

Animal model analyses of additive and non-additive genetic effects for 205 days weight in a Nellore x Hereford multibreed population in Brazil¹

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ABSTRACT

Choosing an appropriate model to obtain reliable estimates of additive and nonadditive genetic effects is essential for the implementation of a sound crossbreeding program. The objective of this study was to assess the importance of direct and maternal breed additive, dominance, and epistatic recombination group effects for 205-d weaning weight (W205) in a large Nellore x Hereford multibreed population using 11 homoscedastic animal models. Four epistatic recombination expressions were evaluated: 1 (Dickerson) = NsHs + NdHd; 2 (Fries) = 0.5(HETs + HETd); 3 (Kinghorn) = 2NaHa; and 4 (Elzo) = 1 - NsNsNdNd - HsHsHdHd; N = Nellore fraction, H = Hereford fraction, HET = heterozygosity, a = animal, s = sire, and d = dam. The data file had 124,638 W205, 3,768 contemporary groups (CG = herd-year-season-management group-sex of calf), 1,078 sires, and 88,750 dams. The pedigree file included 202,475 animals. Fixed effects were CG, cow age at calving (fourth degree polynomial), weaning age as a deviation from 205 d (third degree polynomial), direct and maternal breed additive effects (models M_2 to M_{10}), direct and maternal heterosis (models M_3 to M_{10}), and direct and maternal epistatic recombination effects (direct: models M_{11} to M_{14} ; maternal: models M_{15} , M_{16} , M_{17} , M_{18} , M_{19}). Random effects were direct and maternal additive genetic effects, maternal permanent environmental effects, and residual effects. Additive relationships were accounted for. The Akaike (AIC) and Bayesian (BIC) information criteria were used to compare models. Inclusion of direct and maternal heterosis, and direct and maternal epistatic recombination (all definitions) showed an improvement in model fitting according to AIC and BIC (except for maternal epistatic recombination in models M_{16} and M_{19}). Thus, both heterosis and epistasis need to be accounted for in genetic evaluation models for this multibreed population.

INTRODUCTION

Reliable crossbreeding parameter estimates are required to design a sound crossbreeding program. By extrapolating the estimates obtained from the best fitting model, the merit of untested crossbred genotypes can be predicted. Therefore, the choice of an appropriate genetic model is important for the analysis of a crossbred population data. Models that include genetic interactions such as heterosis, dominance, and epistasis can be more accurate but also more confusing because both selection and mating must be considered rather than just selection. Genetic interactions are not just nuisance terms to subtract from models but can provide useful predictions if presented carefully.

The most commonly applied model in crossbreeding accounts for heterosis and recombination, however, heterosis in that model includes a part of the additive x additive epistasis in addition to dominance. Other alternative genetic models have been developed that allow a separate estimation of heterosis (dominance) and epistatic effects. Thus, it was devised definition and probability expressions for the allelic interactions occurring simultaneously among the alleles, originated from two breeds, at one locus and at two loci for both, subclass and regression models. Some recent results have confirmed the importance of epistatic/recombination effects for analysis of crossbreeding beef cattle field data. There is some evidence that non-additive variation due to *Bos indicus* x *Bos taurus* intralocus interactions may be comparable to additive genetic variation for various growth and carcass traits in beef cattle.

The objectives of this study were to assess direct and maternal breed additive, dominance, and epistatic/recombination fixed genetic effects and to estimate (co)variance components and genetic parameters for adjusted weaning weight at 205 days of age in a Nellore x Hereford multibreed population of beef cattle.

MATERIAL AND METHODS

The data were adjusted weaning weights (kg) at 205 days of age (W205) of animals from a Nellore x Hereford multibreed beef cattle population enrolled by "Conexão Delta G", obtained between 1991 and 2004 from 79 herds. The edited dataset consisted of 124,638 records, including both purebred and crossbred calves of both sexes. Only records of animals produced by AI and with suitable information for calculating direct and maternal dominance and epistatic interaction effects were kept. The Fortran CSET Program was used to check for genetic connectedness due to common sires and maternal grandfamilies among multibreed contemporary groups (CG = herd-year-season-management group-sex of calf). Only CG with at least 8 records were retained. The final dataset included 3,768 CG, 1,078 sires, and 88,750 dams. The pedigree file included 202,475 animals.

In addition to CG, the effect of cow age at calving (CA) in years was modeled as a fourth order polynomial regression on CA across breed groups of dam (BGD). The contributions of polynomial terms above the fourth to model fitting were negligible. Preliminary analyses showed that CA x BGD interaction effects were of little importance to model fitting (less than 0.1% of R²). Previous analysis showed significant weaning age effect, and the effect, as deviation of 205 days, was included as a cubic polynomial regression. Coefficients for direct (β_0) and maternal (β_1) breed additive effects were defined as the proportion of Nellore breed in the breed composition of the calf and the dam, respectively. Consequently, direct and maternal additive breed effects were estimated as deviations from Hereford.

Coefficients for direct (H_d) and maternal (H_m) dominance effects were equal to expected direct and maternal breed heterozygosities. For comparison purposes, coefficients for direct (E_d) and maternal (E_m) epistatic/recombination effects were calculated in four forms: as proposed by Dickerson (1969); based on the *epistazigosity* concept formulated by Fries et al. (2000); according to the epistatic definition of Kinghorn (1980); and as the sum of four possible two loci allelic interactions probabilities corresponding to four different configurations among alleles of two breeds at two loci (Elzo, 1990).

The general model for W205, expressed in matrix notation, was as follows:

$$y = Xb + Fv + Za + Wm + Cpe + e$$

where y = vector of observations; b = vector of fixed partial linear regressions on coefficients for direct and maternal breed additive, dominance, and epistatic/recombination genetic effects; v = vector of fixed non-genetic effects; a = vector of random direct additive genetic effects; m = vector of random maternal additive genetic effects; and e = vector of random residual effects. Incidence matrices X , F , Z , W and C relate records to fixed genetic, fixed environmental, direct genetic, maternal genetic, and maternal permanent environmental effects, respectively. Even though most dams (76.1%) had only one calf record, it was decided to include maternal permanent environmental effect in the models, because 13.4% of dams and 35.1% of granddams had W205 records as calves, and dams with two or more calf records comprised 45.8% of whole data. Homogeneity of variances and no interactions between genetic and non-genetic effects were assumed. Estimates of (co)variance components and other effects included in each model were obtained by the ASREML program (Gilmour et al., 2000).

Eleven models were tested (M_1 to M_{19} and M_{20} ; Table 2). Model M_1 included non-genetic fixed and random additive direct and maternal genetic effects. In models M_2 and M_3 the effects of inclusion of direct and maternal additive and heterotic fixed genetic parameters were tested. In models M_{11} to M_{19} four calculation forms of individual direct (M_{11} models) and maternal (M_{15} models) epistatic/recombination coefficients were tested for comparison. Significance of parameters contribution between models was judged by the Akaike Information Criterion $AIC = -2\log L + 2k$, and the Bayesian Information Criterion $BIC = -2\log L + k\log(n)$, where k = number of independent estimated parameters, and n = total number of observations. Smaller values for AIC and BIC indicate better fit.

RESULTS AND DISCUSSION

The distribution of W205 records by breed-group-of sire (BGS) x breed-group-of dam (BGD) classes is shown in Table 1. The unbalanced distribution and empty or scantily represented BGS x BGD classes are typical of a population produced by an incomplete multibreed mating system. The dataset comprised 44,493 (35.7%) crossbred animals of 85 different genotypes.

The main results from the eleven models tested are shown in Table 2. For all models, the fourth order polynomial regression coefficients (β_0 to β_4) on cow age at calving (CA), and the cubic polynomial regression coefficients (β_0 to β_3) on weaning age deviations of 205 days (WA) were significant and very similar in pattern and values ($\pm$ SE), suggesting independence from the other effects included in the models. For example, the estimated values from M_{10} (chosen model) were 26.72 ± 1.31 , -3.96 ± 0.27 , 0.25 ± 0.02 and -0.006 ± 0.0007 for β_0 , β_1 , β_2 , and -1.27 ± 0.23 , 0.06 ± 0.001 , -0.00001 ± 0.00002 for β_3 to β_4 , respectively.

Table 1. Number of weaning weight records adjusted at 205 days of age by breed-group-of sire (BGS) x breed-group-of dam (BGD) classes in a Brazilian Nellore x Hereford multibreed population

BGD ^A	BGS ^A					
	(0.8-1.0)N	(0.6-0.8)N	(0.4-0.6)N	(0.2-0.4)N	(0.0-0.2)N	Sub-total
(0.8-1.0)N	71,232	0	89	395	23,721	95,437
(0.6-0.8)N	36	2	18	138	2,271	2,465
(0.4-0.6)N	534	4	248	6,110	1,430	8,326
(0.2-0.4)N	148	46	1,099	6,345	338	7,976
(0.0-0.2)N	761	145	385	210	8,933	10,434
Sub-total	72,711	197	1,839	13,198	36,693	124,638

^A N = Nellore breed. Every class contains animals with N fraction equal or lower than the greater limit.

Comparison of AIC and BIC values for M_2 vs. M_1 and M_3 vs. M_2 (Table 2) show significant contribution of linear regressions on fixed genetic direct and maternal additive and heterotic effects to model fitting. These results are in agreement with previous estimates obtained on a smaller sample data of the same population. According to AIC and BIC, the four M_{10} models showed a significant negative direct epistatic/recombination effect in comparison to M_1 . Maternal epistatic/recombination effect (M_{15} models) was significant relative to corresponding M_{10} models in all cases according AIC values. However, BIC values indicate that maternal epistatic/recombination effect in M_{15} and M_{16} was not significant, with values greater than those of M_{17} and M_{18} , respectively. The same result for M_{19} model was found in a previous analysis of smaller dataset from the same population. This is the first time that the epistatic/recombination coefficients for M_{11} and M_{15} models (Elzo, 1990) have been applied to a large field dataset. Their estimates were highly consistent, in values and pattern, with those of the other M_{11} and M_{15} models. Estimates of epistatic effects were negative for E_d and positive for E_m in all M_{10} models, except M_{19} . Contrary to M_{11} and M_{15} , estimates from M_{17} and M_{18} models were larger for H_d than for H_m . However, estimates from M_{11} and M_{15} were in agreement, both for H_d and H_m , with the following interrelationship ($H_{m11} = H_{m15} + \frac{1}{2} E_{m11}$). The estimates of H_d and H_m from M_{11} and M_{15} were comparable to results from other *Bos taurus* x *Bos taurus* and *Bos taurus* x *Bos indicus* multibreed studies.

Sampling correlations among predictor variables indicated dependencies between E_d and H_d (>0.90) for M_{11} and M_{15} models, and between E_m and H_m (>0.94) for M_{17} and M_{18} models. This last two models also showed strong associations between E_d and H_d and between E_m and H_m (>0.95). However, the set of smallest sampling correlations were obtained for M_{11} . Consequently, estimates of effects in M_{11} had the smallest standard errors, expressed as proportion of absolute value of estimated parameters. Based on these criteria, M_{11} was the model of choice for this dataset. A previous result showed that a Dickerson's model yielded the best fit for an experimental multibreed *Bos Taurus* x *Bos Indicus* dataset in Ethiopia.

The H_d and H_m estimates of 10.7% and 12.9% of direct and maternal heterosis were comparable to 9.1% and 15.5% obtained for birth to weaning growth in an Angus x Nellore multibreed population, and 10.3% and 16.9% from a previous sample data of this population. Multicollinearity among predictor variables, due to data imbalance and small proportion of crossbred animals out of purebred and F_1 (15.8%; manifest epistatic/recombination effects), likely contributed to the poor fit of M_{17} and M_{18} models for E_m effect.

The correlations among the four expressions for direct and maternal epistatic/recombination parameters showed some strong associations. Correlations of E_d values for M_{11} were 0.97 with E_d (M_{15}) and 0.94 and 0.95 with E_m for M_{17} and M_{18} , respectively. The correlation of E_m values between M_{11} and M_{15} was 0.99. Values of E_d in M_{11} are correlated with E_m (0.96) for both M_{17} and M_{18} models. The strongest associations (>0.998) were between M_{17} and M_{18} models for both E_d and E_m values. These results suggest the need for further studies on interrelationships among those four expressions to calculate epistatic/recombination effects.

Table 2. Estimates of additive and nonadditive genetic effects, variances and covariances, and genetic parameters for weaning weight (kg) adjusted to 205 days of age in a Brazilian Nellore x Hereford multibreed population

Model / Effects ^A	M ₁	M ₂	M ₃	M ₁₁	M ₁₅	M ₁₇	M ₁₈	M ₁₉	M ₂₀	M ₂₁	M ₂₂
$\beta_0(A_0)$	-22.2	-2.9	-3.1	-2.8	-2.8	-2.8	-3.1	-2.8	-3.1	-3.0	
$\beta_1(A_1)$	37.7	16.6	16.4	15.0	15.1	15.3	16.4	15.0	16.5	15.9	
$\beta_2(H_d)$	18.1	18.5	18.8	18.8	18.8	18.8	32.4	41.2	30.5	37.3	
$\beta_3(H_m)$	15.7	19.5	22.6	27.0	26.8	19.5	16.6	18.4	16.0		
$\beta_{11}(E_d)$			-13.8	-22.4	-20.1	-19.9	-27.7	-44.8	-12.2	-18.8	
$\beta_{15}(E_m)$ ^B				6.1		-0.7		12.1		4.3	
σ_e^2	110.2	74.9	76.2	71.6	70.8	71.3	71.2	71.6	70.8	73.0	72.2
σ_a^2	49.4	41.1	38.5	39.2	39.4	38.8	38.8	39.2	39.4	39.0	39.0
σ_m^2	-14.5	2.9	1.7	2.2	2.6	2.8	2.9	2.2	2.6	2.1	2.5
σ_{pe}^2	65.6	64.7	67.1	67.0	66.7	66.8	66.9	67.0	66.7	67.1	66.9
σ_e'	405.5	395.0	392.0	390.8	390.7	390.7	390.7	390.8	390.7	391.3	391.1
h_d^2	0.27	0.19	0.19	0.18	0.18	0.18	0.18	0.18	0.18	0.19	0.18
h_m^2	0.12	0.10	0.10	0.10	0.10	0.10	0.10	0.10	0.10	0.10	0.10
c^2	0.16	0.16	0.17	0.17	0.17	0.17	0.17	0.17	0.17	0.17	0.17
r_{am}	-0.20	0.05	0.03	0.04	0.05	0.05	0.05	0.04	0.05	0.04	0.05
-2LogL	845458	844666	843652	843616	843596	843592	843592	843614	843594	843634	843628
Param. ^C	3775	3777	3779	3780	3781	3780	3781	3780	3781	3780	3781
AIC ^C	853008	852220	851210	851176	851158	851152	851154	851174	851156	851194	851190
BIC ^C	889751	888982	887992	887967	887959	887943	887955	887965	887957	887985	887991

^A M_1 : $y = \mu + CG + \sum \beta_i (CA)^i + \sum \beta_j (WA)^j + a + m + pe + e$; CG = Contemporary Group (Herd-Year-Season-Sex-Management group); β_i (CA) = Quadratic polynomial regression on cow calving age (CA) in years (CA = 2 to 14); β_j = β_0 to β_4 = partial linear, quadratic, cubic and quartic regression coefficients, respectively; β_i (WA) = Cubic polynomial regression on weaning age (WA) as deviation from 205 days; β_0 to β_4 = partial linear, quadratic and cubic regression coefficients, respectively; a , m , pe = Random additive direct and maternal genetic, a , x m and maternal permanent environmental effects, respectively; e = Random residual effect; $M_2 = M_1 + \beta_2(A_2)$; $M_3 = M_2 + \beta_3(H_d) + \beta_4(H_m)$; $M_{11} = M_1 + \beta_{11}(E_d)$; $M_{15} = M_{11} + \beta_{15}(E_m)$; β_0 to β_4 = Partial linear regression coefficients on direct (A_d) and maternal (A_m) breed additive, direct (H_d) and maternal (H_m) heterosis, and direct (E_d) and maternal (E_m) epistatic/recombination fixed genetic effects, respectively; σ_e^2 , σ_a^2 , σ_m^2 = Genetic additive direct and maternal effect variances, respectively; σ_{pe}^2 = Genetic additive direct-maternal covariance; σ_e' = Maternal permanent environmental variance; σ_e' = Phenotypic variance; h_d^2 , h_m^2 = Heritabilities of direct and maternal effects, respectively; c^2 = (σ_e' / σ_e'); r_{am} = Genetic correlation between direct and maternal effects; σ_e' = Log-likelihood function value of the model.

^B M_{11} , M_{15} , E_d , E_m estimated as proposed by Dickerson (1969, 1973); M_{17} , M_{18} , E_d , E_m estimated according to epistazigosity concept of Fries et al. (2000); M_{19} , M_{21} , E_d , E_m estimated according to Kinghorn (1980, 1982); M_{20} , M_{22} , E_d , E_m estimated according to Elzo (1990).

^C Param. = Number of independent estimated parameters; AIC = Akaike Information Criterion; BIC = Bayesian Information Criterion.

For all models, except M_1 , the estimation of (co)variances and genetic parameters were very consistent in values and pattern. Estimates of direct and maternal heritabilities were 0.18 and 0.10, respectively, and $c^2 = \sigma_e'^2 / \sigma_e'^2$ value was 0.17. The genetic correlation between direct and maternal effects was 0.05 $\pm$ 0.01. These values for heritabilities are in agreement with some previous results from model analyses including maternal permanent environmental effect. The low and positive value of direct-maternal genetic correlation is contrary to most estimates from similar models, which showed medium to high and negative values, suggesting genetic antagonism between direct and maternal effects. It was estimated a value of -0.63 for this correlation on a multibreed *Bos Taurus* population in Canada, and a value of -0.53 for this correlation with a model excluding maternal permanent environmental effect on a smaller sample data from the same multibreed Nellore x Hereford population.

The value estimated for direct-maternal genetic correlation might be determined, at least in part, for a more suitable structure of present data, because some research results indicated that estimates of genetic direct and maternal effects, and the correlation between them are highly dependent of the number of calf records per dam, a sufficient number of dams and maternal granddams with records and of the number of generation present in the dataset analyzed.

CONCLUSIONS

>Breed additive, intralocus nonadditive (heterosis), and interlocus nonadditive (epistasis/recombination) effects were needed to appropriately explain genetic variation in a Nellore x Hereford multibreed population.

>Multicollinearity due to unbalancedness of the Nellore x Hereford multibreed dataset appeared to have affected the estimation of some fixed genetic effects. However, the large estimates obtained for heterosis and epistatic effects would justify additional research work.

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