ADDITIVE, COMPLEMENTARITY (ADDITIVE*ADDITIVE), DOMINANCE, AND EPISTATIC EFFECTS ON PREWEANING WEIGHT GAIN OF HEREFORD x NELORE CALVES

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INTRODUCTION
The primary objective of this work was to obtain estimates of genotypic effects on average daily weight gain (ADG) from a large commercial crossbred population. Another objective was to check or validate results from Fries et al. (2000) on a similar trait and equivalent population but from experimental data and another continent.

MATERIAL AND METHODS
Preweaning records of Hereford x Nelore calves from 29 farms belonging to partners of “Conexão Delta G” breeding program, located in Brazilian states of Mato Grosso, Goiás, Mato Grosso do Sul, São Paulo, Paraná, and Rio Grande do Sul were used. Each of these farms also runs its own breeding program and produces Hereford and Brahford genetics (southern states) or Nelore and Brahford genetics (central regions). This data set does not follow the general pattern of using imported and improved genetics on local unimproved populations.

Final data set contained records from 109,614 animals born from 1974 to 1999 and distributed in 4,665 contemporary groups (CG). CG were defined by the concatenation of identifiers for farm, year, sex, management group/pasture and Julian weaning date. Other environmental effects used to model ADG, with a total of 14 covariates, were: linear and quadratic effects of age of dam nested in sex of calf; linear and quadratic effects of age of calf; and spline functions of Julian date of birth and their linear interactions with latitude (LAT; as in Brito et al. (2002)). Average LAT was 26.56°S [14.0, 31.5]. Average ADG was 0.675 ± 0.164 kg/d [0.25, 1.50].

Covariates for direct (Ad) and maternal (Am) additive effects were defined by the genetic contribution of Nelore genes to the genetic make-up of each individual. Covariates for direct (Cd) and maternal (Cm) complementarity between Nelore and Hereford were calculated as \( Cd = Ad \times (1-Ad) \) and \( Cm = Am \times (1-Am) \). This form of calculating interaction terms helped to reduce multicollinearity. The formulae used to calculate and decompose direct (Hd) and maternal (Hm) heterozygosities were from Bertoli (1991) and Schenkel (1993). To calculate Hd and Hm the genetic composition of the parents and of the maternal grandparents of an individual are needed. All individuals had complete information to calculate Hd. When the genetic composition of the parents of a giving ancestor was not available, it was assumed that the animal was produced by inter se mating. Sires, dams, maternal grandsires and maternal granddams had complete information to calculate their heterozygosities with the following frequencies: 0.76, 0.76, 0.74, and 0.73, respectively. Direct (Ed) and maternal (Em) epistatic effects were modeled by epistazygosity, as in Fries et al. (2000) and calculated as the average heterozygosity present in the
gametes which generated each individual or as the average heterozygosity in the parents of an individual. Covariate means and their standard deviations were: \( \text{Ad}, 0.27 \pm 0.29; \text{Am}, 0.34 \pm 0.40; \text{Hd}, 0.31 \pm 0.36; \text{Hm}, 0.15 \pm 0.24; \text{Ed}, 0.13 \pm 0.19; \) and \( \text{Em}, 0.12 \pm 0.20. \) The average sire had a Nelore composition of 0.21 \pm 0.33. All covariates varied from 0.00 to 1.00, with the exception of \( \text{Em} \) whose maximum value was 0.75. Hence, F\(_2\) individuals were present (maximum value of \( \text{Ed} \) was 1.00) but no dam was an F\(_2\). After absorbing CG effects 46 173 animals had the transformed covariate for \( \text{Ed} \) different from zero. The same was true for 34 278 animals with respect to \( \text{Em} \), and 34,079 animals with respect to both \( \text{Ed} \) and \( \text{Em} \).

A large number (47 931) of calves were produced by AI, mainly from highly selected native Nelore and Hereford sires. Some Brahford semen was imported, mainly from Argentina and most of these sires were 3/8 Brahmans. Since Nelore contributed to the formation of Brahmans no distinction was made with this respect.

**RESULTS AND DISCUSSION**

Environmental effects were in line with results from Paz (1999) and Brito (2002). A model with environmental effects (4,678 df) and classificatory variables for genotypes (by concatenating sire and dam genetic compositions; 95 df) and genotype by latitude interactions (157 df) resulted in a \( R^2=0.62 \). Sequential sum of squares (SS1) for genotypes, after environmental effects and before genotype* latitude interactions was 18.3983. SS1 for these interactions was 9.5462.

### Table 1. Estimates of regression coefficients containing combinations of direct (d) and maternal (m) additive (A), heterotic (H), epistatic (E), and complementarity (C), modeling genotypic effects on preweaning average daily weight gain (kg/d). Last row contains the sum of sequential sum of squares (Σ SS1) of the genotypic effects considered

<table>
<thead>
<tr>
<th>Models</th>
<th>Σ SS1</th>
<th>12.1163</th>
<th>12.5181</th>
<th>12.9767</th>
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<tbody>
<tr>
<td>AH</td>
<td>-0.03517***</td>
<td>-0.03335***</td>
<td>-0.03690***</td>
<td></td>
</tr>
<tr>
<td>AHE</td>
<td>0.12741***</td>
<td>0.12310***</td>
<td>0.11718***</td>
<td></td>
</tr>
<tr>
<td>AHEC</td>
<td>0.03634***</td>
<td>0.03659***</td>
<td>0.11227***</td>
<td></td>
</tr>
<tr>
<td>Em</td>
<td>0.04678***</td>
<td>0.06238***</td>
<td>-0.03219*</td>
<td></td>
</tr>
<tr>
<td>Ed</td>
<td>-0.02555***</td>
<td>0.03196**</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cd</td>
<td>-0.00948*</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cm</td>
<td>-0.29562***</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

\( p<0.05; \) \( ** p<0.005; \) \( *** p<0.0005. \)

Table 1 shows results from preliminary modelings of genotypic effects. The traditional additive-dominance model (AH), with 4 df, explained 65.85% of the SS1 for genotypes but produced a significant lack-of-fit (lof) test. The addition of E to the models brought even more evidence to the H components. These results for epistatic effects are in agreement with the ones from Arthur et al. (1999) and Fries et al. (2000) who used similar models on experimental Brahford data from Grafton.

Adding C components produced significant estimates, but brought the Variance Inflation Factors (VIF) of the E components to range between 5 to 13 ; of the H components to around 20 ; and of the C components to around 30. When interactions of these effects with latitude were added, most VIF went to the thousands. Therefore, ridge techniques were recommended.
For being able to use PROC REG from SAS, CG had to be absorbed beforehand. For preventing the shrinkage of the remaining environmental effects, estimates obtained from the classificatory genotypic model were used to correct observations for these environmental effects. Interactions between all 8 genotypic covariables with linear (LAT1), quadratic (LAT2), and cubic (LAT3) functions of latitude were tested. Overall, the range of ridge values tested varied from 0 to 100. Higher order interaction terms, which produced inconsistent results (p-values higher than 0.05 or change of signs) at different ridge constants, where dropped from the model. Lower order interaction terms were kept if higher order ones were significant. Too many models produced equivalent results, with similar R² and difficulties for the interpretation of the results. Since one of the objectives of this work was to examine/check models containing dominance and epistatic effects, all terms involving interactions of these effects with latitude were removed. Considering only the interactions between latitude and A and C terms, R² was kept almost the same. Hm component was still varying too wildly according to which interaction terms were used. Estimates became stable when the restriction of equality of Hd and Hm regression coefficients was imposed. When choices of competitive models narrowed down, the value of the ridge constant became more relevant. Figure 1a lists the genotypic terms of the final model and their interactions with functions of LAT and shows their estimates as ridge values went from 0.00 to 0.10. The function “harmonic mean of the absolute t-values” (HARM_AT) helped to identify (local optimum) the smallest possible ridge values (small shrinkage is desirable), which will produce uniform (harmonic mean of t-values) significant results. Figure 1b shows the calculated t-values and values of HARM_AT, which offer some objective support in the decision process.

Figure 1. (a) Estimates of genotypic values from the “Delta G” Braford population as ridge values varying from 0.0 to 0.1; (b) t-values and the harmonic mean of their absolute values

Figure 2 was obtained using the estimates (ridge value=0.06) given in Figure 1a to predict ADG from stabilized (after generation F4) synthetic lines at each 0.1 interval (Hereford=0; Nelore=1) at different latitudes. The result was unexpected but easily interpreted. In the tropics, highly adapted genotypes are required and they do better than highly heterotic ones.
At latitude 16 no pure Hereford calves were present (under commercial conditions, would not survive)

At tropical latitudes purebred Nelores do better.

CONCLUSION
There exist maternal and individual additive, complementarity, dominance and epistatic effects on preweaning gain, as well as interactions of these genotypic effects with location (latitude);
There is a significant lack of fit for the additive-dominance models;
A working hypothesis that can be formulated is that part of the heterotic effects estimated under the additive-dominance model may be originated from complementarity, that is, from across breed additive*additive effects;
The relevance of the latitude*genotype interaction estimates obtained suggests the exploration of other geoclimatic indicators/markers and geostatistic techniques in order to better explain/describe genotype*environment response surfaces.

REFERENCES