

GENETIC ANTAGONISM BETWEEN GROWTH AND MATERNAL ABILITY IN NELORE CATTLE

J.P. Eler¹, J.B.S. Ferraz¹, R.B. Lobo² and L.A. Josakian³

ABSTRACT

This study evaluated direct and maternal effects on 205 and 365 day weights (W205 and W365) of 7415 Nelore calves, sired by 59 bulls and raised on pasture in the state of São Paulo, Brazil. Thirteen variance and covariance components for several different sets of related animals were estimated by least squares procedure and equated to their expected causal components. The system of equations gave estimates of heritability for direct effects (h^2_D) and for maternal effects (h^2_M). Estimates of h^2_D were 0.26 for W205 and 0.18 for W365. The estimates of h^2_M were 0.28 for W205 and 0.18 for W365. The estimates of genetic correlations between the direct and maternal effects ($r_{A \times M}$) were -0.91 for both traits, suggesting a severe antagonism between the effects of genes for growth and genes for maternal ability. Estimates of total heritability (h^2_T) were only 10% of those obtained by the usual paternal half-sib correlation. These results suggest that analyses that do not consider maternal effects in the Nelore breed overestimate genetic progress and long term response may be less than has been predicted.

INTRODUCTION

Nelore is the most common of the *Bos indicus* breeds in Brazil and selection for increased weight has been widely applied.

Birth and weaning weights are controlled by two kinds of genotypes in beef cattle. There are two routes of gene expression: the first, direct, is the expression of the genes in the same individual in which the trait is measured (direct animal effect). The second, indirect, is the expression of the genes in the mother of the animal, related to its maternal ability (maternal effect, i.e., the capacity of the mother in providing some environment to the progeny, during gestation and nursing).

Several authors (Dickerson, 1947; Koch and Clark, 1955; Hohenboken and Brinks, 1971; Beltran Bru, 1978) reported negative correlations between direct and maternal

effects in beef cattle, which was also found in Nelore cattle raised in the tropics by Eler *et al.* (1989). The negative correlation should reduce the response to selection for traits for which maternal effects are important. In phenotypic selection, a positive response to selection for increasing growth rate should be associated with a decrease in maternal ability and part of the genetic progress obtained in one generation should be canceled in the next generation, due to poorer maternal ability of the cows.

The objectives of this study were:

- evaluate the maternal effect and the relationship between direct and maternal effects on weights of Nelore calves;
- estimate heritability coefficients for those weights, considering both the direct and maternal effects;
- estimate the genetic correlation between direct and maternal effects.

MATERIAL AND METHODS

Records of weights at 205 and 365 days (W205 and W365) from 7,415 calves, sired by 59 different bulls of Nelore breed, born from 1975 to 1987 and raised on pasture in a herd of the state of São Paulo, Brazil were analysed. The data set came from the recording system of

¹ Departamento de Zootecnia, Faculdade de Zootecnia e Engenharia de Alimentos da Universidade de São Paulo, Caixa Postal 23, 13630-000 Pirassununga, SP, Brasil. Send correspondence to J.P.E.

² Departamento de Genética, Faculdade de Medicina de Ribeirão Preto, Universidade de São Paulo, 14049-900 Ribeirão Preto, SP, Brasil.

³ Associação Brasileira de Criadores de Zebu (ABCZ), Uberaba, MG, Brasil.

Associação Brasileira de Criadores de Zebu (ABCZ), the breeders' association for zebu breeds in Brazil.

Due to the types of analysis and some restrictions imposed, eight different files were generated, each analysed by least squares methods (Harvey, 1985), according to four linear models. The effects included in the models were:

- Y_{ijk} = W205 or W365
 μ = overall mean
 a_i = random effect of the i^{th} bull (cow, maternal grandsire or family of full sibs or 3/4 sibs). 3/4 sibs are paternal half sibs with dams that are paternal half sibs.
 F_j = set of fixed effects (sex, year, season of birth and age of dam at calving)
 X = weight of sire or dam
 MX = mean weight of sire or dam
 e_{ij} = random error NID (0, σ^2)

The different models used were:

$$Y_{ij} = \mu + F_j + e_{ij} \quad \text{Model 1}$$

This model was used to estimate the phenotypic variance (σ_p^2). As the data are adjusted for the fixed effects, the error mean square is the phenotypic variance ($MSE = \sigma_e^2 = \sigma_p^2$).

$$Y_{ijk} = \mu + a_i + F_j + e_{ijk} \quad \text{Model 2}$$

Model 2 was used to estimate:

a) the variance components for sires (σ_s^2) and progeny within sires (σ_{ws}^2). Assuming no inbreeding and random mating, σ_s^2 is the covariance among half paternal half sibs (cov_{PHS}).

b) the least squares constants for fixed effects.

c) in another data set in which the family structure was based on the dam, this model was used to estimate the variance components of dam (σ_D^2) and progeny within dam (σ_{WD}^2). In this case, the expected value of σ_D^2 is the covariance among maternal half sibs (cov_{MHS}).

d) the variance component for 3/4 sib families (σ_{TQS}^2) and within 3/4 sib families (σ_{WTQS}^2). In this case, the expected value of σ_{TQS}^2 is the covariance among 3/4 sibs.

e) the variance component for full sib families (σ_{FS}^2) and within full sib families (σ_{WFS}^2), where the expected value of σ_{FS}^2 is the covariance among full sibs.

f) the variance components for maternal grandsire (σ_{MGS}^2) and within maternal grandsire (σ_{WMGS}^2). In this analysis, σ_{MGS}^2 is the covariance among cousins with dams that are paternal half sibs.

$$Y_{ijk} = \mu + a_i + b(X-MX) + e_{ijk} \quad \text{Model 3}$$

This model was used to estimate the covariance offspring - dam (cov_{oD}), from data previously adjusted for fixed effects, with the least squares constants from Model 2.

$$Y_{ijk} = \mu + b(X-MX) + e_{ij} \quad \text{Model 4}$$

Model 4 was used to estimate the covariance offspring-sire (cov_{oS}), from data previously adjusted, as in Model 3.

The causal (co)variance components were estimated using the method described by Willham (1963). The method consists of equating the different variance components for groups of relatives to their expected values. These components and their expected values are shown in Table I. This results in a system of equations which estimate each causal component of variance and covariance. As the number of relationships available (n) was larger than the number of components to be estimated (p), these solutions were obtained by least squares procedures, as proposed by Eisen (1967) and Beltran Bru (1978). The solutions were obtained by:

$$b = (X'X)^{-1}x'y, \text{ where}$$

b = vector of causal components

x = matrix of theoretical expectations for (co)variances of each group of relatives (family).

Y = least square estimates of the (co)variance components for each family.

The description of this method can be found in Willham (1963) and Eler (1987). The causal components estimated, directly related to the genetic parameters, were:

a) the variance component of the direct additive effects of the own genes of the calf (σ_{Ao}^2);

b) the variance component of the additive effects of the genes of the cow, responsible for its maternal ability (σ_{Am}^2);

c) the covariance component between the direct and maternal effects (σ_{AoAm}).

Heritabilities for direct effects (h_o^2) and maternal effects (h_m^2) were estimated, respectively, by the ratios σ_{Ao}^2/σ_p^2 and σ_{Am}^2/σ_p^2 , where σ_p^2 is the phenotypic variance. Heritability of the total genetic contribution of the individuals (h_T^2) for each trait can be estimated by the regression of additive breeding value on the phenotypes, as proposed by Dickerson (1947): $h_T^2 = (\sigma_{Ao}^2 + 3/2 \sigma_{AoAm} + 1/2 \sigma_{Am}^2)$.

The genetic correlation between direct and maternal effects is given by:

$$r_{AoAm} = \sigma_{AoAm}/(\sigma_{Ao}^2 \cdot \sigma_{Am}^2)^{1/2}$$

The regression coefficient of the direct breeding value on maternal breeding value is:

$$b_{AoAm} = \sigma_{AoAm}/\sigma_{Am}^2.$$

Table I - Expected values of the variance components in terms of causal variance components (based on Dickerson, 1947).

Component	σ_{Λ}^2	σ_{β}^2	$\sigma_{\Lambda OAM}$	σ_{DODM}	$\sigma_{\Lambda m}^2$	$\sigma_{\beta m}^2$	σ_{EO}^2	σ_{EOEM}	$\sigma_{\beta m}^2$
σ_{ξ}^2	1/4	0	0	0	0	0	0	0	0
σ_{WS}^2	3/4	1	1	0	1	1	1	0	1
σ_{β}^2	1/4	0	1	0	1	1	0	0	1
σ_{WD}^2	3/4	1	0	0	0	0	1	0	0
σ_{MGS}^2	1/16	0	1/4	0	1/4	0	0	0	0
σ_{WMGS}^2	11/16	1	3/4	0	3/4	1	1	0	1
σ_{TQS}^2	5/16	1/16	1/4	0	1/4	0	0	0	0
σ_{WTQS}^2	11/16	15/16	3/4	0	3/4	1	1	0	1
σ_{FS}^2	1/2	1/4	1	0	1	1	0	0	1
σ_{WFS}^2	1/2	3/4	0	0	0	0	1	0	0
σ_{OD}	1/2	0	5/4	1	1/2	0	0	1	0
σ_{OS}	1/2	0	1/4	0	0	0	0	0	0
σ_{β}^2	1	1	1	0	1	1	1	0	1

RESULTS AND DISCUSSION

Least squares means, heritability and correlations

The least squares means were 157.6 ± 0.4 kg for W205 and 220.8 ± 0.6 kg for W365. The heritability coefficients, estimated by correlation among paternal half sibs were 0.36 ± 0.06 for W205 and 0.18 ± 0.04 for W365. The estimate of genetic correlation (r_G) between W205 and W365 was 0.32 ± 0.15 . The phenotypic correlation (r_P) was 0.62.

Causal (co)variance components

Table II gives the estimated variance and covariance components. These values were used in the Y vector to estimate the causal components. The estimates of causal (co)variance components for W205 and for W365 are presented in Table III. The phenotypic variance is the sum of all the causal components except the environmental covariance (σ_{EOEM}).

Direct and maternal genetic effects

In the extensive system of beef cattle production, normally used in Brazil, maternal ability is mainly milk production.

Estimates of heritability coefficients for direct genetic effect (h_o^2) and maternal genetic effect (h_m^2) are presented in Table IV. The estimates indicate that both

Table II - Variance and covariance components of 205 (W205) and 365 (W365) day weight of Nelore calves (kg^2).

Component	W205	W365
σ_{ξ}^2	39.56	36.24
σ_{WS}^2	397.21	745.86
σ_{β}^2	90.03	95.92
σ_{WD}^2	326.52	688.02
σ_{MGS}^2	11.31	11.19
σ_{WMGS}^2	400.66	766.21
σ_{TQS}^2	39.33	49.76
σ_{WTQS}^2	389.85	722.05
σ_{FS}^2	113.04	127.73
σ_{WFS}^2	290.74	626.55
σ_{OD}	35.96	87.80
σ_{OS}	28.70	36.98
σ_{β}^2	417.95	780.01

W205 and W365 are affected by genes of the own calf and genes from its mother for maternal ability, in approximately equal parts. The estimates for W205 are similar to those reported by Deese and Koger (1967) for Brahman calves. Hohenboken and Brinks (1971) in

Table III - Estimates of causal (co)variance components for 205 (W205) and 365 (W365) days of Nelore calves (kg^2).

Component	W205 estimate	% of σ_{T}^2	W365 estimate	% of σ_{T}^2
σ_{Ao}^2	109.40	26	138.18	18
σ_{Do}^2	0.24	0	51.98	7
σ_{AoAm}	-104.00	-25	-128.42	-17
σ_{Am}^2	118.67	28	143.04	18
σ_{Eo}^2	244.12	58	528.92	68
σ_{EoEm}	51.92	-	107.72	-
σ_{Em}^2	49.88	12	42.35	6
σ_{T}^2	418.31	100	776.05	100

Table IV - Estimates of genetic parameters for 205 (W205) and 365 (W365) day weight of Nelore calves.

Genetic parameter*	W205	W365
h_{o}^2	0.26	0.18
h_{m}^2	0.28	0.18
r_{AoAm}	-0.91	-0.91
b_{AoAm}	-0.88	-0.90
h_{T}^2	0.03	0.02

*This method does not allow estimation of standard errors.

Hereford breed, Beltran Bru (1978) in Brahman and Eler *et al.* (1989) reported a larger contribution of maternal genes to W205 for Nelore.

The estimates of heritability for W365 point to a significant contribution of genes for maternal ability (18%). Persistence of maternal influence on post weaning weight would indicate that compensatory gain is not enough to cancel the differences that occurred at weaning. This point should be carefully considered if W365 is a selection criterion.

Although the heritabilities are low to moderate, for both traits (0.18 to 0.28), response to selection is expected.

Genetic and environmental correlations between direct and maternal effects

The values for these parameters are presented in Table IV. They are directly related to the covariance estimates. The covariance between direct and maternal genetic effects (σ_{AoAm}) was negative for both traits.

Several papers (Deese and Koger, 1967; Hohenboken and Brinks, 1971; Foulley and Lefort, 1978) consider the possibility of this covariance being inflated by a negative environmental covariance (σ_{EoEm}), although those authors did not report estimates for this component. In our study, σ_{EoEm} was estimated. Due to the extensive system used in this herd, without any supplementation, probably the heifers were fed at a limited level, so that their future maternal ability was not affected.

As the covariance between direct and maternal genetic effect was negative, the correlation between those two effects (r_{AoAm}) and the regression of the genetic direct effect on the maternal genetic effect (b_{AoAm}) was also negative for both traits (Table IV). The regression shows the magnitude of the linear dependency of direct genetic effects on maternal ones, while the correlation shows the strength of that dependency. The observed negative genetic correlations suggested an antagonism between the genes for growth and the ones for maternal ability. These results confirm reports by Deese and Koger (1967), Brown and Galvez (1969), Hohenboken and Brinks (1971), Vesely and Robison (1971), Beltran Bru (1978) and Togashi and Yokouchi (1982). The values obtained in this analysis are in agreement with those of mixed model procedures (Bertrand *et al.*, 1987; Wright *et al.*, 1991; Johnson *et al.*, 1992).

Total heritability

The estimates of total heritability (h_{T}^2 , Dickerson, 1947) were 0.03 for W205 and 0.02 for W365, due to the highly negative covariance between the direct animal effect and the maternal genetic effect. Compared to the values of heritability, obtained from correlation among half sibs (0.26 for W205 and 0.18 for W365), the estimates of h_{T}^2 corresponded to about 10%. The main effect of this severe reduction in the estimates is on selection programs, generally based on estimates from half sib analyses. If selection programs do not consider the maternal effects, response to selection can be much smaller than originally predicted. Part of the direct genetic gain in one generation is offset by a reduction in maternal ability, expressed in the next generation.

Permanent and temporary environment and dominance effects

The component σ_{Em}^2 accounts for the part of variance, due to permanent environmental effects on the maternal ability of the cow. The values of this parameter show that this effect was the cause of 12% (W205) or 6% (W365) of the total phenotypic variance. There is some possibility that cows, with some handicap due to past diseases or even lost have, therefore with reduced milk

production, could have contributed to differences in maternal ability, reducing the phenotypic variance of W205. Also one group of cows had a low nutritional level when calves, that could have affected their maternal performance. As the animals of this herd were raised on pasture, without any supplementation, there is no chance that a group was overfed as calves. The permanent environmental effects should affect mainly milk production and W205, which is reflected in W365.

The variance component due to dominance effects (σ_D^2), was close to zero in W205 and explained 7% of the variability in W365, which agrees with Hill (1965), who reported that this component should be small for growth traits. Deese and Koger (1967), analysing weaning weight of Brahman, also did not find any variability due to dominance effects.

The residual component (σ_{Eo}^2), the variance due to the temporary direct effect of environment on weight of calves, contributed 58% of the phenotypic variance of W205 and 68% of W365. The magnitude of this component should indicate that those traits were strongly affected by non genetic causes, which makes the considerations of breeding programs to select for those growth weights still more complex.

Limitations of the model

According to Foulley and Lefort (1978), the limitations to the model of Wilham are related to:

- a) confounding of components
- b) errors of specific sources
- c) unknown accuracy of estimates

In this analysis, there were confoundings between σ_{Em}^2 and σ_{Dm}^2 , and also between σ_{EoEm} and σ_{DODm} . The results obtained were, actually, joint estimates of both components.

Epistasis is one of the specific sources of errors in this analysis. In the theoretical development of the model, it was assumed that epistasis was not important. However, this component is part of the expected values of some covariances among relatives, such as full sibs and some cousins. Therefore, the assumption of no importance of epistasis can bias the estimates.

Hohenboken and Brinks (1971) did not find epistatic effects to be important for cattle weight. This method does not allow calculation on standard errors of estimates. This is probably the biggest weakness of the method. Some individuals are present, simultaneously, in different groups of animals (different relationships), what could also induce errors in the estimates (Eisen, 1967). Foulley and Lefort (1978), based on this information, concluded that the Method of Wilham is only justified due

to the practical difficulties of geneticists in interpreting the biological phenomena involved in selection.

It is necessary to develop better methods to estimate maternal effects, possibly based on embryo transfer or mixed model procedures (Crow and Howell, 1982). In this analysis it is unknown if the genetic correlation of -.91 is true, but the negative sign of the estimate is probably correct.

CONCLUSIONS

The conclusions of this study were:

- a) maternal effect is an important source of variation for weights of calves at 205 and 365 days;
- b) the genetic correlation between direct and maternal effects was negative for both traits and the values of estimates were around -0.9, which indicates a strong antagonism among the genes involved in the determination of growth of calves and maternal ability;
- c) the permanent environment effects were important for maternal ability expressed as weaning weight of calves, indicating that problems related to health and management should affect milk production of the cows in this herd;
- d) the environmental correlation between direct and maternal effects (r_{EoEm}) could not be detected in either W205 or W365; and,
- e) due to the negative genetic correlation between direct and maternal effects (r_{AOAm}), maternal effects should be included in any breeding program, to improve genetic progress.

ACKNOWLEDGMENTS

We are thankful to Associação Brasileira de Criadores de Zebu (ABCZ) for permitting the utilization of the records, to Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) for partially funding this project, to Centro de Apoio à Informática da Faculdade de Medicina de Ribeirão Preto, USP for help in performing the analyses, and to Dr. L.D. Van Vleck, University of Nebraska, USA for suggestions.

Publication supported by FAPESP.

RESUMO

Com o objetivo de avaliar os efeitos genéticos direto e materno em um rebanho da raça Nelore, treze componentes de (co)variância de várias famílias de indivíduos aparentados (componentes entre e dentro de família) foram estimados em sete análises separadas. Os valores obtidos foram iguais às suas respectivas esperanças teóricas (componentes causais de variância e de covariância), formando um sistema de equações cuja solução pelo método dos quadrados mínimos forneceu uma estimativa dos componentes causais e dos parâmetros genéticos. As características

avaliadas foram peso aos 205 (W205) e 365 (W365) dias de idade. Para o componente genético direto, os valores estimados para o coeficiente de herdabilidade (h_c^2) foram 0,26 (W205) e 0,18 (W365). Para o componente materno (h_m^2), os valores foram 0,28 e 0,18 respectivamente. O método utilizado não permite obter os erros-padrão das estimativas. A correlação genética entre os efeitos direto e materno (r_{AOAM}) foi estimada em -0,91 para ambos os pesos analisados. Isto indica um antagonismo entre os efeitos dos genes para potencial de crescimento e dos genes para habilidade materna. A herdabilidade baseada na contribuição genética total (h_t^2) correspondeu a 10% do valor dos coeficientes de herdabilidade obtidos pelo método usual de correlação entre meio-irmãos paternos, indicando que se os programas de seleção forem estabelecidos com base nos valores estimados pelo método usual, que não considera o efeito materno, a resposta à seleção poderá ser menor do que prevista.

REFERENCES

- Beltran Bru, J.J.** (1978). Evaluation of direct and maternal effects on weaning traits in Brahman Cattle. Doctoral Thesis. University of Florida, Gainesville, FL.
- Bertrand, J.K. and Benyshek, L.L.** (1987). Variance and covariance estimates for maternally influenced beef growth traits. *J. Anim. Sci.* 64: 728-734.
- Brown, C.J. and Galvez, M.** (1969). Maternal and other effects on birth weight of beef calves. *J. Anim. Sci.* 28: 162-167.
- Crow, G.H. and Howell, W.E.** (1982). Genetic parameters of the maternal grandsire contribution to beef cattle weaning weights. *Can. J. Anim. Sci.* 62: 1057-1062.
- Deese, R.E. and Koger, M.** (1967). Maternal effects on preweaning growth rate in cattle. *J. Anim. Sci.* 26: 250-253.
- Dickerson, G.E.** (1947). Composition of hog carcass as influenced by heritable differences in rate and economy of gain. *Iowa Agric. Exp. Sta. Bul.* 354.
- Eisen, E.J.** (1967). Mating designs for estimating direct and maternal genetic variances and direct-maternal genetic covariances. *Can. J. Genet. Cytol.* 9: 13-22.
- Eler, J.P.** (1987). Avaliação dos efeitos genéticos direto e materno em características ponderais de bovinos da raça Nelore criados no Estado de São Paulo. Doctoral Thesis. Faculdade de Medicina, USP, Ribeirão Preto, SP.
- Eler, J.P., Lobo, R.B. and Rosa, A.N.** (1989). Influência de fatores genéticos e de meio em pesos de bovinos da raça Nelore criados no Estado de São Paulo. *Rev. Soc. Bras. Zoot.* 18: 112-123.
- Foulley, J.L. and Lefort, G.** (1978). Methodes d'estimation des effets directs et maternels en selection animale. *Ann. Genet. Sel. Anim.* 10: 475-496.
- Harvey, W.R.** (1985). User's guide for LSMLMW: Mixed Model least squares and maximum likelihood computer program. Ohio State University, mimeo, pp. 46.
- Hill, J.R.** (1965). The inheritance of maternal effects in beef cattle. Doctoral Thesis, North Carolina State University, Raleigh, NC.
- Hohenboken, W.D. and Brinks, J.S.** (1971). Relationship between direct and maternal effects on growth in herefords: III - Covariance of paternal half-brother and sister performance. *J. Anim. Sci.* 32: 35-42.
- Johnson, Z.B., Wright, D.W., Brown, C.J., Bertrand, J.K. and Brown Jr., A.H.** (1992). Effect of including relationships in the estimation of genetic parameters of beef calves. *J. Anim. Sci.* 70: 78-88.
- Kock, R.M. and Clark, R.T.** (1955). Genetic and environmental relationship among economic characters in beef cattle: III - Evaluating maternal environment. *J. Anim. Sci.* 14: 979-996.
- Togashi, K. and Yokouchi, K.** (1982). Maternal effects on preweaning growth traits in Hereford Cattle. *Hpn. J. Zootech. Sci.* 53: 883-843.
- Vesely, J.A. and Robison, O.W.** (1971). Genetic and maternal effects on preweaning growth and type scores in beef calves. *J. Anim. Sci.* 32: 825-831.
- Willham, R.L.** (1963). The covariance between relatives for characters composed of components contributed by related individuals. *Biometrics* 19: 18-26.
- Wright, D.W., Johnson, Z.B., Brown, C.J. and Wildens, S.** (1991). Variance and covariance estimates for weaning weight of Senepol Cattle. *J. Anim. Sci.* 69: 3945-3951.

(Received December 2, 1992)