

Modeling breed additive and non-additive genetic effects using a Angus x Nellore crossbred population



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ABSTRACT

The objectives of this study were to estimate fixed genetic (both additive and non-additive) effects and test different non-additive models. These effects included direct and maternal joint breed additive effects, direct and maternal complementarity (or profit heterosis), direct and maternal heterosis (dominance) and direct and maternal epistatic loss non-additive effects. A large crossbred Angus x Nellore population with approximately 300,000 records for weaning gain (WG) and 150,000 records for post-weaning gain (PG) was used. Phenotypic scores for weaning (WC) and post-weaning (PC) conformation, weaning (WP) and post-weaning (PP) precocity, weaning (WM) and post-weaning (PM) muscling and scrotal circumference (SC) were also used. All models included the fixed contemporary group effect and random animal, maternal genetic and permanent environment effects. Each model was tested against all other models for all nine traits using the likelihood ratio test. The complete model, including all additive and non-additive effects and the model without complementarity, were seen to be the best options to analyze this crossbred population. However, least squares may not be the best methodology due to possible collinearity among estimates that may inflate the variance. In the complete model most effects were statistically significant ($P < 0.01$) for weaning traits, except for direct and maternal breed additive effects and direct complementarity effect for WM. For post-weaning traits, the direct complementarity effect for phenotypic scores (PC, PP and PM) and the maternal heterosis effect for PG, PC, PM, were not statistically significant. For scrotal circumference the maternal complementarity, direct and maternal heterosis and maternal epistatic loss effects were not statistically significant. All other effects were statistically significant ($P < 0.01$). For the model without complementarity, the direct breed additive

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effect for PG and PP was not statistically significant, including the maternal breed additive effect for WC, WD, PP and PM and maternal heterosis, direct and maternal epistatic loss effects for SC. Considering all models, significant direct breed additive effect was mostly positive for weaning traits and was negative for all post-weaning and SC. The significant maternal breed additive and maternal complementarity effects for SC were all negative. The significant direct and maternal epistatic loss effects were negative for all traits and for all models, except for PG in the complete model and for weaning traits in the model including only breed additive and epistatic loss effects. We conclude that the fixed genetic effects are mostly significant, thus it is important to include them in the model when evaluating crossbred animals and the models including breed additive effects, heterosis and epistatic loss with or without complementarity were the more appropriate.

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1. Introduction

Widely used in tropical and sub-tropical climate countries, crossbreeding systems are based on the exploration of various genetic effects resulting from existing differences between breeds. Among these effects are the breed additive effect and the non-additive effects of the combination of the involved breeds (joint additive effect), as well as heterosis and epistatic loss effects.

The breed additive effect comprehends the individual effects of each of the involved breeds; as long-term selection within a breed increased frequencies of non-allelic genes that jointly produce favorable extra effects (Fries et al., 2002). The non-additive effect of the combination of breeds involved in the crossbreeding, that causes a multiplicative relation among the additive actions was defined by Kinghorn (1993) as “profit heterosis”. The heterosis effect is mainly due to the dominance effects on the genes and can be considered as the recovery from the depression due to accumulated consanguinity. A linear relationship between heterozygosity and heterosis retention has been found (Fries et al., 2000; Gregory et al., 1991). The epistatic loss effect comprehends an additional deviation from the genotypic value occasioned by the non-additive combination when more than one locus is considered in the analysis (Falconer and Mackay, 1996). According to VanRaden (2006), talking about crossbred animals, “If non-additive effects are subtracted and only additive effects are reported, selection may not be optimal”.

The models that estimate simultaneously additive and heterosis effects or estimate direct additive effects after the adjustment of the data for heterosis based on the expected heterozygosity are the most common basic models of multi-racial populations breeding programs for beef cattle. These models have been used in crossbred populations in Brazil (Lopes et al., 2010), Africa (Theunissen et al., 2013), Australia (Arthur et al., 1999), Canada (Rosso et al., 2005a), Colombia (Vergara et al., 2009a, 2009b), Ethiopia (Demeke et al., 2003a, 2003b), USA (Elzo and Wakeman, 1998) and Uruguay (Lema et al. 2011).

The inclusion of complementarity effect in the model was suggested by Fries et al. (2000) and reaffirmed by Piccoli et al. (2002). According to Pimentel et al. (2006), when referring to crossbred animals in a tropical environment, we can consider that two groups of genes were acting, one related to the growth potential and the other to adaptation. The multiplicative relation among their effects could be interpreted as

complementarity. A large number of studies do not consider complementarity as an important effect, but Piccoli et al. (2002) found that the magnitude of heterosis estimates is reduced when the complementarity (additive*additive interactions) is included in the model, indicating that under the additive-dominance model the heterosis estimation may be due to a non-linear additive effect. According to these authors this effect becomes more evident when the model also includes an epistatic loss effect.

The inclusion of the epistatic loss effect in the additive-dominant model was also suggested by Fries et al. (2000) and reaffirmed by Piccoli et al. (2002) with the objective of achieving a better explanation of the existing genetic variation among different breed compositions. The genotype at a locus can influence the genotype effect of a second locus and may inhibit gene expression of the second locus in the phenotype. Recent studies suggest that the epistatic loss effect strongly and negatively influenced crossbred animals' levels of production (Cardoso et al., 2008, Lema et al., 2011), although some researchers choose do not include epistasis in the models, such as Vergara et al. (2009b), Legarra et al. (2007) and Arthur et al. (1999).

As the main objective of crossbreeding systems is taking advantage from non-additive genetic effects among breeds, obtaining reliable estimates of the parameters involved in crossbreeding systems and thus being able to predict the performance of the crossed genotypes is an important step for the successful development of a breeding program (Cardoso et al., 2008).

The main objective of this study was to test different additive and non-additive genetic models. We also aim to estimate the fixed genetic effects (joint breed direct and maternal additive effects and complementarity (or profit heterosis), heterosis and epistatic loss direct and maternal non-additive effects), involving crosses between Angus and Nellore beef cattle breeds.

2. Materials and methods

2.1. Data

Data from different breed compositions resulting from crosses between Angus and Nellore cattle was used. This data came from more than 200 herds distributed in the Brazilian provinces of Rio Grande do Sul, Paraná, São Paulo, Mato Grosso do Sul, Mato Grosso and Goiás and also from

Table 1
Absolute and relative frequencies of observations among coefficients of fixed genetic effects, grouped in classes of 0.125, ranging from zero to one.

Classes	aa	am	ca	cm	ha	hm	ea	em
0.000	27135	37561	27135	89677	27107	89598	54852	103209
0.125	522	145	1013	200	17	3	35	6
0.250	7140	2385	257161	195431	731	98	66553	23795
0.375	18626	84046			3110	24370	9924	26693
0.500	84259	65641			136291	132697	120060	121670
0.625	11868	8575			43545	9490	20810	6273
0.750	33676	34416			36052	14284	12576	3527
0.875	2050	420			3120	232	494	130
1.000	32	52120			35335	14538	6	5
Total	285,309	285,309	285,309	285,309	285,309	285,309	285,309	285,309

aa, am, ca, cm, ha, hm, ea, em: coefficients used to estimate direct and maternal breed additive genetic effects, direct and maternal complementarity, heterosis and epistatic loss non-additive genetic effects, respectively. Classes include fractions equal or smaller than the mentioned value. Percentages in parentheses were expressed as relative frequencies.

Paraguay. All herds were participants of “Programa Natura de Melhoramento Genético de Bovinos” (Natura Cattle Breeding Program). Absolute and relative frequencies of observations among coefficients are presented in Table 1.

2.1.1. Traits

Nine traits were used in this analysis: weaning gain (WG), post-weaning gain (PG), phenotypic scores of conformation (WC), precocity (WP) and muscling (WM) taken at weaning, phenotypic scores of conformation (PC), precocity (PP) and muscling (PM) at post-weaning as well as scrotal circumference (SC) adjusted for animal weight and age. The phenotypic score for each trait is given on a five-point scale, where one is the worst, and five is the best score for each management group. The number of used observation is presented in Table 3.

2.2. Predictor variables of fixed genetic effects

2.2.1. Breed additive effect

The contribution of Nellore genes in the genetic composition of the animal and their dams were used to estimate the direct (**aa**) and maternal (**am**) genetic effect of breed. To avoid dependence in incidence matrix columns, only the Nellore coefficient was used, giving us an estimate as a deviation from the Angus breed performance.

2.2.2. Complementarity

The coefficients proposed by Kinghorn (1993) and used by Fries et al. (2000), Piccoli et al. (2002), Cardoso et al. (2008) were used to estimate the complementarity effects. The direct complementarity (**ca**) coefficient is described as $ca = aa * (1.0 - aa)$ and the maternal complementarity (**cm**) coefficient is described as $cm = am * (1.0 - am)$ where **aa** is the Nellore fraction of the animal breed and **am** is the Nellore fraction of the dam breed.

2.2.3. Heterosis effect

To estimate the direct (**ha**) and maternal (**hm**) heterosis effects, the heterozygosity coefficients were used as described by Bertoli (1991) and Schenkel (1993), also used by Cardoso

Table 2

Fixed genetic effects included in the genotypic models considered in this study.

Model	Effects included on γ							
	aa	am	ca	cm	ha	hm	ea	em
A	x	x						
AC	x	x	x	x				
AH	x	x			x	x		
AE	x	x					x	x
ACH	x	x	x	x	x	x		
ACE	x	x	x	x			x	x
AHE	x	x			x	x	x	x
ACHE	x	x	x	x	x	x	x	x

aa, am, ca, cm, ha, hm, ea, em: direct and maternal breed additive genetic effects, direct and maternal complementarity non-additive genetic effects, direct and maternal heterosis non-additive genetic effects, direct and maternal epistatic loss non-additive genetic effects, respectively.

Table 3

Number of animals (A) and contemporary groups (CG) used in the analysis.

Trait		Weight gain		Conformation		Precocity		Muscling		Scrotal circumference	
		TOTAL	CONNED (%)	TOTAL	CONNED (%)	TOTAL	CONNED (%)	TOTAL	CONNED (%)	TOTAL	CONNED (%)
A	W	294,045	284,628 (97)	288,182	279,582(97)	276,264	268,333 (97)	286,350	277,734 (97)		
	PW	148,443	138,102 (93)	149,091	144,264 (98)	141,188	136,802 (97)	147,392	142,580 (97)	46,269	40,092 (87)
CG	W	9242	6615 (72)	8840	6433 (73)	8312	6011 (72)	8807	6398 (73)		
	PW	11,398	7044 (62)	3535	2496 (71)	3304	2318 (70)	3506	2471 (70)	4222	2445 (58)

W: weaning phenotypes; **PW:** post-weaning phenotypes; **CONNED. (%)**: number (and percentage) of animals(A)/contemporary groups(CG) connected to the analyzed data.

et al. (2008), Cardoso and Tempelman (2004), Pimentel et al. (2006) and Roso et al. (2005b). These coefficients are given by $\mathbf{ha} = (1 - \sum_{i=1}^2 (\text{Sire breed}_i * \text{Dam breed}_i))$ and $\mathbf{hm} = (1 - \sum_{i=1}^2 (\text{Maternal Grand Sire breed}_i * \text{Maternal Grand Dam breed}_i))$ where $i=1$ refers to Angus breed proportion and $i=2$ refers to Nellore breed proportion. When the breed composition of a cow was not known (all products had known breed composition) the cow was considered as *inter se* mating.

2.2.4. Epistatic loss effect

To estimate the direct (**ea**) and maternal (**em**) epistatic loss effects, the epistazigosity coefficients were used as proposed by Fries et al. (2000,2002) and also used by Cardoso et al. (2008), Pimentel et al. (2006), Carvalheiro et al. (2006) and Roso et al. (2005a,b). These coefficients are given by $\mathbf{ea} = \frac{1}{2} [\text{Hs} + \text{Hd}]$ and $\mathbf{em} = \frac{1}{2} [\text{Hmgs} + \text{Hmgd}]$, where Hs is the sire's heterozygosity, Hd is the dam's heterozygosity, Hmgs is the maternal grand sire heterozygosity and Hmgd is the maternal grand dam heterozygosity. When the breed composition of a cow was not known (all products had known breed composition) the cow was considered as *inter se* mating.

2.3. Statistical analysis

2.3.1. The (co)variance components

The (co)variance components were previously estimated using model (1), including all effects (fixed effects of environment, fixed genetic effects, random direct, maternal and permanent environmental effects and residual). The Restricted Maximum Likelihood (REML) method with the DMU (Madsen and Jensen, 2000) software was used. The convergence criterion was 10^{-12} .

2.3.2. Genotypic models

The general model is described by Eq. (1). The pair-traits WG–PG, WC–PC, WP–PP, WM–PM and WG–SC were analyzed in a two-trait analysis using this model with the systematic inclusion of fixed genetic terms, in order to compare models and effects.

$$\mathbf{y} = \mathbf{X}\boldsymbol{\beta} + \mathbf{W}\boldsymbol{\gamma} + \mathbf{Z}\boldsymbol{\alpha} + \boldsymbol{\varepsilon} \quad (1)$$

where **y** is the vector of observations of trait 1 and trait 2; **β** is the vector of fixed effects of environment, which includes contemporary group (herd, year, season, sex, phenotype collect date and manage group); **γ** is the vector of fixed

genetic effects; **α** is the vector combining the random direct (a), maternal (m) and permanent (p) environmental effects, i.e. $\boldsymbol{\alpha} = [a' \ m' \ p']'$, and **ε** is the vector of random residual effects. Incidence matrices **X**, **W** and **Z** relate records to fixed environmental effects, to fixed genetic effects and to random direct and maternal additive genetic and permanent environment effects, respectively.

The vectors of random effects **α** and **ε** were assumed to

$$\text{have (co)variance} = \mathbf{V}(\boldsymbol{\alpha}) = \begin{bmatrix} \mathbf{A} \otimes \mathbf{G}_a & \mathbf{A} \otimes \mathbf{G}_{am} & \mathbf{0} \\ \mathbf{A} \otimes \mathbf{G}_{am} & \mathbf{A} \otimes \mathbf{G}_m & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{I} \otimes \mathbf{P}_e \end{bmatrix}$$

and $\mathbf{V}(\boldsymbol{\varepsilon}) = \mathbf{I} \otimes \mathbf{R}$. **A** is the additive numerator relationship matrix among animals and **I** is the identity matrix;

$$\mathbf{G}_a = \mathbf{G}_a = \begin{bmatrix} \sigma_{a1}^2 & \sigma_{a1a2} \\ \sigma_{a1a2} & \sigma_{a2}^2 \end{bmatrix}, \mathbf{G}_m = \begin{bmatrix} \sigma_{m1}^2 & \sigma_{m1m2} \\ \sigma_{m1m2} & \sigma_{m2}^2 \end{bmatrix}, \mathbf{G}_{am} = \begin{bmatrix} \sigma_{a1m1} & \sigma_{a1m2} \\ \sigma_{a2m1} & \sigma_{a2m2} \end{bmatrix}, \mathbf{P}_e = \begin{bmatrix} \sigma_{p1}^2 & \sigma_{p1p2} \\ \sigma_{p1p2} & \sigma_{p2}^2 \end{bmatrix} \text{ and } \mathbf{R} = \begin{bmatrix} \sigma_{e1}^2 & \sigma_{e1e2} \\ \sigma_{e1e2} & \sigma_{e2}^2 \end{bmatrix}$$

where σ^2 refers to variance and σ refers to covariance; **a** refers to direct additive genetic, **m** to maternal additive genetic **p** to permanent environmental effects and **e** to residual; **1** refers to the first and **2** to the second trait on a two-trait analysis.

The complete general model above (1) was analyzed and also with reductions. The difference among compared models was in **γ** vector, which includes different fixed genetic effects. Eight models were analyzed: model **A** which includes in **γ** only the breed additive effect (direct and maternal); model **AC** which includes in **γ** the breed additive effect (direct and maternal) and complementarity (joint additive) effects (individual and maternal); model **AH** which includes in **γ** the breed additive effect (direct and maternal) and dominance (heterosis) effects (individual and maternal); model **AE** which includes in **γ** the breed additive effect (direct and maternal) and epistatic loss effects (individual and maternal); model **ACH** which includes in **γ** the breed additive effect (direct and maternal), complementarity effects (individual and maternal) and dominance (heterosis) effects (individual and maternal); model **ACE** which includes in **γ** the breed additive effect (direct and maternal), complementarity effects (individual and maternal) and epistatic loss effects (individual and maternal); model **AHE** which includes in **γ** the breed additive effect (direct and maternal), dominance (heterosis) effects (individual and maternal) and epistatic loss effects (individual and maternal) and the complete model **ACHE** which includes

in γ the breed additive effect (direct and maternal), complementarity effects (individual and maternal), dominance (heterosis) effects (individual and maternal) and epistatic loss effects (individual and maternal). (Table 2) In total, eight models were analyzed for each trait using the least squares methodology in a two-trait analysis. Data was pre-adjusted for fixed effects of animal age, dam age and birth date (julian). Scrotal circumference was pre-adjusted for age and weight. GenSys Consultores Associados developed the analysis programs in Fortran 95.

The Likelihood Ratio, as described by Regazzi and Silva (2004), was used to compare the models for each model pair.

2.3.3. Connectedness analysis

A connectedness analysis between contemporary groups was carried out according to Roso et al. (2004), using the total number of direct genetic links between contemporary groups due to common sires and dams. Contemporary groups with more than 2 calves and with at least 5 ten direct links and two classes of direct or maternal fixed effects were considered connected and retained for analysis. Roso et al. (2004) found that as the degree of connectedness among test groups decreases, the accuracy of comparisons of EBVs of bulls in different test groups also decreases. As one of the final objectives of a genetic evaluation is to obtain accurate EBVs, we tested the connectedness, using only connected animals and contemporary groups in this analysis. The number of animals and contemporary groups for each trait before and after the connectedness analysis is presented in Table 3.

2.3.4. Collinearity diagnosis

Principal components (PC), condition index (CI) and variance inflation factor (VIF) were used to perform a collinearity diagnosis. CI was obtained for each eigenvalue by computing $CI_i = \sqrt{\lambda_{max}/\lambda_i}$, where λ_{max} is the largest eigenvalue and λ_i is the i th eigenvalue of the correlation

matrix between predictor variables of the fixed genetic effects. The condition number (k) is the condition index of the highest value. VIF was given by $VIF = 1/(1 - R_i^2)$, where R_i is the determination coefficient. (Schabenberger and Pierce, 2002).

3. Results and discussion

3.1. The models

The significance of the comparisons of the models against reductions is presented in Table 4. Of the 198 realized comparisons (22 between each two of the eight models, for each of the nine analyzed traits), using the Likelihood ratio test and testing under a significance level of $P > 0.001$, 40 comparisons (20%) were not significant. Of these, 45% were for scrotal circumference. The nullity hypothesis was rejected, indicating that for each of the 158 significant comparisons the tested models presented a significant difference in at least one of the considered parameters.

All models tested against reduced **A**, **AC** and **AE** models, presented significant differences except for SC, showing that for all other traits these models are not the best models to use to crossbreed animals.

The **AH** reduction model did not show significant difference from **ACH** for most traits, but did with **ACE**, **AHE** and **ACHE** models. If **AH** and **ACH** are not truly different, we may suppose that **ca** and/or **cm** are not really important to these traits. Lopes et al. (2010), testing different models to estimate genetic effects in Angus x Nellore crosses, found that the “joint additive effect does not substantially improve the adjustment”. Carvalheiro et al. (2006), studying Hereford–Nellore crosses, suggest that complementarity seems to be important but should be further investigated to better comprehend the effect and how to model it.

Table 4
Significance of the models tested against the each possible reduced model.

model reduction	AC A	AH A	AE A	ACH A	ACE A	AHE A	ACHE A	ACH AC	ACE AC	AHE AC	ACHE AC	ACH AH	ACE AH	AHE AH	ACHE AH	ACH AE	ACE AE	AHE AE	ACHE AE	ACHE ACH	ACHE ACE	ACHE AHE
trait																						
WG	***	***	***	***	***	***	***	***	***	***	***	ns	***	***	***	***	***	***	***	***	ns	ns
WC	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	ns	***
WP	***	***	***	***	***	***	***	***	***	***	***	ns	***	***	***	***	***	***	***	***	ns	ns
WM	***	***	***	***	***	***	***	***	***	***	***	ns	***	***	***	***	***	***	***	***	ns	***
PG	***	***	***	***	***	***	***	***	***	***	***	ns	***	***	***	***	***	***	***	***	ns	ns
PC	***	***	***	***	***	***	***	***	***	***	***	ns	***	***	***	***	***	***	***	***	ns	ns
PP	***	***	***	***	***	***	***	***	***	***	***	ns	***	ns	***	***	***	***	***	***	ns	***
PM	***	***	***	***	***	***	***	***	***	***	***	ns	ns	ns	ns	***	***	***	***	***	ns	ns
SC	***	**	**	**	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns

ns: non significant; **A**: model including only the breed additive (direct and maternal) effect; **AC**: model including the breed additive (direct and maternal) and complementarity (direct and maternal) effects; **AH**: model including the breed additive (direct and maternal) and heterosis (direct and maternal) effects; **AE**: model including the breed additive (direct and maternal) and epistatic loss (individual and maternal) effects; **ACH**: model including the breed additive (direct and maternal), complementarity (individual and maternal) and heterosis (individual and maternal) effects; **ACE**: model including the breed additive (direct and maternal), complementarity (direct and maternal) and epistatic loss (direct and maternal) effects; **AHE**: model including the breed additive (direct and maternal), heterosis (direct and maternal) and epistatic loss effects (direct and maternal) and the complete model **ACHE**: the breed additive (direct and maternal), complementarity (direct and maternal), heterosis (direct and maternal) and epistatic loss (direct and maternal) effects.

** $P < 0.01$.

*** $P < 0.001$.

Table 5

Correlation between the coefficients used on estimation of fixed genetic effects. Weaning gain below and post-weaning gain above diagonal.

	aa	am	ca	cm	ha	Hm	ea	em
aa	1	0.7552	0.7172	0.1195	0.6607	0.1165	0.2652	0.0884
am	0.7435	1	0.5577	-0.1375	0.7379	-0.1200	-0.1077	-0.1281
ca	0.6726	0.5298	1	0.5073	0.7559	0.4548	0.5513	0.4241
cm	0.0724	-0.1810	0.4774	1	-0.0052	0.9013	0.8373	0.8362
ha	0.6015	0.6970	0.7288	-0.0323	1	-0.0025	-0.0425	-0.0012
hm	0.0711	-0.1628	0.4247	0.8998	-0.0242	1	0.8760	0.5367
ea	0.2210	-0.1416	0.5259	0.8305	-0.0792	0.8719	1	0.5630
em	0.0521	-0.1610	0.4000	0.8339	-0.0248	0.5345	0.5540	1

aa, am, ca, cm, ha, hm, ea, em: direct and maternal breed additive effect, direct and maternal complementarity, heterosis and epistatic loss non-additive effects, respectively.

The comparison of **ACHE/ACE** did not present any significance and **ACHE/AHE** presented non-significant comparisons for a larger number of traits. Observing **ACHE/ACE** we might suppose **ha** or **hm** were not important to improve the adjustment of the tested models thus the models are equivalent. However, if we consider the significance of the comparison **ACH/AC** a possible confounding may exist when **ha/hm** or **ea/em** are not present in the model. According to [VanRaden \(2006\)](#) "Breed differences contain additive, dominance, and epistatic effects that are confounded if only two breeds are considered...". When using simpler models, joint additive and epistatic effects appear to be mixed in the heterosis effect ([Pimentel et al. 2006](#)).

For weaning traits, the determination coefficient (R^2) (not shown) was highest and the mean square error (MSE) was lower for the **ACE** model and for post weaning traits the **AHE** model had the highest R^2 and lowest MSE.

Although **ACHE** did not differ statistically from **ACE** and **AHE** for most traits, the **ACE** model produced very high magnitude of the estimates. These high estimates hinder the biological interpretation and lead us to assume that this is not the best model to use. The **ACHE** and **AHE** models seem more parsimonious to use with crossbred animals.

A wide variety of forms of interactions may be manifested in a crossbred animal, often estimated as a single component, called heterosis. This estimated heterosis value is, actually, the liquid balance of all the gene interactions that are present in the animal. Models that include non-additive effects can be more precise, but also more confusing. Although genetic interactions are complicated terms to extract from models, they can provide useful predictions if used carefully. Breeders must continue selecting for additive merit, but can also improve non-additive merit, considering these interactions in breeding programs where crossbred animals are used ([VanRaden, 2006](#)).

[Bueno et al. \(2011\)](#), studying epistasis on genetic evaluation models, concluded that simpler models used to evaluate bovine composites might wrongly identify various additive and non-additive effects as a heterosis effect. Breed additive, heterosis and epistatic loss effects, as well as direct and maternal effects, should be included in models to evaluate crossbred beef cattle. ([Bueno et al., 2012](#); [Lema et al., 2011](#); [Cunha et al., 2009](#); [Cardoso et al., 2008](#); [Kippert et al., 2008](#); [Carvalho et al., 2006](#))

Complementarity effects are more controversial. [Cardoso et al. \(2008\)](#) and [Piccoli et al. \(2002\)](#) found that they are as

important as the other non-additive effects; however, [Lopes et al. \(2010\)](#) concluded "The inclusion of joint additive effects does not substantially improve the adjustment promoted by the analysis models, besides inserting a bias attributed to multicollinearity". [Carvalho et al. \(2006\)](#) argue that complementarity seems important but should be further investigated.

3.1.1. Collinearity analysis

3.1.1.1. Correlation between predictor variables. The correlation between the coefficients used for the estimation of the fixed genetic effects for WG and PG are presented in [Table 5](#).

In total, 46% of the correlations between the pairs for WG and 50% for PG, present values superior to 0.5, indicating medium to high correlations between the pairs. This high correlation may indicate multicollinearity between the coefficients; therefore, the coefficient pairs must not be the only verified factor as the existing relationship between three or more coefficients can also be interfering in this multicollinearity.

For all analyzed traits (WG, WC, WP, WM, PG, PC, PP, PM and SC), the highest correlation was found between the coefficients for maternal complementarity and maternal heterosis, followed by the correlation of maternal and direct epistatic loss with maternal complementarity. This high correlation might be the reason why significant differences were not detected between the **ACH/AH** and **ACHE/ACE** reductions.

When complementarity is removed from the model (not shown), the highest correlation is between maternal heterosis and direct epistatic loss, keeping values around 0.85 for all traits. This high correlation may be due to the difficulty in separating the coefficients of maternal complementarity and maternal heterosis and direct epistatic loss, resulting from data structure and from a possible linear dependence (multicollinearity) involving the predictors.

When we remove the maternal component of heterosis from the analysis of PG, PC and PM (maternal heterosis was not significant for these traits) the highest correlation remains between complementarity and epistatic loss, with very close values.

3.1.1.2. Principal components and conditional index. The first principal component allows us to perceive a possible collinearity between the values of the direct (**ca**) and maternal complementarity (**cm**), maternal heterosis (**hm**),

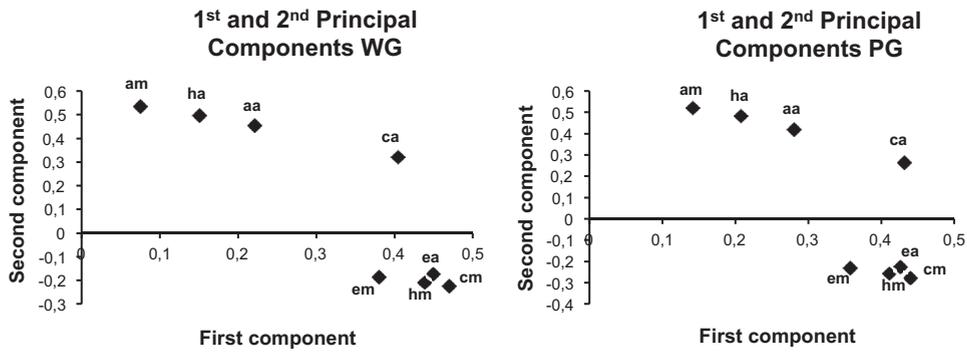


Fig. 1. First and second principal components for weaning gain (WG) and post-weaning gain (PG) traits. **aa**: direct breed additive effect, **ca**, direct complementarity effect, **ha**: direct heterosis effect, **ea**: direct epistatic loss effect. **am**: maternal breed additive effect, **cm**: maternal complementarity effect, **hm**: maternal heterosis effect, **em**: maternal epistatic loss effect.

direct (**ea**) and maternal (**em**) epistatic loss estimates. These estimates may be confounded for these traits. The second principal component shows that the breed direct (**aa**) and maternal (**am**) additive effect, direct heterosis (**ha**) and direct complementarity (**ca**) effect opposes to the maternal complementarity (**cm**), maternal heterosis (**hm**) and direct (**ea**) and maternal (**em**) epistatic loss effects, showing again a possible confounding between these estimators (Fig. 1).

When there is no collinearity, the eigenvalues, condition index and condition numbers are all one. With increasing collinearity, eigenvalues are both larger and smaller than one (eigenvalue close to zero indicates multicollinearity problem) and the condition index and number will increase (Schabenberger and Pierce, 2002). According to Schabenberger and Pierce (2002), if the value of the condition number of the matrix is lower than the upper threshold of 30, this indicates problems of multicollinearity. The highest condition index we found was 21.2493 for WG. The other CIs were 21.0631 for WC, 20.4443 for WP, 20.8205 for WM, 24.4637 for PG, 22.8341 for PC, 21.9954 for PP, 22.3479 for PM and 28.5690 for SC. Lema et al. (2011) also used the threshold of 30. They found condition number of 28.3 and concluded that collinearity was not a problem.

Multicollinearity can occur when one or more variables are dependent on others present in the same model. When using non-additive models, we are using breed composition (individual, parents and grandparents) to estimate all coefficients (breed direct, complementarity, heterosis and epistatic loss). High correlations between variable pairs may be indicative of multicollinearity (Roso et al., 2005b). The higher the collinearity, the higher the standard errors and, wider the confidence intervals. The *t* statistics tend to be very small in this case. When multicollinearity is present, it is therefore difficult to reject the null hypothesis (Schabenberger and Pierce, 2002). Even if there is multicollinearity among the used estimators, we reject most of our null hypotheses in the present study.

3.1.1.3. Variance inflation factor. The variance inflation factor (VIF) indicates the variance inflation of each regression coefficient compared with an orthogonal situation. Usually values above 10 for VIF suggest that multicollinearity may be causing problems in the estimation (Schabenberger and Pierce, 2002).

The variance inflation factor (VIF) analysis for the models **ACHE**, **AHE** and **ACE** are presented in Table 6.

The VIF shows that the estimates had their variance inflate up to 110 times (SC) when compared to an orthogonal condition (VIF=1) for the model **ACHE**. (Table 6) Roso et al. (2005b) suggested the use of ridge regression to solve the problem of multicollinearity; however, Cardoso et al. (2008), comparing the least squares and ridge regression methodologies, showed that, although the most consistent results were generated by the ridge regression technique, the estimates of genotypic effects, with and without the use of this technique, generate similar predicted values, and this occurred for all tested traits.

This possible collinearity can be partially explained as all estimators are based on the breed composition of individuals, which is restricted to 1. In addition, the fact that the breed composition of an individual is equal to the average of the breed composition of their parents interferes with this collinearity. In practice, we are using the same information to predict different effects seen from different angles.

For the **ACE** model, except PP, all other traits presented FIV higher than ten for maternal complementarity and higher FIV for direct and maternal epistatic loss than **AHE** model. For the **AHE** and **ACH** models, only SC produced a FIV higher than ten. The **AC**, **AH**, **AE** and **A** models did not present any FIV above ten. These results may indicate that the greatest problem for collinearity is complementarity, as **cm** always showed the highest values.

3.2. Fixed genetic effects estimates

Estimates of fixed genetic effects are presented in Table 7. All regression coefficients for WG and WM are statistically significant ($P < 0.01$), as are most coefficients for the other traits (WC, WP, PG, PC, PP, PM). Scrotal circumference presents 30% of the total statistically non-significant coefficients. Among the non-significant effects, there were some maternal components for post-weaning traits, which were not expected to be significant. Contrary to this, the non-significance of the direct and maternal breed additive and direct complementarity effects for WM (models **ACHE**, **ACH** and **AHE**) was not expected nor was the direct breed additive effect for PG (model **AHE**) and for PP (models **ACE** and **AHE**).

Table 6
Variance inflation factor (VIF) estimated (ACHE, AHE and ACE models).

Model ACHE									
	WG	WC	WP	WM	PG	PC	PP	PM	SC
aa	3.544	3.593	3.455	3.503	4.174	4.024	3.823	3.853	6.054
am	3.712	3.892	4.024	3.844	4.030	4.323	4.854	4.230	4.773
ca	13.730	13.935	13.815	13.355	21.228	19.661	19.140	18.183	22.848
cm	69.093	67.611	62.564	66.808	86.393	75.271	68.870	74.077	110.851
ha	8.896	8.886	8.460	8.672	13.638	12.444	11.416	11.911	13.541
hm	36.929	36.343	34.335	36.021	45.887	41.392	38.361	40.770	51.637
ea	13.924	14.158	13.918	13.975	18.166	17.214	16.603	16.795	21.906
em	17.169	16.908	15.957	16.755	20.864	18.359	17.366	18.199	28.671
model AHE									
aa	3.544	3.592	3.454	3.502	4.165	4.010	3.798	3.837	6.053
am	3.481	3.606	3.659	3.561	3.775	3.993	4.317	3.902	4.415
ha	2.216	2.285	2.370	2.249	2.568	2.596	2.839	2.521	3.421
hm	5.124	5.172	5.073	5.132	5.383	5.301	5.177	5.218	6.661
ea	6.330	6.380	6.250	6.313	7.012	6.784	6.586	6.655	10.394
em	1.496	1.491	1.453	1.481	1.511	1.474	1.448	1.459	1.705
model ACE									
aa	3.465	3.502	3.369	3.414	4.008	3.865	3.675	3.699	5.686
am	3.672	3.849	3.980	3.802	3.960	4.254	4.781	4.164	4.588
ca	3.399	3.561	3.840	3.441	3.973	4.080	4.728	3.831	5.716
cm	10.189	10.147	9.704	10.032	10.926	10.329	9.781	10.147	15.204
ea	5.745	5.764	5.726	5.689	6.341	6.124	6.134	5.988	9.462
em	4.501	4.477	4.291	4.439	4.673	4.467	4.278	4.418	5.917

aa, am, ca, cm, ha, hm, ea, em: direct and maternal breed additive genetic effects, direct and maternal complementarity non-additive genetic effects, direct and maternal heterosis non-additive genetic effects, direct and maternal epistatic loss non-additive genetic effects, respectively; **WG:** weaning gain; **PG:** post-weaning gain; **WC:** weaning conformation; **PC:** post-weaning conformation; **WP:** weaning precocity; **PP:** post-weaning precocity; **WM:** weaning muscling; **PM:** post-weaning muscling; **SC:** scrotal circumference adjusted to age.

The breed additive effect relates to the Angus and must be considered as a deviation from Angus performance as the Nellore gene proportion increases. The direct breed additive direct effect (**aa**) was positive for weaning traits and negative for post-weaning traits and SC for most of the tested models, showing that as the Nellore (*B. indicus*) gene proportion increases, the general weaning growth rate increases and the general post-weaning growth rate decreases. For **A, AC** and **AE** models, **aa** was negative for all traits. The positive or negative effect does not mean that the animals are heavier or lighter; it is just the gene effect. The final animal weight will be a balance of all involved effects. Negative values were reported for weaning weight for Nellore (Lopes et al., 2010) and positive for Brahman (Elzo and Wakeman, 1998), both as deviation from Angus. A positive value of **aa** for weaning weight was reported by Lema et al. (2011) and negative values for average pre-weaning daily gain were reported by Cardoso et al. (2008) and for pre-weaning gain by Carvalheiro et al. (2006). These effects considered Nellore as a deviation from Hereford. Kippert et al. (2008) studying 205 day and 550 day weights found negative values for both periods, weaning and post-weaning, even though neither the complementarity nor epistatic loss effects were considered. Cardoso et al. (2008), studying Nellore x Hereford crosses also found negative values of **aa** for all traits (WC, WP, WM, PC, PP, PM and SC).

The maternal breed additive effect (**am**) was positive for most of models and traits except for SC, showing that as the

Nellore genes proportion increase the calf performance also increase, but with a small scrotal circumference. Negative values of **am** for WC (model **ACE**), WP (models **ACHE, ACE** and **AHE**) and WM (models **ACE** and **AHE**) may indicate poorer performance in conformation, precocity and muscling at weaning for the Nellore genes. We did not find literature testing these models with these traits. Positive values of **am** for 205 day and 550 day weights were reported by Kippert et al. (2008) and for weaning weight by Lopes et al. (2010). Lema et al. (2011), using a model without a complementarity effect, found strongly negative values for Nellore breed as a deviation from Hereford. They suggest their environment was less restricted, explaining the better performance for the British breed compared to Zebu. All models presented negative values of **am** for SC. Cardoso et al. (2008), studying crosses between Hereford and Nellore found negative values of **am** only for post-weaning precocity.

Complementarity can be considered as what Kinghorn (1993) called “profit heterosis”. If we consider this effect as the joint action of two gene pools, as suggested by Pimentel et al. (2006), these results can be interpreted as additive interaction between two different traits, independent of dominance (heterosis) or epistasis. When we consider a tropical or a temperate environment, the change in performance when we move the genetic composition from 0.00 to 0.25 *Bos indicus* is not necessarily equivalent for the move from 0.75 to 1.00. What we are considering here is a quadratic effect between two breeds as suggested by

Table 7

Regression coefficients of breed additive and non-additive genetic effects of pre and post-weaning traits in Angus x Nellore crosses.

	ACHE		ACH		ACE		AHE		AC		AH		AE		A									
WG																								
aa	1.405	(0.323)	**	1.881	(0.302)	**	4.776	(0.319)	**	4.429	(0.323)	**	-1.504	(0.295)	**	1.810	(0.271)	**	-5.551	(0.295)	**	-2.535	(0.257)	**
am	2.111	(0.195)	**	4.322	(0.183)	**	1.513	(0.194)	**	2.957	(0.189)	**	6.085	(0.172)	**	4.238	(0.181)	**	6.970	(0.172)	**	4.739	(0.152)	**
ca	16.269	(1.605)	**	3.350	(1.079)	**	58.021	(0.798)	**			**	40.823	(0.768)	**			**			**			**
cm	36.701	(2.339)	**	5.190	(0.747)	**	90.059	(0.898)	**			**	27.964	(0.395)	**			**			**			**
ha	8.079	(0.365)	**	14.437	(0.245)	**			**	11.356	(0.182)	**			**	14.573	(0.174)	**			**			**
hm	3.872	(0.665)	**	15.026	(0.251)	**			**	21.465	(0.248)	**			**	16.346	(0.116)	**			**			**
ea	-3.821	(0.541)	**			**	-20.403	(0.347)	**	-10.531	(0.365)	**			**			**	8.096	(0.194)	**			**
em	-11.616	(0.559)	**			**	-24.588	(0.286)	**	-3.070	(0.165)	**			**			**	-5.002	(0.163)	**			**
PG																								
aa	-1.090	(0.405)	**	-4.681	(0.371)	**	-1.115	(0.397)	**	-0.172	(0.405)	ns	-10.265	(0.362)	**	-3.038	(0.326)	**	0.638	(0.357)	ns	-6.705	(0.303)	**
am	1.892	(0.235)	**	2.529	(0.217)	**	1.457	(0.232)	**	1.373	(0.227)	**	6.577	(0.202)	**	2.468	(0.214)	**	4.734	(0.204)	**	11.593	(0.179)	**
ca	21.586	(2.204)	**	17.294	(1.365)	**	55.084	(0.953)	**			**	52.577	(0.919)	**			**			**			**
cm	-12.820	(3.018)	**	-6.783	(0.889)	**	-6.212	(1.073)	**			**	-28.680	(0.467)	**			**			**			**
ha	6.112	(0.522)	**	12.215	(0.321)	**			**	13.145	(0.227)	**			**	14.567	(0.216)	**			**			**
hm	0.594	(0.858)	ns	-5.025	(0.293)	**			**	-2.627	(0.294)	**			**	-5.610	(0.135)	**			**			**
ea	-8.452	(0.706)	**			**	-15.337	(0.417)	**	-5.886	(0.438)	**			**			**	-13.226	(0.227)	**			**
em	1.496	(0.714)	*			**	-1.854	(0.338)	**	-0.510	(0.192)	**			**			**	-1.097	(0.190)	**			**
WC																								
aa	0.107	(0.014)	**	0.126	(0.013)	**	0.241	(0.013)	**	0.224	(0.014)	**	-0.002	(0.012)	ns	0.087	(0.011)	**	-0.099	(0.012)	**	-0.030	(0.011)	**
am	0.023	(0.008)	**	0.091	(0.008)	**	-0.011	(0.008)	ns	0.004	(0.008)	ns	0.160	(0.007)	**	0.069	(0.008)	**	0.122	(0.007)	**	0.099	(0.006)	**
ca	0.376	(0.067)	**	-0.399	(0.045)	**	1.490	(0.034)	**			**	0.819	(0.033)	**			**			**			**
cm	1.310	(0.097)	**	0.160	(0.031)	**	2.808	(0.037)	**			**	0.725	(0.017)	**			**			**			**
ha	0.222	(0.015)	**	0.471	(0.010)	**			**	0.251	(0.008)	**			**	0.406	(0.007)	**			**			**
hm	0.091	(0.028)	**	0.418	(0.010)	**			**	0.677	(0.010)	**			**	0.427	(0.005)	**			**			**
ea	-0.229	(0.023)	**			**	-0.737	(0.014)	**	-0.524	(0.015)	**			**			**	0.150	(0.008)	**			**
em	-0.423	(0.023)	**			**	-0.779	(0.012)	**	-0.131	(0.007)	**			**			**	-0.178	(0.007)	**			**
PC																								
aa	-0.123	(0.019)	**	-0.185	(0.018)	**	-0.062	(0.019)	**	-0.046	(0.019)	*	-0.412	(0.017)	**	-0.270	(0.016)	**	-0.261	(0.018)	**	-0.371	(0.015)	**
am	0.142	(0.012)	**	0.215	(0.011)	**	0.126	(0.012)	**	0.130	(0.012)	**	0.360	(0.010)	**	0.214	(0.011)	**	0.284	(0.010)	**	0.415	(0.009)	**
ca	0.190	(0.106)	ns	-0.918	(0.066)	**	1.526	(0.048)	**			**	0.955	(0.046)	**			**			**			**
cm	0.665	(0.139)	**	0.084	(0.043)	ns	1.425	(0.051)	**			**	-0.195	(0.024)	**			**			**			**
ha	0.336	(0.025)	**	0.648	(0.015)	**			**	0.385	(0.011)	**			**	0.526	(0.011)	**			**			**
hm	0.027	(0.040)	ns	0.113	(0.014)	**			**	0.346	(0.014)	**			**	0.077	(0.007)	**			**			**
ea	-0.326	(0.034)	**			**	-0.788	(0.020)	**	-0.529	(0.021)	**			**			**	-0.204	(0.011)	**			**
em	-0.235	(0.033)	**			**	-0.467	(0.016)	**	-0.089	(0.009)	**			**			**	-0.100	(0.009)	**			**
WP																								
aa	0.036	(0.015)	*	0.029	(0.014)	*	0.189	(0.014)	**	0.170	(0.015)	**	-0.092	(0.013)	**	-0.005	(0.012)	ns	-0.146	(0.014)	**	-0.099	(0.012)	**
am	-0.045	(0.010)	**	0.023	(0.009)	**	-0.105	(0.009)	**	-0.087	(0.009)	**	0.084	(0.008)	**	0.005	(0.009)	ns	0.038	(0.008)	**	0.038	(0.007)	**
ca	0.180	(0.073)	**	-0.914	(0.049)	**	1.144	(0.039)	**			**	0.311	(0.037)	**			**			**			**
cm	1.063	(0.103)	**	-0.191	(0.034)	**	3.149	(0.041)	**			**	0.635	(0.019)	**			**			**			**
ha	0.196	(0.016)	**	0.483	(0.011)	**			**	0.170	(0.009)	**			**	0.388	(0.008)	**			**			**
hm	0.200	(0.030)	**	0.528	(0.011)	**			**	0.770	(0.011)	**			**	0.442	(0.005)	**			**			**
ea	-0.305	(0.025)	**			**	-0.858	(0.016)	**	-0.709	(0.017)	**			**			**	0.116	(0.009)	**			**
em	-0.432	(0.025)	**			**	-0.919	(0.013)	**	-0.216	(0.007)	**			**			**	-0.261	(0.007)	**			**
PP																								

Table 7 (continued)

	ACHE		ACH		ACE		AHE		AC		AH		AE		A									
aa	-0.122	(0.022)	**	-0.195	(0.020)	**	0.000	(0.021)	ns	-0.020	(0.022)	ns	-0.442	(0.020)	**	-0.227	(0.020)	**	-0.394	(0.017)	**			
am	0.042	(0.015)	**	0.111	(0.014)	**	-0.015	(0.015)	ns	0.002	(0.014)	ns	0.290	(0.013)	**	0.118	(0.014)	**	0.192	(0.012)	**	0.385	(0.010)	**
ca	0.187	(0.120)	ns	-1.189	(0.075)	**	1.873	(0.060)	**				0.974	(0.056)	**									
cm	0.402	(0.155)	**	-0.153	(0.050)	**	1.728	(0.058)	**				-0.379	(0.030)	**									
ha	0.406	(0.027)	**	0.782	(0.017)	**				0.456	(0.014)	**				0.636	(0.013)	**						
hm	0.113	(0.044)	*	0.164	(0.015)	**				0.386	(0.016)	**				0.059	(0.008)	**						
ea	-0.410	(0.038)	**				-1.028	(0.023)	**	-0.658	(0.024)	**				-0.290	(0.012)	**						
em	-0.225	(0.037)	**				-0.607	(0.018)	**	-0.148	(0.011)	**				-0.156	(0.010)	**						
WM																								
aa	0.017	(0.014)	ns	0.011	(0.013)	ns	0.151	(0.014)	**	0.125	(0.014)	**	-0.092	(0.013)	**	-0.030	(0.012)	*	-0.199	(0.013)	**	-0.109	(0.011)	**
am	0.005	(0.009)	ns	0.082	(0.008)	**	-0.027	(0.009)	**	-0.016	(0.009)	ns	0.134	(0.008)	**	0.056	(0.008)	**	0.092	(0.008)	**	0.048	(0.007)	**
ca	0.089	(0.071)	ns	-0.882	(0.048)	**	0.886	(0.036)	**				0.174	(0.035)	**									
cm	1.248	(0.102)	**	0.130	(0.033)	**	3.211	(0.040)	**				0.931	(0.018)	**									
ha	0.178	(0.016)	**	0.415	(0.011)	**				0.131	(0.008)	**				0.314	(0.008)	**						
hm	0.161	(0.029)	**	0.496	(0.011)	**				0.771	(0.011)	**				0.481	(0.005)	**						
ea	-0.222	(0.024)	**				-0.741	(0.015)	**	-0.611	(0.016)	**							0.213	(0.009)	**			
em	-0.409	(0.024)	**				-0.851	(0.013)	**	-0.146	(0.007)	**				-0.191	(0.007)	**						
PM																								
aa	-0.206	(0.021)	**	-0.267	(0.019)	**	-0.144	(0.021)	**	-0.158	(0.021)	**	-0.461	(0.019)	**	-0.335	(0.017)	**	-0.293	(0.019)	**	-0.414	(0.016)	**
am	0.042	(0.013)	**	0.093	(0.012)	**	0.014	(0.013)	ns	0.022	(0.013)	ns	0.225	(0.011)	**	0.091	(0.012)	**	0.160	(0.011)	**	0.286	(0.010)	**
ca	0.092	(0.115)	ns	-0.836	(0.072)	**	1.421	(0.053)	**				0.851	(0.050)	**									
cm	0.551	(0.150)	**	0.026	(0.047)	ns	1.264	(0.056)	**				-0.245	(0.026)	**									
ha	0.333	(0.027)	**	0.596	(0.017)	**				0.368	(0.012)	**				0.488	(0.012)	**						
hm	0.007	(0.043)	ns	0.092	(0.015)	**				0.272	(0.015)	**				0.049	(0.007)	**						
ea	-0.261	(0.036)	**				-0.738	(0.022)	**	-0.443	(0.023)	**							-0.204	(0.012)	**			
em	-0.202	(0.036)	**				-0.426	(0.017)	**	-0.088	(0.010)	**				-0.093	(0.010)	**						
SC																								
aa	-1.589	(0.121)	**	-1.909	(0.107)	**	-1.649	(0.117)	**	-1.648	(0.121)	**	-2.010	(0.105)	**	-1.846	(0.087)	**	-1.776	(0.095)	**	-1.864	(0.073)	**
am	-0.889	(0.062)	**	-0.938	(0.052)	**	-0.904	(0.060)	**	-0.949	(0.059)	**	-0.984	(0.046)	**	-0.993	(0.051)	**	-0.943	(0.051)	**	-0.875	(0.042)	**
ca	1.187	(0.489)	*	1.156	(0.337)	**	1.039	(0.245)	**				1.736	(0.236)	**									
cm	-0.345	(0.797)	ns	-0.566	(0.215)	**	0.219	(0.295)	ns				-0.623	(0.109)	**									
ha	-0.092	(0.114)	ns	0.048	(0.078)	ns				0.151	(0.057)	**				0.250	(0.055)	**						
hm	0.197	(0.222)	ns	0.055	(0.074)	ns				0.095	(0.080)	ns				-0.014	(0.034)	ns						
ea	-0.367	(0.175)	*				-0.269	(0.115)	*	-0.198	(0.121)	ns							-0.142	(0.059)	*			
em	-0.037	(0.194)	ns				-0.172	(0.088)	ns	-0.082	(0.047)	ns				-0.098	(0.047)	*						

ns: non significant; **aa, am, ca, cm, ha, hm, ea, em**: direct and maternal breed additive genetic effects, direct and maternal complementarity, heterosis and epistatic loss non-additive genetic effects, respectively. **WG, WC, WP, WM**: weaning gain, conformation, precocity, muscling respectively; **PG, PC, PP, PM**: post-weaning gain, conformation, precocity, muscling respectively; **SC**: Scrotal circumference; standard error are in parenthesis.

* $P < 0.05$.

** $P < 0.01$.

Kinghorn (1993). The complementarity coefficient reaches its maximum value at $\frac{1}{2}$ Angus $\frac{1}{2}$ Nellore animals, which presents a complementarity coefficient of 0.25. According to Cardoso et al. (2008), if for a trait such as weaning gain, **am** is the additive effect due to the Nellore dam maternal instinct (defense and calf care), heat and parasites tolerance and ability to digest food with low nutritional value and turn it into milk with high solids, while (**1-am**) represents the maternal breed additive effect due to high feed intake and high conversion rate from the Angus breed. Thus **cm** ($=\mathbf{am}^*(1,0-\mathbf{am})$) represents an extra effect due to both gene pools (Cardoso et al., 2008). This may explain the significance for this effect for these two specific breeds.

Direct complementarity (**ca**) presented positive values for models **ACHE**, **ACE** and **AC**, but negative values for weaning and post weaning phenotypic scores using the **ACH** model (WC, WP, WM, PC, PP, PM). These negative values may imply that Nellore cows, although producing heavier calves may produce less harmonious calves in terms of conformation, precocity and musculature, both at weaning and post weaning. For the **ACHE** model, **ca** was not statistically significant for WM, PC, PP and PM. Cardoso et al. (2008) found negative values for all weaning traits and SC and positive values for post-weaning traits for Hereford x Nellore crosses. Carvalho et al. (2006) reported negative values for pre-weaning gain ($-65.38(3.78)$) for an equivalent model, also with Hereford x Nellore crosses. Lopes et al. (2010) reported a value of 21.82 for direct complementarity for weaning weight of Angus x Nellore crosses.

Maternal complementarity (**cm**) presented the highest magnitude effect for all traits and also the highest standard errors, followed by direct complementarity. These coefficients presented the highest FIV, especially for SC. For the **ACHE** model, **am** was 36.70 for WG and -12.82 for PG. Carvalho et al. (2006) reported a value of 61.38 for pre-weaning gain for Hereford X Nellore crosses when estimating **am** with ordinary least squares methodology and 11.94 when using ridge regression methodology. They assume that multicollinearity can cause these high values that have a difficult biological interpretation (Carvalho et al., 2006). **cm** ranged from 1.0 to 1.3 for weaning and 0.4–0.7 for post-weaning phenotypic scores with the **ACHE** model. Similar values (between 0.78 and 1.47 for WC, WP and WM) were reported by Cardoso et al. (2008) for Hereford x Nellore crosses. For Angus x Nellore crosses, Lopes et al. (2010) reported negative values for **cm** (-45.52 for weaning weight). It is difficult to find results for the complementarity effect for many traits in the literature, but it seems that the presented values are very high. Perhaps with other estimation methodology, as is the case of Carvalho et al. (2006) and Cardoso et al. (2008) who used ridge regression, these values would be smaller and more reliable.

Unlike the complementarity, heterosis is widely studied and interest is increasing in epistatic loss. Lopes et al. (2010), Vergara et al. (2009b), Kippert et al. (2008), Elzo and Wakeman (1998) estimated heterosis and/or epistatic loss in Angus x Nellore or Angus x Brahman or Angus X Zebu crosses; Lema et al. (2011), Cardoso et al. (2008), Carvalho et al. (2006), Pimentel et al. (2006), Piccoli et al. (2002), Arthur et al. (1999) worked on heterosis and/or epistatic loss with Hereford x Nellore or Hereford x Brahman crosses and

Bueno et al. (2011), Roso et al. (2005a), Demeke et al. (2003a, 2003b) and Abdel-Aziz (2003) studied heterosis and/or epistasis with another crossbreed cattle. These authors also tested different models and/or methodologies to estimate non-additive genetic effects. The range for direct and maternal heterosis effects is wide and usually positive. When estimates of heterosis effect are negative, it usually has a very low magnitude. For epistatic loss, the estimates frequently changed from negative to positive.

The direct heterosis effect (**ha**) was positive and statistically significant for all traits, except for SC, in **ACHE** and **ACH**. When complementarity or epistatic loss were included in the model, but not both (models **AHE** and **ACH**), estimated values of **ha** remained close one to each other, but when compared to the **ACHE** model, the estimated values of **ha** are around half the previous value. It is possible that the estimates for complementarity or epistasis decrease heterosis estimates, because when the model does not include complementarity and/or epistatic loss effects, heterosis estimates were much higher. In the same manner, when the model does not include heterosis, complementarity effects increased significantly. This probably refers to what Dickerson (1973) commented as recombination effects between joint gametes which may be confounded with heterosis effects. These effects are then estimated as heterosis or complementarity, if the complementarity is included in the model, and represent the sum of all interactions for each locus and among every gene that affects the trait.

Maternal heterosis was not statistically significant for SC in all tested models. For the **ACHE** model, **hm** was not statistically significant for most post-weaning traits (PG, PC and PM). For all other situations, **hm** was statistically significant. **ha** was positive for all models and traits except for PG in the **ACH**, **AHE** and **AH** models. Lema et al. (2011), Lopes et al. (2010), Cardoso et al. (2008) and Kippert et al. (2008) found positive values for direct and maternal heterosis and greater values for **hm** than **ha**.

Epistatic effects are understood as interaction of genes at different loci. When breeds were formed, benefic interactions between genes were selected and produced linkage disequilibrium among them. When breeds are crossed, these interactions may be broken. Crossbred animals may be out of harmony and epistasis, if important, is a negative effect (Kinghorn, 1993). Recombination loss is a measure to attempt to all deviations from linear association of heterosis with degree of heterozygosity (Dickerson, 1973) and “epistatic loss” is “proportional to the probability that two non-allelic genes in the diploid individual are from different breeds” (Kinghorn, 1980). What we are estimating here are the interactions between non-allelic genes due to crossbred mating.

Estimates for direct epistatic loss effect were negative and statistically significant for all traits, except for weaning traits in the **AE** model and SC in the **AHE** model. The estimate for the maternal component of epistatic loss effect for post-weaning gain was positive and negative for all other traits and models. The epistatic loss effect for scrotal circumference was statistically significant ($P < 0.05$) only for the **AE** model. Cardoso et al. (2008) studying Hereford x Nellore crosses, found positive estimates to epistatic loss for all weaning traits and negative values for post-weaning traits, as found here in the **AE** model. Lema et al. (2011) found negative

effects for direct and positive for maternal components for all traits. The negative epistatic loss effect may be explained as the broken positive interaction, if they exist.

Even if most full models are significantly different from their reduced versions and the most tested effects are significant, when we look at the rank of animal EBVs, we find 70% of coincidence in the first 10% for all tested models.

4. Conclusion

Considering the high significance of most comparisons between models and their reduced versions we conclude that the best models are ACHE and AHE. ACHE includes all effects and they were mostly significant but this model has many effects with extremely high estimated values, which may have been caused by a collinearity of the predictor variable. We suggest further studies around collinearity in the specific case of this model, perhaps using the ridge regression methodology can solve this. AHE model proved extremely interesting, especially with regard to minor estimated standard errors for the effects of heterosis and epistasis compared with the ACHE model with FIV lower than ten for all traits, except SC. The fixed genetic effects of breed, complementarity, heterosis and epistatic loss effects are really acting behind the models. If the interaction between different alleles effectively exists, even if their magnitudes are unstable, we must include them in the models to evaluate crossbred animals, under a risk of selection bias. The results depend on the breeds and environment where the animals are maintained. The results presented here are from Angus x Nelore crosses, reared on extensive pastures in South America.

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References

- Abdel-Aziz, M., 2003. Estimation of additive, maternal and non-additive genetic effects of preweaning growth traits in a multibreed beef cattle project. *Anim. Sci.* 74, 169–179.
- Arthur, P.F., Hearnshaw, H., Stephenson, P.D., 1999. Direct and maternal additive and heterosis effects from crossing *Bos indicus* and *Bos taurus* cattle: cow and calf performance in two environments. *Livest. Prod. Sci.* 57, 231–241.
- Bertoli, C.D., 1991. Sistema Cruza – Controle de produção e avaliação dos valores genéticos dentro de uma população bovina sintética M. Sc. Dissertation. Universidade Federal do Rio Grande do Sul, Porto Alegre, RS233.
- Bueno, R.S., Torres, R.A., Ferraz, J.B.S., Lopes, P.S., Eler, J.P., Almeida e Silva, M., Euclides, R.F., Mattos, E.C., 2011. Inclusão da epistasia em modelo de avaliação genética de bovinos de corte compostos. *Arq. Bras. Med. Vet. Zootec.* 63, 948–953.
- Bueno, R.S., Torres, R.D.A., Ferraz, J.B.S., Lopes, P.S., Eler, J.P., Mourão, G.B., Almeida e Silva, M., Mattos, E.C., 2012. Estimation methods of non-additive effects for characteristics of weight and scrotal circumference in crossbred beef cattle. *R. Bras. Zootec.* 41, 1140–1145.
- Cardoso, F.F., Tempelman, R.J., 2004. Hierarchical Bayes multiple-breed inference with an application to genetic evaluation of a Nelore–Hereford population. *J. Anim. Sci.* 82, 1589–1601.
- Cardoso, V., Queiroz, S.A., Fries, L.A., 2008. Estimates of genotypic effects on pre and post-weaning performance in Hereford × Nelore populations. *Rev. Bras. Zootec.* 37, 1763–1773.
- Carvalho, R., Pimentel, E.C.G., Cardoso, V., Queiroz, S.A., Fries, L.A., 2006. Genetic effects on preweaning weight gain of Nelore–Hereford calves according to different models and estimation methods. *J. Anim. Sci.* 84, 2925–2933.
- Cunha, E.E., Euclides, R.F., Torres, R.D., Sarmento, J.L.R., Carneiro, P.L.S., Carneiro, A.P.S., 2009. Impacts of ignoring the non-additive genetic effects of dominance on animal genetic evaluation. *Rev. Bras. Zootec.* 38, 2354–2361.
- Demeke, S., Naser, F.W.C., Schoeman, S.J., 2003a. Early growth performance of *Bos taurus* × *Bos indicus* cattle crosses in Ethiopia: evaluation of different crossbreeding models. *J. Anim. Breed. Genet.* 120, 39–50.
- Demeke, S., Naser, F.W.C., Schoeman, S.J., 2003b. Early growth performance of *Bos taurus* × *Bos indicus* cattle crosses in Ethiopia: estimation of individual crossbreeding effects. *J. Anim. Breed. Genet.* 120, 245–257.
- Dickerson, G.E., 1973. Inbreeding and heterosis in animals. In: *Proceedings of the Symposium on Animal Breeding and Genetics in Honor of Dr. J.L. Lush, Blacksburg*, p. 54–77.
- Elzo, M., Wakeman, D.L., 1998. Covariance components and prediction for additive and nonadditive preweaning growth genetic effects in an Angus–Brahman multibreed herd. *J. Anim. Sci.* 76, 1290–1302.
- Falconer, D.S., Mackay, T.F.C., 1996. *Introduction to Quantitative Genetics*, 4th edition Longman group, Essex, UK.
- Fries, L., Johnston, D., Hearnshaw, H., Graser, H., 2000. Evidence of epistatic effects on weaning weight in crossbred beef cattle. *Asian-Aus J. Anim. Sci.* 13B, 242.
- Fries, L.A., Schenkel, F.S., Roso, V.M., Brito, F.V., Severo, J.L.P., and Piccoli, M.L., 2002. “Epistazogosity” and epistatic effects. In: *Proceedings of the 7th World Congress on Genetics Applied to Livestock Production*, August 19–23, Montpellier, 2002.
- Gregory, K.E., Cundiff, L.V., Koch, R.M., 1991. Breed effects and heterosis in advanced generations of composite populations for preweaning traits of beef cattle. *J. Anim. Sci.* 69, 947–960.
- Kinghorn, B.P., 1980. The expression of “Recombination Loss” in quantitative traits. *J. Anim. Breed. Genet.* 97, 138–143.
- Kinghorn, B.P., 1993. *Design of Livestock Breeding Programs*. AGBU–UNE, 187–203.
- Kippert, C.J., Roberto, P., Rorato, N., Lopes, J.S., Weber, T., Boligon, A.A., 2008. Direct, maternal additive genetic and heterozygotic effects for pre- and post-weaning traits in a multi-breed Aberdeen Angus–Nelore population. *Rev. Bras. Zootec.* 37, 1383–1391.
- Legarra, a., Bertrand, J.K., Strabel, T., Sapp, R.L., Sánchez, J.P., Misztal, I., 2007. Multi-breed genetic evaluation in a Gelbvieh population. *J. Anim. Breed. Genet.* 124, 286–295.
- Lema, O.M., Gimeno, D., Dionello, N.J.L., Navajas, E.A., 2011. Pre-weaning performance of Hereford, Angus, Salers and Nelore crossbred calves: individual and maternal additive and non-additive effects. *Livest. Sci.* 142, 288–297.
- Lopes, J.S., Rorato, P.R.N., Weber, T., Araújo, R.O., de, Dornelles, M.D.A., Comin, J.G., 2010. Pre-weaning performance evaluation of a multi-breed Aberdeen Angus × Nelore population using different genetic models. *Rev. Bras. Zootec.* 39, 2418–2425.
- Madsen, P., Jensen, J., 2000. *A User's Guide to DMU. A Package for Analysing Multivariate Mixed Models*. Danish Inst. of Agric. Sci. (DIAS), Tjele, Denmark.
- Pimentel, E.C.G., Queiroz, S.A., Carvalho, R., Fries, L.A., 2006. Estimates of genetic effects in crossbred calves by different models and estimation methods. *Rev. Bras. Zootec.* 35, 1020–1027.
- Piccoli, M.L.; Roso, V.M.; Brito, F.V., Severo, J.L.P., Schenkel, F.S. and Fries, L.A., 2002. Additive, complementarity (additive*additive), dominance, and epistatic effects on preweaning weight gain of Hereford x Nelore calves. In: *Proceedings of the 7th World Congress on Genetics Applied to Livestock Production*, 2002, Montpellier, p.275–278.
- Regazzi, A.J., Silva, C.H.O., 2004. Teste para verificar a igualdade de parâmetros e a identidade de modelos de regressão não-linear. i. dados no delineamento inteiramente casualizado. *Rev. Mat. E Estat.* 22 (3), 33–45.
- Roso, V.M., Schenkel, F.S., Miller, S.P., 2004. Degree of connectedness among groups of centrally tested beef bulls. *Can. J. Anim. Sci.* 84, 37–47.
- Roso, V.M., Schenkel, F.S., Miller, S.P., Schaeffer, L.R., 2005a. Estimation of genetic effects in the presence of multicollinearity in multibreed beef cattle evaluation. *J. Anim. Sci.* 83, 1788–1800.
- Roso, V.M., Schenkel, F.S., Miller, S.P., Wilton, J.W., 2005b. Additive, dominance, and epistatic loss effects on preweaning weight gain of crossbred beef cattle from different *Bos taurus* breeds. *J. Anim. Sci.* 83, 1780–1787.

- Schabenberger, O., Pierce, F.J., 2002. *Contemporary Statistical Models for the Plant and Soil Sciences*. Ed Taylor and Francis Group, New York.
- Schenkel, F.S., 1993. *Calculo das Heterozigoses*. 1993. GenSys Consultores Associados, Porto Alegre3.
- Theunissen, A., Scholtz, M.M., Neser, F.W.C., MacNeil, M.D., 2013. Crossbreeding to increase beef production: additive and non-additive effects on weight traits. *S. Afr. J. Anim. Sci.* 43, 143–152.
- VanRaden, P.M., 2006. Predicting genetic interactions within and across breeds. In: *Proceedings of the 8th World Congress on Genetics Applied to Livestock Production*, 2006.
- Vergara, O.D., Ceron-Muñoz, M.F., Arboleda, E.M., Orozco, Y., Ossa, G.A., 2009a. Direct genetic, maternal genetic, and heterozygosity effects on weaning weight in a Colombian multibreed beef cattle population. *J. Anim. Sci.* 87, 516–521.
- Vergara, O.D., Elzo, M.A., Ceron-Muñoz, M.F., Arboleda, E.M., 2009b. Weaning weight and post-weaning gain genetic parameters and genetic trends in a Blanco Orejinegro–Romesinuano–Angus–Zebu multibreed cattle population in Colombia. *Livest. Sci.* 124, 156–162.