the dam's maternal ability, and vice-versa (Mercadante *et al.*, 1995).

Many authors have reported negative genetic correlations between direct and maternal effects for several traits and breeds. Therefore, the inclusion of maternal effect in the models for estimation of genetic parameters has been suggested (Sousa *et al.*, 1995, Cobucci *et al.*, 1997), as well as for genetic evaluations (Reyes *et al.*, 1994).

The Tabapuã is a Zebu polled breed used for beef production, which has a white or gray hair coat and pigmented skin. The purpose of this study was to estimate (co)variance components, heritabilities and genetic correlations between direct and maternal effects of pre and post-weaning weights of Tabapuã cattle raised on pasture, in different regions of Brazil. Estimates obtained with single-trait analyses with four different models, were compared to quantify the importance of direct and maternal genetic effects, as well as maternal permanent environmental effect.

Materials and Methods

Weight data were obtained from the Brazilian Zebu Breeders Association (ABCZ), for a 21 year period (1975 – 1995) for animals raised on pasture on farms in several different regions of Brazil. The information was provided by the National Beef Cattle Research Center (CNPGC), which belongs to the Brazilian Agricultural Research Corporation (Embrapa).

Weights were adjusted to standard ages of 205 days (weaning), 365 days (one year) and 550 days (yearling), using the daily gain between the two weightings closest to each of these standard ages.

Data summary of the three traits studied is shown in Table 1.

To estimate variance and covariance components, as well as the genetic parameters for W205, W365 and W550, four different univariate animal models were compared for all three traits. These models contained the random direct genetic effects, with and without maternal genetic effects and the maternal permanent environmental effects, as well as the fixed effects of contemporary group (farm, federation unit,

Table 1. Descriptive statistics for the body weight traits

	Traits ^a		
	W205	W365	W550
No. of animals	30.746	27.701	18.493
No. of animals in A ⁻¹	41.420	37.561	26.523
Mean (kg)	170.3	222.4	286.4
Standard deviation (kg)	24.1	36.3	55.4
Coefficient of variation (%)	14.39	16.32	19.34

^aW205, W365 and W550 = body weights at 205, 365 and 550 days of age, respectively.

sex, season and year of birth), and age of dam at calving as a covariable (linear and quadratic effects).

Model 1 included the animal's direct additive genetic effect. Model 2 also included the uncorrelated permanent environmental effects. Model 3 included the animal's direct genetic effects and the dam's maternal genetic effect. Model 4 included all three effects: direct genetic, maternal genetic and permanent environmental effects.

The most complete model, model 4 in matrix form can be described as:

$$Y = X\beta + Za + Mm + Wpe + e,$$

where,

Y is the vector of observations (W205, W365 and W550); β is the vector of fixed effects in the model, associated with the incidence matrix X; a is the vector of random direct genetic effects associated with the incidence matrix Z; m is the vector of maternal genetic effects associated with the incidence matrix M; pe is the vector of the random maternal permanent environmental effects associated with the incidence matrix W; and e is the vector of the random residual effects.

The maternal and the direct genetic effects are assumed to be correlated with each other, while the residual and permanent environment effects are not correlated with each other, nor are they correlated with the genetic effects. The basic structure of variance and covariance matrix for model 4 can be described as:

The estimated components of variance and

$$V \begin{bmatrix} a \\ m \\ pm \\ e \end{bmatrix} = \begin{bmatrix} A\sigma_a^2 & A\sigma_{am} & 0 & 0 \\ A\sigma_{am} & A\sigma_m^2 & 0 & 0 \\ 0 & 0 & I\sigma_{pm}^2 & 0 \\ 0 & 0 & 0 & I\sigma_e^2 \end{bmatrix},$$

where A is the relationship matrix among animals and I is an identity matrix of appropriate order.

covariance included: σ_p^2 , the phenotypic variance; σ_a^2 , the direct additive genetic variance; σ_m^2 , the maternal additive genetic variance; σ_{pm}^2 , the variance due to the dam's permanent environmental effect; σ_e^2 , the residual variance; and σ_{am} , the covariance between the direct and the maternal genetic effects. The following parameters are derived from the estimates of these components: $\hat{h}_a^2 = \sigma_a^2 / \sigma_p^2$ = direct heritability, $\hat{h}_m^2 = \sigma_m^2 / \sigma_p^2$ = maternal heritability and $\hat{h}^2 = (\sigma_a^2 + \sigma_m^2) / \sigma_p^2$ = total heritability, which according to Willham (1972) is the regression of the entire genotype of an animal (direct and maternal) on its phenotype, where σ_p^2 = phenotypic variance of the trait under consideration, given by: $\sigma_p^2 = \sigma_a^2 + \sigma_m^2 + \sigma_{pm}^2 + \sigma_e^2$. The correlation between the direct and the maternal genetic effects, $\rho_{am} = \sigma_{am} / (\sigma_a \sigma_m)^{1/2}$, and the proportion of the permanent environmental effect relative to the total phenotypic variation, $c^2 = \sigma_{pm}^2 / \sigma_p^2$, were also computed.

The estimates of the variance and covariance components and the genetic parameters were obtained by the derivative free restricted maximum likelihood method (DFREML), using the MTDFREML (Multiple Trait Derivative-Free Restricted Maximum Likelihood) programs developed by Boldman *et al.* (1993).

The statistical comparison of one model with another was made using the likelihood ratio test, which determines the difference between the logarithms of the likelihood functions (log L), and compares it to a Chi-square value. Deviations of logarithms of likelihood were obtained from models that differed in only one random factor. These deviations were then multiplied by two, the product of which constituted the λ . This λ was then compared with the value from the Chi-square table (χ^2) with one degree of freedom at a 95% probability level, according to the following rule (Dobson, 1990):

$\lambda = 2 (\log \text{likelihood of model [b]} - \log \text{likelihood of model [a]})$

If $\lambda \geq \chi^2_{1, 0.95}$, model [b] is accepted as fitting the data significantly better than model [a]. If $\lambda < \chi^2_{1, 0.95}$, model [a] and model [b] are not significantly different, where a is the model with n parameters and b is the model with $n+1$ parameters.

Results and Discussion

The estimates of total phenotypic, additive direct, additive maternal, permanent environmental, and residual variances, and the covariances between direct and maternal genetic effects for the weights at 205, 365 and 550 days of age, as well as log L, are shown in Tables 2, 4 and 6, respectively. Estimates of genetic parameters are summarized in Tables 3, 5 and 7, respectively, and values of I, for models comparison, are shown in Table 8.

Table 2. Estimates of (co)variance components (kg²) for standardized weight at 205 days of age (W205)

Model	$\hat{\sigma}_p^2$	$\hat{\sigma}_a^2$	$\hat{\sigma}_m^2$	$\hat{\sigma}_{pm}^2$	$\hat{\sigma}_e^2$	$\hat{\sigma}_{am}$	Log L
Model 1	436.68	117.83	-	-	318.85	-	-190.72
Model 2	426.97	63.53	-	39.82	323.62	-	-47.57
Model 3	427.77	67.57	64.28	-	323.48	-27.56	-10.21
Model 4	427.23	67.24	42.72	19.02	320.79	-22.54	0

$\hat{\sigma}_p^2, \hat{\sigma}_a^2, \hat{\sigma}_m^2, \hat{\sigma}_{pm}^2, \hat{\sigma}_e^2, \hat{\sigma}_{am}$ = components of phenotypic, additive direct, additive maternal, permanent environmental and residual variances, and covariance between direct and maternal effects, respectively.

Log L = log likelihood, expressed as a deviation from Model 4.

l = log likelihood, expressed as twice the deviation from Model 4.

Weight at weaning (W205)

Weaning weight was strongly influenced by maternal genetic and permanent environmental effects (Models 2, 3 and 4). The estimates of $\hat{\sigma}_p^2$ and $\hat{\sigma}_a^2$ obtained by Model 1 were biased upward when compared with those obtained by the other models. When the permanent environmental effect was added (Model 2), a substantial increase in log L compared to Model 1 occurred, showing the importance of this effect on weight at weaning (Table 8). The inclusion of this effect decreased the estimate of $\hat{\sigma}_p^2$ with regard to Model 1, and $\hat{\sigma}_a^2$ was responsible for 9% of the total variation in W205. In fact, part of the $\hat{\sigma}_a^2$ obtained with Model 1 (117.83 kg²) was due to the dam’s effect (Model 2). The inclusion of this effect, resulted in a decrease of 44.4% for $\hat{\sigma}_p^2$ and $\hat{\sigma}_a^2$ (Table 3).

When W205 was analyzed with Model 3, which included the maternal genetic effect of the dam, instead of the permanent environmental effect, the estimate of $\hat{\sigma}_p^2$ increased slightly (Table 2), resulting in a slight increase in the estimate of direct heritability (h_a^2), when compared to Model 2 (Table 3). The inclusion of the maternal genetic effect resulted in a substantial improvement in log L compared to Model 1, and demonstrated the strong maternal effect on weight at weaning (Table 8). The direct and maternal heritability estimates were similar: 0.16 and 0.15, respectively.

Model 4, which included both maternal genetic

and permanent environmental effects was substantially better than model 3 (Table 8). Model 4 reduced the estimate of $\hat{\sigma}_p^2$ by partitioning the variance of total dam maternal effects into genetic and permanent environmental portions.

Direct heritability estimates obtained in this study for weight at 205 days were low, indicating that the expected genetic progress by selection are not to be high (Table 3).

The estimate of the correlation between direct and maternal genetic effects was high and negative (-0.42), which indicates an antagonism between these effects, making total heritability smaller than the direct heritability (Table 3).

Weight at one year (W365)

Though relatively less important, the maternal effects (additive and permanent environmental) remained evident after weaning (Tables 4 and 5), and were responsible for 6.6 to 2.7% of the phenotypic variance of body weight at 365 days of age, and when included in the model, contributed to a decrease in direct heritability from 0.24 (Model 1) to 0.17 (Models 3 and 4) (Table 5).

Estimates of direct heritability obtained in this study for weight at 365 days of age, are within the range of those reported by many authors for different breeds and methods (Eler *et al.*, 1995; Reyes *et al.*, 1994; Salles, 1995).

According to the estimates obtained using Model

Table 3. Estimates of genetic parameters for standardized weight at 205 days of age

Model	\hat{h}_a^2	\hat{h}_m^2	\hat{h}_T^2	\hat{r}_{GDM}	C_{DM}	\hat{c}^2	\hat{e}^2
Model 1	0.27	-	0.27	-	-	-	0.73
Model 2	0.15	-	0.15	-	-	0.09	0.76
Model 3	0.16	0.15	0.14	-0.42	-0.06	-	0.76
Model 4	0.16	0.10	0.15	-0.42	-0.05	0.04	0.75

$\hat{h}_a^2, \hat{h}_m^2, \hat{h}_T^2, \hat{r}_{GDM}, C_{DM}, \hat{c}^2$ and \hat{e}^2 = direct, maternal and total heritabilities, genetic correlation between direct and maternal effects, covariance between direct and maternal effects as a proportion of the phenotypic variance, variance due to the permanent environment as a proportion of the total phenotypic variance, and fraction of total phenotypic variance due to the residual effects, respectively.

Table 4. Estimates of covariance components (kg²) for standardized weight at 365 days of age

Model	$\hat{\sigma}_p^2$	$\hat{\sigma}_a^2$	$\hat{\sigma}_m^2$	$\hat{\sigma}_{pm}^2$	$\hat{\sigma}_e^2$	$\hat{\sigma}_{am}$	log L
Model 1	725.64	177.52	-	-	548.12	-	-73.83
Model 2	715.46	119.38	-	46.41	549.66	-	-2.99
Model 3	719.25	121.68	47.31	-	557.99	-7.72	-89.78
Model 4	715.90	121.94	19.20	36.43	548.04	-9.71	0

$\hat{\sigma}_p^2, \hat{\sigma}_a^2, \hat{\sigma}_m^2, \hat{\sigma}_{pm}^2, \hat{\sigma}_e^2, \hat{\sigma}_{am}$ = components of phenotypic, additive direct, additive maternal, permanent environmental and residual variances, and covariance between direct and maternal effects, respectively.

3 for W365, and as with W205, it is clear that the maternal heritability (\hat{h}_m^2) was overestimated, not including the maternal permanent environmental effect in the model, as is shown by the estimates with Model 4. Failure to include the maternal permanent environmental effect in the Model could explain the estimate of maternal heritability of 0.14 reported by Mercadante and Lôbo (1997), for the Nelore breed.

The estimate of maternal heritability of 0.07 (Table 5), obtained from Model 3, is similar to the estimate of 0.06 obtained by Robinson and O'rourke (1992), for the Brahman breed, and equals that of Magnabosco *et al.* (1996). Nevertheless, it is smaller than estimates by ELER *et al.* (1995), Reyes *et al.* (1994) and Salles (1995), for the Nelore breed. However, when Model 4 was used, the estimate became equal to 0.03, much smaller than the estimates reported in the literature.

The estimates of covariance between direct and maternal genetic effects were negative (-7.72 provided by Model 3 and -9.71 by Model 4), which are similar to those (-7.79 and -8.99) obtained by Mercadante and Lôbo (1997), when the same models were utilized.

The estimates of correlation between direct and maternal genetic effects for W365 were negative and small in magnitude: -0.10 and -0.20 with Models 3 and 4 respectively. They were, however, higher than those obtained by Mercadante and Lôbo (1997). A possible cause of such negative correlations is the

fact that a negative environmental covariance between the dam and her progeny is not considered (Baker 1990; Meyer, 1992 and Swalve, 1993).

Total heritability estimates (\hat{h}_T^2) obtained for body weight at 365 days of age ranged from 0.16 to 0.24. Model 1 provided the highest value, mainly because it did not account for maternal effects.

An a he his you me I as in on is An a he his you me I as in on is An a he **Weight at yearling (W550)**

As expected, the influence of the maternal effect on the estimates of \hat{h}_T^2 was smaller for this trait (Table 6, Model 2), as the offspring becomes less dependent on its dam (Sousa *et al.*, 1999). The estimate of \hat{h}_T^2 under Model 2 was less than that obtained by Model 1. The permanent environmental effect was responsible for 2.3% of the total variation (Table 7, Model 2).

The estimate of \hat{h}_T^2 with Model 3, which considered the maternal genetic effect instead of the permanent environmental effect, was 5.3% greater than that obtained with Model 2 (Table 6), increasing the estimate (Table 7). The estimate of \hat{h}_T^2 was responsible for 3.6% of the total phenotypic variation (Table 7).

Finally, the analysis with model 4 provided a higher estimate of \hat{h}_T^2 than that obtained with Model 2, and lower than those obtained with Models 3 and 1 (Table 6). The estimate of \hat{h}_T^2 was 12.6% smaller than that obtained with Model 3, and was about 55.3% smaller than that obtained with Model 2.

The covariances between direct and maternal effects were negative (-21.50 and -29.02, for models

Table 5. Estimates of genetic parameters for standardized weight at 365 days

Model	\hat{h}_a^2	\hat{h}_m^2	\hat{h}_T^2	\hat{r}_{Gam}	C_{am}	\hat{c}^2	\hat{e}^2
Model 1	0.24	-	0.24	-	-	-	0.76
Model 2	0.17	-	0.17	-	-	0.06	0.77
Model 3	0.17	0.07	0.19	-0.10	-0.01	-	0.78
Model 4	0.17	0.03	0.16	-0.20	-0.01	0.05	0.77

$\hat{h}_a^2, \hat{h}_m^2, \hat{h}_T^2, \hat{r}_{Gam}, C_{am}, \hat{c}^2$ and \hat{e}^2 = direct, maternal and total heritabilities, genetic correlation between direct and maternal effects, covariance between direct and maternal effects as a proportion of the phenotypic variance, variance due to the permanent environment as a proportion of the total phenotypic variance, and fraction of total phenotypic variance due to the residual effects, respectively.

Table 6. Estimates of covariance components (kg²) for standardized weight at 550 days of age

Model	$\hat{\sigma}_p^2$	$\hat{\sigma}_a^2$	$\hat{\sigma}_m^2$	$\hat{\sigma}_{pm}^2$	$\hat{\sigma}_e^2$	$\hat{\sigma}_{am}$	Log L
Model 1	1682.05	256.84	-	-	1425.21	-	-9.64
Model 2	1674.98	216.88	-	38.06	1420.03	-	-3.58
Model 3	1679.37	228.43	54.71	-	1417.73	-21.50	-6.81
Model 4	1675.25	225.06	47.83	17.00	1414.38	-29.02	0

$\hat{\sigma}_p^2, \hat{\sigma}_a^2, \hat{\sigma}_m^2, \hat{\sigma}_{pm}^2, \hat{\sigma}_e^2, \hat{\sigma}_{am}$ = components of phenotypic, additive direct, additive maternal, permanent environmental and residual variances, and covariance between direct and maternal effects, respectively.

λ = log likelihood, expressed as twice the deviation from the model with the highest value.

Table 7. Genetic parameters for adjusted weight at 550 days of age

Model	\hat{h}_a^2	\hat{h}_m^2	\hat{h}_T^2	\hat{r}_{Gam}	C_{am}	\hat{c}^2	\hat{e}^2
1	0.15	-	0.15	-	-	-	0.85
2	0.13	-	0.13	-	-	0.02	0.85
3	0.14	0.04	0.13	-0.19	-0.01	-	0.84
4	0.13	0.03	0.12	-0.28	-0.01	0.01	0.84

$\hat{h}_a^2, \hat{h}_m^2, \hat{h}_T^2, \hat{r}_{Gam}, C_{am}, \hat{c}^2$ and \hat{e}^2 = direct, maternal and total heritabilities, genetic correlation between direct and maternal effects, covariance between direct and maternal effects as a proportion of the phenotypic variance, variance due to the permanent environment as a proportion of the total phenotypic variance, and fraction of total phenotypic variance due to the residual effects, respectively.

Table 8. Differences between λ values from four models used in one-trait analyses for weights at 205 (W205), 365 (W365) and at 550 (W550) days of age

Models	λ		
	W205	W365	W550
Log L [2] – log L [1]	286.26*	141.68*	12.12*
Log L [3] – log L [1]	361.04*	327.23*	5.66*
Log L [4] – log L [2]	95.16*	5.98*	7.16*
Log L [4] – log L [3]	20.42*	179.56*	13.62*

*Significant (P<0.05)

3 and 4, respectively), contributing to a slight decrease in the total heritabilities when compared to direct heritabilities. Permanent environmental effects were low.

The estimates of direct and total heritability for W550 were low, indicating that the expected genetic progress through selection would not be high.

Conclusions

Direct heritability estimates were, in general, higher than estimates of total heritability. This means that, when maternal and permanent environmental effects are not considered, genetic parameter estimates are overestimated, and consequently the estimates of breeding values will be unreliable.

Given the low estimates of direct and total heritability obtained for these herds, information on relatives should be included in the selection process.

Estimates of the correlation between maternal and direct genetic effects were negative, showing an antagonism between these effects.

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