NON-GENETIC, ADDITIVE AND NON-ADDITIVE GENETIC EFFECTS FOR ANIMAL MODEL ANALYSES OF WEANING WEIGHTS IN A NELLORE x HEREFORD MULTIBREED POPULATION IN BRAZIL

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SUMMARY

Reliable estimates of genetic parameters are essential for planning economically viable multibreed programs. Additive direct (A_D) and maternal (A_M), dominance direct (H_D) and maternal (H_M), and epistatic direct (E_D) and maternal (E_M) genetic effects were estimated for 205-day weaning weights using data from a Brazilian Nellore x Hereford multibreed population (42,822 calves, 620 sires, 31,381 dams). Estimates from the model with the smallest standard errors were -4.30 ± 3.65 kg, 10.46 ± 2.83 kg, 16.65 ± 2.35 kg, 27.45 ± 2.44 kg, -21.77 ± 5.38 kg and 10.87 ± 2.57 kg for A_D, A_M, H_D, H_M, E_D and E_M, respectively. Multicollinearity affected estimates. Results need to be revalidated with a larger and more balanced multibreed dataset.

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 (Kinghorn and Vercoe, 1989).

The most commonly applied model in crossbreeding studies was proposed by Dickerson (1969, 1973). This model accounts for heterosis and recombination loss, however, heterosis in this model includes a part of the additive x additive epistasis in addition to dominance (Demeke *et al.*, 2003). Other authors, such as Kinghorn (1980, 1982), Koch *et al.* (1985) and Wolf *et al.* (1995) developed alternative genetic models that allow a separate estimation of heterosis (dominance) and epistatic effects. Some recent results have confirmed the importance of epistatic/recombination effects for analysis of crossbreeding beef cattle field data (Fries *et al*., 2000; Pimentel *et al*., 2004; Roso *et al.,* 2005).

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 (Elzo and Wakeman, 1998; Elzo *et al.,* 1998a,b; Elzo *et al.,* 2001).

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 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 1974 and 1999 from 39 herds.

The edited dataset consisted of 42,822 records, including both purebred and crossbred calves of both sexes. Only records of animals produced by AI and with complete information for calculating direct and maternal dominance and epistatic interaction effects were kept. The Fortran CSET Program (Elzo, 2002) was used to check for genetic connectedness due to common sires and maternal grandsires among multibreed contemporary groups (CG = herd-year-season-management group-sex of calf). Only CG with at least 10 records were retained. The final dataset included 1,292 CG, 620 sires, and 31,381 dams. The pedigree file contained 71,282 animals.

In addition to CG, the effect of cow age at calving (CA) 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 0.2 % of R^2). Coefficients for direct ($\mathbf{A_D}$) and maternal ($\mathbf{A_M}$) 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 ($\mathbf{H_D}$) and maternal ($\mathbf{H_M}$) dominance effects were equal to expected direct and maternal breed heterozygosities.

For comparison purposes, coefficients for direct ($\mathbf{E_D}$) and maternal ($\mathbf{E_M}$) epistatic/recombination loss effects were calculated in three forms: as proposed by Dickerson (1969, 1973), according to the epistatic loss (hypothesis ***x***) of Kinghorn (1980, 1982), and based on the *epistazigosity* concept formulated by Fries *et al.* (2000).

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

$$\boldsymbol{y = Xb + Fv + Za + Wm + e}$$

where ***y*** = vector of observations; ***b*** = vector of fixed partial linear regressions on coefficients for direct and maternal breed additive, dominance, and epistatic/recombination loss 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*** and ***W*** relate records to fixed genetic, fixed environmental, direct genetic and maternal genetic effects, respectively. The vectors of random effects ***a***, ***m***, and ***e*** were assumed to have (co)variance matrices equal to $A\sigma_a^2$, $A\sigma_m^2$ and $I\sigma_e^2$, respectively, where ***A*** is the additive numerator relationship matrix among animals and ***I*** is an identity matrix. Covariance between ***a*** and ***m*** was assumed to be equal to $A\sigma_{am}$. Homogeneity of variances and no interactions between genetic and non-genetic effects were assumed. Estimates of (co)variance components and the other effects included in each model were obtained using the ASREML program (Gilmour *et al.,* 2000).

The maternal permanent environmental effect was not included in any model because the structure of data prevented to adequately estimate that effect. Most dams (76.8%) had only one calf record, and a small proportion of dams (11.4%) and no granddams had W205 records as calves.

Nine models were tested (M_1 to M_7, and M_{71}, M_{72}; Table 2). Model M_1 included non-genetic fixed and random additive direct and maternal genetic effects. In models M_2 to M_7 the effects of inclusion of each of the fixed genetic parameter to be estimated were tested. Models M_{71} and M_{72} differed from M_7 in the calculation form of epistatic/recombination loss coefficients.

Significance of each parameter contribution between models was judged by Akaike Information Criterion *AIC =-2logL + 2k* (Akaike, 1974) and Bayesian Information Criterion *BIC= -2logL + klog(n)* (Schwarz, 1978), where *k* = number of independent estimated parameters, and *n* = total number of observations. Smaller values for *AIC* and *BIC* indicate better fit.

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	2,010	0	0	25	10,369	12,404
(0.6-0.8)N	41	2	16	157	357	573
(0.4-0.6)N	231	0	109	910	870	2,120
(0.2-0.4)N	136	0	421	1,898	208	2,663
(0.0-0.2)N	542	118	165	110	24,127	25,062
Sub-total	2,960	120	711	3,100	35,931	42,822

[A] N - Nellore breed. Every class contains animals with N fraction equal or greater than the lower limit.

RESULTS AND DISCUSSION

The distribution of W205 records by breed-group-of sire x breed-group-of dam classes is shown in Table 1. The unbalanced distribution and some BGS x BGD empty classes are typical of a population produced by an incomplete multibreed mating system (Elzo and Reyes, 2004). The dataset comprised 16,690 (39%) crossbreed animals of 53 different genotypes.

The main results from the nine models tested are shown in Table 2. For all models, the fourth order polynomial regression coefficients on cow age at calving (CA) were very similar in pattern and values (± SE), suggesting independence from other effects included in the models. For example, the estimated values from M_{71} were 41.25 ± 2.60, -6.42 ± 0.58, 0.44 ± 0.05 and -0.012 ± 0.002 for β_1 to β_4, respectively.

The contribution to model fitting of each individual linear regression on fixed genetic direct and maternal additive, dominance and epistatic effects from M_1 to M_7 was significant according to the *AIC* and *BIC* values (Table 2), except for the comparison of M_7 and M_6 for maternal epistatic effects, where *AIC* values were equal, and the *BIC* value for M_7 was larger than for M_6, indicating a lesser fit for M_7 than for M_6. Estimates of epistatic effects were negative for E_D and positive for E_M in M_7, M_{71} and M_{72}, but with large differences in magnitude. In M_{72} estimates were larger for H_D (38.0 kg) than for H_M (16.6 kg). Contrarily, higher estimates of H_D (15.2 to 16.7 kg) than for H_M (21.8 to 30.1 kg) were obtained in M_5, M_6, M_7, and M_{71}, which values are in agreement with results from Roso and Fries (2000). However, estimates from M_{71} and M_{72} are in agreement with the interrelationship ($\mathbf{H_{M71} = H_{M72} + ½ E_{M72}}$) demonstrated by Wolf *et al.* (1995). Multicollinearity among predictor variables due to data imbalance and empty classes, and the small proportion of crossbreed animals, out of purebred and F_1, which should manifest epistatic/recombination effects, likely contributed to the poor fit of M_7 for E_M and some instability of estimated parameters.

Sampling correlations among predictor variables indicated dependencies between E_D and H_M (0.92) and E_M and H_M (0.78) in M_7. Model M_{72} showed strong associations between E_D and H_D (0.96) and E_M and H_M (0.95), and, in contrast with M_7 and M_{71}, also high correlations between E_D and A_D (0.66) and A_M (0.78). The smallest sampling correlations were obtained in M_{71}. Consequently, estimates of effects in M_{71} had the smallest standard errors. Based on these criteria, M_{71} was the most adequate model for this dataset. Similarly, Demeke *et al.* (2003) found that a Dickerson model yielded the best fit for an experimental dataset in Ethiopia.

The following estimates (± SE) were obtained from M_{71}: -4.30 ± 3.65 kg, 10.46 ± 2.83 kg, 16.65 ± 2.35 kg, 27.45 ± 2.44 kg, -21.77 ± 5.38 kg and 10.87 ± 2.57 kg for A_D, A_M, H_D, H_M, E_D and E_M, respectively. The H_D and H_M estimates represent 10.3% and 16.9% of direct and maternal heterosis, respectively, which are comparable to corresponding 13.3% and 22.6% obtained in Angus x Nellore multibreed population (Roso and Fries, 2000). Contrary to expectation, the value of h_m^2 (0.36) was higher than h_a^2 (0.18) and the value of the correlation between direct and maternal genetic effects was negative and rather high (-0.52). These values may be consequence of the unbalanced structure of the dataset, thus they will need to be reconfirmed with a larger and more balanced dataset.

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_4	M_5	M_6	M_7	M_{71}	M_{72}
$\beta_5(A_D)$		16.7	3.3	-2.7	-6.5	-4.3	-4.5	**-4.3**	-4.4
$\beta_6(A_M)$			22.8	21.5	13.8	12.1	11.7	**10.5**	10.5
$\beta_7(H_D)$				8.7	15.6	15.2	15.8	**16.7**	38.0
$\beta_8(H_M)$					21.8	30.0	30.1	**27.5**	16.6
$\beta_9(E_D)$ [B]						-16.0	-16.4	**-21.8**	-42.8
$\beta_{10}(E_M)$ [B]							2.1	**10.9**	21.5
σ_a^2	101.8	110.4	98.7	96.7	94.4	90.1	90.2	**89.8**	89.8
σ_m^2	183.5	187.8	181.0	180.9	179.0	177.4	177.3	**177.2**	177.2
σ_{am}	-72.8	-79.6	-70.4	-69.5	-68.3	-65.8	-65.7	**-65.6**	-65.6
σ_p^2	495.2	496.8	493.2	492.7	490.6	489.5	489.6	**489.4**	489.3
h_a^2	0.21	0.22	0.20	0.20	0.19	0.18	0.18	**0.18**	0.18
h_m^2	0.37	0.38	0.37	0.37	0.36	0.36	0.36	**0.36**	0.36
r_{am}	-0.53	-0.55	-0.53	-0.53	-0.53	-0.52	-0.52	**-0.52**	-0.52
-2LogL	299916	299882	299806	299790	299668	299652	299650	**299642**	299640
Param. [C]	1296	1297	1298	1299	1300	1301	1302	**1302**	1302
AIC [C]	302508	302476	302402	302388	302268	302254	302254	**302246**	302244
BIC [C]	313738	313714	313649	313644	313532	313527	313536	**313528**	313526

[A] M1: y = μ + CG + Σ{βi (CA)i}+ a + m + am + ε; CG = Contemporary Group (Herd-Year-Season-Sex-Management. group); βi (CA)i = Quartic polynomial regression on cow calving age (CA) in years (CA = 2 to 14), βi = β1 to β4 = partial linear, quadratic, cubic and quartic regression coefficients, respectively; *a*, *m*, *am* = Random additive direct and maternal genetic, and *a* x *m* effects, respectively; ε = Random residual effect; M2 = M1 + β5(AD); M3 = M2 + β6(AM); M4 = M3 + β7(HD); M5 = M4 + β8(HM); M6 = M5 + β9(ED); M7 = M6 + β10(EM); β5 to β10 = Partial linear regression coefficients on direct (AD) and maternal (AM) breed additive, direct (HD) and maternal (HM) heterosis, and direct (ED) and maternal (EM) epistatic/recombination loss fixed genetic effects, respectively.
σ_a^2, σ_m^2 = Genetic additive direct and maternal effect variances, respectively; σ_{am} = Genetic additive direct-maternal covariance; σ_p^2 = Phenotypic variance; h_a^2, h_m^2 = Heritabilities of direct and maternal effects, respectively; r_{am} = Genetic correlation between additive direct and maternal effects; *LogL* = Log of likelihood function value of the model.
[B] M_7 -E_D, E_M estimated according to *epistazigosity* concept of Fries *et al.* (2000); M_{71} -E_D, E_M estimated as proposed by Dickerson (1969, 1973); M_{72} -E_D, E_M estimated according to Kinghorn (1980, 1982).
[C] *Param.* -Number of independent estimated parameters; *AIC* -Akaike Information Criterion; *BIC* -Bayesian Information Criterion.

CONCLUSIONS

➢**The statistical model with only breed additive and dominance effects was insufficient to appropriately explain genetic and environmental variability in a Nellore x Hereford multibreed field dataset. Both heterosis and epistasis were important genetic effects that needed to be accounted for.**

➢ **Multicollinearity appeared to have affected the estimation of genetic and environmental effects. However, the large estimates obtained for heterosis and epistatic effects would justify additional research work with larger, and perhaps more balanced datasets to validate these results and to gain a better understanding of the genetic and economic characteristics of this multibreed population.**