Direct and maternal breed additive and heterosis effects on growth traits of beef cattle raised in southern Brazil[1]

Willian S. Leal,[†,2] Michael D. MacNeil,[‡,‖] Henry Gomes Carvalho,[$] Ricardo Zambarda Vaz,[†] and Fernando F. Cardoso[†,$]

[†]Department of Animal Science, Federal University of Pelotas, Pelotas – Rio Grande do Sul, 96010-900, Brazil; [‡]Delta G, 145 Ice Cave Rd., Miles City, Montana, MT; [‖]Department of Animal Wildlife and Grassland Sciences, University of the Free State, PO Box 339, Bloemfontein 9300, South Africa; and [$]Embrapa Pecuária Sul, Rodovia BR-153, Km 632,9 Vila Industrial, Zona Rural, Caixa Postal 242, CEP 96401-970, Bagé, Rio Grande do Sul, Brazil

ABSTRACT: The objective of this study was to compare growth from birth to slaughter of different breed groups that were raised in Rio Grande do Sul, Brazil and estimate the consequent breed additive and heterosis effects. Caracu (C), Hereford (H), and Nelore (N) sires were mated with Angus (A) dams, and A sires were mated with H and N dams to produce a first generation of crossbred progeny that was contemporary with purebred A, H, and N calves. Heifers from this first generation (G_1) were mated with Brangus (**BN**) and Braford (**BO**) sires to produce a second generation (G_2) of progeny. Data were analyzed to estimate breed group means, individual and maternal breed additive effects, and heterosis effects on birth weight, weaning weight, preweaning average daily gain, yearling weight, postweaning average daily gain, fattening phase initial weight (around 19 mo), final weight (around 24 mo), average daily gain in the fattening phase, and age at slaughter. In general, crossbred calves outperformed purebred calves. Angus-N and CA crossbred cows weaned heavier calves. Individual taurine-indicine heterosis (Z) significantly increased weaning weight. The AN, NA, and CA steers were heaviest at yearling, whereas NA, CA, AN, and HA had the greatest final weights. However, AH steers were 1 mo older at slaughter than NA contemporaries. Taurine breed effects on postweaning traits and final weight were greater than for N. Maternal breed effects on birth weight and average daily gain in the fattening phase were greater for A and H than for N. In conclusion, heterosis effects were sufficiently large for use of N to be recommended as a component of such systems, despite their relatively low-breed additive effects compared with taurine breeds. Moreover, germplasm from the tropically adapted *Bos taurus* C may be particularly useful when increased milk production is desired. With the breed and heterosis effects derived in the present study, it is possible to predict the performance and infer which breed and breed crosses will perform better in crossbreeding systems designed for the subtropical conditions of southern Brazil and similar regions.

Key words: crossbreeding, indicine, performance, steers, taurine

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[2]Corresponding author: wl.zootecnia@hotmail.com

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INTRODUCTION

Use and benefits of crossbreeding have been widely reported (e.g., Gregory *et al.*, 1966; Cundiff, 1970; Williams *et al.*, 2010). Crossbred animals grow more rapidly and are better adapted, particularly when the parental breeds are genetically distant (e.g., *Bos Taurus* and *Bos indicus* crosses). This better performance occurs due to the combination of breed complementarity of breed additive effects and heterosis (Gregory *et al.*, 1966; Cundiff, 1970). In addition to the genetic effects on individual performance, heterosis also enables crossbred dams to increase milk production and thus provides a maternal environment that supports greater preweaning growth.

Dickerson (1969, 1973) presented mathematical models to partition breed groups into their genetic components allowing estimation of direct and maternal breed additive effects, and individual and maternal heterosis. Henderson (1977) proposed estimating these effects using multiple regression methods and using them in prediction of untested crosses. Robison *et al.* (1981) and MacNeil *et al.* (1982) provide early examples of the use of these approaches. However, the use of this approach to design optimal breed combinations and crossbreeding systems entails the availability of reliable parameter estimates under the local conditions and systems where the crossbred animals will be raised. Therefore, the aim of this study was to partition variation among breed groups into breed additive and heterosis effects on growth traits that were recorded from birth to slaughter of beef cattle that had been raised in southern subtropical part of Brazil.

MATERIALS AND METHODS

All experimental procedures that involved animals were approved by the Committee for Ethics in Animal Experimentation from the Federal University of Pelotas (Pelotas, Brazil; Process CEEA No. 8250-2015).

This study was conducted from 2006 to 2016 at Embrapa Pecuária Sul Research Center of the Brazilian Agricultural Research Corporation (Embrapa), located in the city of Bagé, Rio Grande do Sul State, Brazil. The regional climate is subtropical, according to Koppen classification, with precipitation evenly distributed throughout the year (1350 mm average). Numerous environmental stressors include cold during winter (min. 9.4 °C to max. 16 °C on average), heat during summer (min. 19.5 °C to max. 27.8 °C on average), infestation of *Erasgostis plana* weed in pastures, and external parasites, particularly *Rhipicephalus microplus* ticks.

Data

Caracu (C—taurine), Hereford (H—taurine), and Nelore (N—indicine) sires were mated with Angus (A—taurine) dams, and A sires were mated with H and N dams to produce a first generation of crossbred progeny that was contemporary with purebred A, H, and N calves. Heifers from this first generation (G_1) were mated to advanced generation Brangus (**BN**—composite 3/8 N 5/8 A) and Braford (**BO**—composite 3/8 N 5/8 H) sires to produce a second generation (G_2) of progeny. Sires were chosen to represent commercial seedstock from locally available semen and herd clean up bulls. There were 14 A, 8 H, 8 C, 6 BN, 2 BO, and 9 N sires and 147 A, 73 H, and 58 N cows. These cows were kept in the herd as long as they were calving, allowing for a single failure during their productive lives. All animals of the different breed compositions were managed as a single herd. Males were castrated at weaning and heifers were exposed to bulls at 2 yr of age.

Body weights were recorded at birth (BW—occurred between September and December), weaning at approximately 7 mo of age (WW), long-yearling at approximately 18 mo of age (W18), at the beginning of a fattening phase (around 19 mo), and at slaughter (around 24 mo). Average daily gain (ADG) was calculated from birth to weaning, from weaning to yearling, and during fattening phase. Males and females were managed together until weaning, and then males were backgrounded in native pasture. In 2008 and 2009, castrated males were fattened on cool-season pasture. In 2010 and 2011, the steers were fattened in cool-season pasture or in a feedlot. A minimum of 3 mm of rib-eye fat thickness—measured by ultrasound—was used as a criterion to determine harvest point. All genetic groups were represented in both feeding systems. Replacement females were raised exclusively on native pastures. Performance of G_2 calves was recorded only until they were weaned.

Statistical Analyses

Data were analyzed in R Package (R Core Team, 2017) using the following model:

$$Y_{ijklm} = \mu + BG_i + G_j + CA_k + CA_k^2 + DA_l + DA_l^2 + e_{ijklm}$$

In this model, Y_{ijk} is an observation from the kth calf of the ith breed group (BG_i) that was reared in the jth contemporary group (G_j), with its kth age and lth age of its dam equal to CA_k and DA_l, respectively, and e_{ijklm} is a random deviation $(0, \sigma_e^2)$ of the observation from its expectation given the model. Here, G is defined by the season (before or after Julian day 292) and year of birth of the calf and its sex. The DA effects were only included in the analyses of preweaning traits.

Constraining individual and maternal breed additive effects of Nelore to zero was necessary in order to obtain a unique solution, when the BG effects were decomposed in a series of linear genetic coefficient effects as follows:

$$BG = b_1 g_A^i + b_2 g_C^i + b_3 g_H^i + b_4 h_t^i + b_5 h_z^i + b_6 g_A^m + b_7 g_C^m + b_8 g_H^m + b_9 h_t^m + b_{10} h_z^m$$

In the foregoing equation, b_i are breed additive effects of Angus, Caracu, and Hereford, respectively, for i = 1, 2, and 3; estimates of individual heterosis as expressed by taurine crosses and crosses of taurine and indicine breeds, respectively, for i = 4 and 5; maternal breed additive effects of Angus, Caracu, and Hereford, respectively, for i = 6, 7, and 8; and maternal heterosis effects as expressed by taurine crosses and crosses of taurine and indicine breeds, respectively, for i = 9 and 10. g^i represent the breed proportions for A = Angus (g_A^i), C = Caracu (g_C^i), and H = Hereford (g_H^i) that define the breed composition of calves, and likewise, g^m represent the breed proportions of the dams (A, C, and H) of calves. Following the work of Gregory and Cundiff (1980), individual and maternal heterosis effects were assumed proportional to expected heterozygosity of the individual and its dam (h^i and h^m, respectively). The heterosis effects were further partitioned into whether the heterozygosity resulted from the combination of alleles from 2 taurine breeds (subscript t) or from a taurine breed and an indicine breed (subscript z). Genetic expectations of each BG are shown in Table 1. Predicted

Table 1. Fractional coefficients of breed effects for genetics groups in the study: g^i = individual additive effect, g^i = maternal additive effect, h^i = individual heterosis, h^m = maternal heterosis; with subscripts A = Angus, H = Hereford, C = Caracu, N = Nelore, BO = Braford, BN = Brangus, t = taurine breed crosses, and z = taurine-indicine crosses

Genetics group[1]	Breed and heterosis effects											
	g_A^i	g_H^i	g_C^i	g_N^i	h_t^i	h_z^i	g_A^m	g_H^m	g_C^m	g_N^m	h_t^m	h_z^m
Purebred												
A	1	0	0	0	0	0	1	0	0	0	0	0
H	0	1	0	0	0	0	0	1	0	0	0	0
N†	0	0	0	1	0	0	0	0	0	1	0	0
G_1												
CA	0.5	0	0.5	0	1	0	1	0	0	0	0	0
HA	0.5	0.5	0	0	1	0	1	0	0	0	0	0
NA	0.5	0	0	0.5	0	1	1	0	0	0	0	0
AH	0.5	0.5	0	0	1	0	0	1	0	0	0	0
AN	0.5	0	0	0.5	0	1	0	0	0	1	0	0
G_2*												
(BN)A	0.8125	0	0	0.1875	0	0.375	1	0	0	0	0	0
(BO)A	0.5	0.3125	0	0.1875	0.625	0.375	1	0	0	0	0	0
(BN)CA	0.5625	0	0.25	0.1875	0	0.375	0.5	0	0.5	0	1	0
(BO)CA	0.25	0.3125	0.25	0.1875	0.3125	0.375	0.5	0	0.5	0	1	0
(BN)HA	0.5625	0.25	0	0.1875	0.3125	0.375	0.5	0.5	0	0	1	0
(BO)HA	0.25	0.5625	0	0.1875	0.3125	0.375	0.5	0.5	0	0	1	0
(BN)NA	0.5625	0	0	0.4375	0	0.5	0.5	0	0	0.5	0	1
(BO)NA	0.25	0.3125	0	0.4375	0.3125	0.5	0.5	0	0	0.5	0	1
(BN)AH	0.5625	0.25	0	0.1875	0.3125	0.375	0.5	0.5	0	0	1	0
(BO)AH	0.25	0.5625	0	0.1875	0.3125	0.375	0.5	0.5	0	0	1	0
(BN)H	0.3125	0.5	0	0.1875	0.625	0.375	0	1	0	0	0	0
(BO)H	0	0.8125	0	0.1875	0	0.375	0	1	0	0	0	0
(BN)AN	0.5625	0	0	0.4375	0	0.5	0.5	0	0	0.5	0	1
(BO)AN	0.25	0.3125	0	0.4375	0.3125	0.5	0.5	0	0	0.5	0	1
(BN)N	0.3125	0	0	0.6875	0	0.625	0	0	0	1	0	0
(BO)N	0	0.3125	0	0	0	0.625	0	0	0	1	0	0

[1]Breed of sire is identified by the first symbol in crossbred groups.

†Nelore breed effects were set equal to zero in the model in order to obtain a unique solution.

*Second generation.

means for breed groups and crossbreeding systems were estimated with the R contrast function (Max *et al.*, 2013).

For postweaning traits, the model did not include maternal heterosis because the performance of G_2 calves was not recorded after weaning. The interaction of sex and genetic group was also evaluated in preliminary analyses but was discarded because it was not significant ($P > 0.05$).

RESULTS

Breed Additive and Heterosis Effects

For the 3 preweaning traits, effects of individual and maternal heterosis were consistently greater in indicine × taurine crosses than in crosses among taurine breeds (Table 2). The maternal-breed additive effects indicated that N dams suppressed birth weight in comparison with the taurine dams, which had similar maternal effect. The C maternal breed additive effect indicates that C dams may provide an environment for greater weaning weight than the other breeds. During the postweaning period (Table 3), the individual breed additive effects indicate greater growth potential for A, C, and H than for N, with the former breeds being similar to each other. Both taurine-taurine and taurine-indicine individual heterosis effects also increased growth, with the latter effects again being substantially greater than the former. The maternal breed additive effect of H on W18 was negative ($P < 0.01$).

Individual and maternal breed additive effects of A and H on ADG during the fattening period were positive, as were the individual breed additive effects of all 3 taurine breeds on initial and final weight (Table 3). As in the postweaning period, both taurine-taurine and taurine-indicine individual heterosis effects also increased growth during the finishing period. Taurine breed effects were positive and significant for ADG in fattening phase. Individual breed effect A increased age at slaughter as deviation from N, with taurine × indicine heterosis decreasing age at slaughter. There were unexpected maternal breed additive effects of A on final weight and A and H on ADG during the finishing period.

Genetic Group Performance Differences

Birth weight ranged from 28.89 to 36.63 kg (Table 4). The NA animals had 16.9% greater birth weight when compared with their parental breeds. In G_2, the use of terminal sires on HA and CA dams increased birth weight. The use of Angus as dam breed in the crossbreeding with Nelore also resulted in increased birth weight. Preweaning ADG (range: 0.558 to 0.817 kg/day) was greater for calves born to NA, AN, and CA dams that were mated with BN and BO sires. Purebred (A, H, C, and N), and G_1 and G_2 taurine-taurine crossbred calves grew more slowly in preweaning phase. Thus, calves born to NA and AN dams mated with BN and BO sires had the greatest weaning weights. Calves from CA dams were somewhat lighter at weaning than those from NA and AN dams. Purebred, G_1 taurine crossbred, and purebred dams mated with BN and BO, weaned the lightest calves.

During the postweaning phase, purebred calves grew less rapidly compared with the crossbred animals (Table 5) and were the purebreds H had the greatest and N the least ADG. At 18 mo of age, AN and NA were heaviest, followed by CA and HA.

Table 2. Estimates of individual and maternal breed effects and heterosis effects on preweaning growth traits

	Preweaning		
Effects[1]	Birth weight kg	Weaning weight kg	ADG kg/d
g^i_A	−0.06 ± 1.48	3.78 ± 7.17	0.04 ± 0.03
g^i_H	0.71 ± 1.69	2.06 ± 8.16	0.03 ± 0.04
g^i_C	−2.87 ± 2.07	11.45 ± 9.68	0.11 ± 0.04*
g^m_A	4.92 ± 0.99***	0.45 ± 4.91	−0.03 ± 0.02
g^m_H	5.25 ± 1.19***	−8.44 ± 5.90	−0.09 ± 0.03**
g^m_C	5.79 ± 1.61***	17.16 ± 7.82*	0.04 ± 0.03
h^i_t	0.81 ± 0.61	4.31 ± 2.91	0.02 ± 0.01
h^i_z	2.86 ± 0.73***	21.75 ± 3.49***	0.11 ± 0.01***
h^m_t	0.61 ± 0.53	10.48 ± 2.65***	0.05 ± 0.01***
h^m_z	1.19 ± 0.54*	27.05 ± 2.70***	0.13 ± 0.01***

[1]g^i = individual breed effect; g^i = maternal breed effect; h^i = individual heterosis; h^m = maternal heterosis; with subscripts A = Angus, C = Caracu, H = Hereford, t = taurine breed crosses, and z = taurine-indicine crosses.

*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

Table 3. Individual and maternal breed effects, individual and maternal heterosis for weight at yearling (W18), postweaning ADG, and fattening phase growth traits

	Postweanning[1]		Fattening phase[2]			
Effects[3]	W18 kg	ADG kg	Initial weight[4] kg	Final weight[5] kg	ADG kg	Age at slaughter months
g_A^i	24.35 ± 9.79*	0.09 ± 0.02***	0.14 ± 13.44	34.42 ± 14.60*	0.15 ± 0.05**	0.74 ± 0.28**
g_H^i	36.99 ± 12.25**	0.12 ± 0.02***	26.25 ± 15.10	50.77 ± 16.33**	0.16 ± 0.06**	0.17 ± 0.32
g_C^i	56.56 ± 13.84***	0.16 ± 0.03***	45.67 ± 17.44**	63.43 ± 19.06**	−0.01 ± 0.07	−0.42 ± 0.38
g_A^m	−5.48 ± 6.91	−0.04 ± 0.01*	18.33 ± 9.38	26.72 ± 9.98**	0.09 ± 0.04**	−0.35 ± 0.20
g_H^m	−17.08 ± 9.48	−0.03 ± 0.02	−1.40 ± 12.11	19.74 ± 12.91	0.14 ± 0.05**	0.06 ± 0.26
h_t^i	17.40 ± 4.56***	0.03 ± 0.01***	25.33 ± 6.31***	22.67 ± 7.04**	0.07 ± 0.03**	−0.07 ± 0.14
h_z^i	63.19 ± 4.86***	0.12 ± 0.01***	76.66 ± 6.27***	67.26 ± 7.50***	0.07 ± 0.03**	−0.90 ± 0.16***

[1]Steers and heifers.

[2]Just steers.

[3]g^i = individual breed effect; g^i = maternal breed effect; h^i = individual heterosis; h^m = maternal heterosis; with subscripts A = Angus, H = Hereford, C = Caracu, t = taurine breed crosses, and z = taurine-indicine crosses.

[4]Age around 19 mo.

[5]Age around 24 mo.

*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

Table 4. Estimated means and standard errors for preweaning traits of the genetic groups that were evaluated

		Birth weight kg		Weaning weight kg	
Genetic group[1]	*N*		*n*		ADG kg
Purebred					
A	67	33.7 ± 0.5 (19)	65	154.9 ± 2.6 (20)	0.62 ± 0.02 (19)
H	43	34.8 ± 0.7 (13)	43	144.2 ± 3.6 (24)	0.56 ± 0.02 (24)
N	35	28.9 ± 0.8 (24)	31	150.6 ± 4.5 (22)	0.61 ± 0.02 (20)
G_1					
CA	75	33.1 ± 0.6 (20)	74	163 ± 2.9 (16)	0.68 ± 0.02 (15)
HA	56	34.9 ± 0.6 (12)	55	158.3 ± 2.9 (18)	0.62 ± 0.02 (18)
NA	46	36.6 ± 0.6 (1)	43	174.7 ± 3.4 (7)	0.71 ± 0.02 (8)
AH	42	35.3 ± 0.6 (11)	40	149.4 ± 3.2 (23)	0.58 ± 0.02 (23)
AN	39	31.7 ± 0.7 (21)	37	174.3 ± 3.7 (8)	0.74 ± 0.02 (7)
G_2					
(BN)A	58	34.8 ± 0.4 (14)	55	162.3 ± 2 (17)	0.66 ± 0.02 (17)
(BO)A	33	35.6 ± 0.4 (9)	26	164.5 ± 2.2 (15)	0.68 ± 0.02 (16)
(BN)H	42	36 ± 0.5 (6)	38	155.2 ± 2.8 (19)	0.61 ± 0.02 (21)
(BO)H	10	35.8 ± 0.6 (8)	9	152 ± 3.1 (21)	0.59 ± 0.02 (22)
(BN)N	23	30.6 ± 0.5 (23)	22	165.4 ± 3 (13)	0.70 ± 0.02 (9)
(BO)N	7	30.9 ± 0.6 (22)	7	164.9 ± 3.2 (14)	0.69 ± 0.02 (10)
(BN)CA	108	35.4 ± 0.4 (10)	97	184.4 ± 2.6 (6)	0.77 ± 0.02 (6)
(BO)CA	45	35.9 ± 0.5 (7)	34	185.2 ± 2.9(5)	0.78 ± 0.01 (5)
(BN)HA	86	36.1 ± 0.4 (4)	73	169.3 ± 2.6 (9)	0.69 ± 0.02 (11)
(BO)HA	36	36.3 ± 0.5 (2)	28	168.7 ± 2.7 (11)	0.69 ± 0.02 (13)
(BN)NA	97	33.9 ± 0.4 (17)	89	190.9 ± 2.4 (3)	0.81 ± 0.02 (3)
(BO)NA	33	34.4 ± 0.4 (15)	27	191.7 ± 2.6 (1)	0.82 ± 0.02 (1)
(BN)AH	43	36.1 ± 0.4 (5)	39	169.3 ± 2.6 (10)	0.69 ± 0.02 (12)
(BO)AH	13	36.3 ± 0.5 (3)	11	168.7 ± 2.7 (12)	0.69 ± 0.02 (14)
(BN)AN	54	33.9 ± 0.4 (18)	50	190.9 ± 2.5 (4)	0.81 ± 0.02 (4)
(BO)AN	19	34.4 ± 0.4 (16)	15	191.7 ± 2.6 (2)	0.82 ± 0.02 (2)

Ranking of groups is given in parentheses.

[1]A = Angus; C = Caracu; H = Hereford; N = Nelore; BO = Braford; BN = Brangus; Breed of sire is identified by the first symbol in crossbred groups.

As would be expected from the 18-mo weights, initial weights going into the finishing phase were greater for NA and AN compared with the other groups (Table 5) and 22% superior to the A and N means. The CA steers showed superior initial weights compared with the purebreds (A, H, and

Table 5. Estimated means and standard error for yearling and fattening phase traits

Genetic group[3]	N	Yearling[1]		n	Fattening phase[2]			
		W18 kg	ADG kg		Initial weight[4] kg	Final weight[5] kg	ADG kg	Age months
A	63	296.5 ± 3.8(7)	0.39 ± 0.01 (7)	30	304.7 ± 7.4 (7)	458.2 ± 6.4 (7)	1.02 ± 0.02 (4)	25.26 ± 0.13 (6)
H	40	297.5 ± 5.3 (6)	0.42 ± 0.01 (6)	40	311.1 ± 8.1 (6)	467.6 ± 7.2 (6)	1.08 ± 0.02 (3)	25.39 ± 0.14 (8)
N	30	277.6 ± 6.1 (8)	0.33 ± 0.01 (8)	28	286.2 ± 8.6 (8)	397.1 ± 8.5 (8)	0.78 ± 0.03 (8)	24.86 ± 0.17 (4)
CA	69	329.9 ± 3.4 (3)	0.45 ± 0.01 (3)	20	352.8 ± 6.9 (3)	495.4 ± 5.7 (2)	1.01 ± 0.02 (6)	24.60 ± 0.11 (3)
HA	54	320.2 ± 4.1 (4)	0.43 ± 0.01 (5)	22	343.1 ± 7.3 (4)	489.1 ± 6.5 (3)	1.10 ± 0.02 (2)	24.90 ± 0.15 (5)
NA	41	347.5 ± 4.9 (2)	0.47 ± 0.01 (2)	25	381.3 ± 8.9 (1)	508.3 ± 8.1 (1)	1.01 ± 0.03 (5)	23.99 ± 0.16 (1)
AH	38	308.6 ± 5.2 (5)	0.44 ± 0.01 (4)	21	323.3 ± 8.6 (5)	482.1 ± 7.5 (4)	1.14 ± 0.03 (1)	25.31 ± 0.15 (7)
AN	35	352.9 ± 5.1 (1)	0.50 ± 0.01 (1)	19	362.9 ± 6.9 (2)	481.5 ± 7.2 (5)	0.92 ± 0.02 (7)	24.33 ± 0.13 (2)

Ranking of genetic groups is given in parentheses.

[1]Male and female.

[2]Just male.

[3]A = Angus; C = Caracu; H = Hereford; N = Nelore. Sire breed is represented by the first letter in G_1 crosses.

[4]Age around 19 mo.

[5]Age around 24 mo.

N). Between A and H, crossbred HA had the greater performance. During the fattening phase, AH and HA steers had the greatest ADG, followed by H steers. Between taurine-indicine crossbred, NA grew most rapidly. Age at slaughter ranged from 23.99 to 25.39 mo, with NA and AN steers being harvested youngest. The purebreds and taurine crossbreds were older at harvest than taurine-indicine and C × taurine crossbreds. Despite this difference in age, crossbred steers were generally heavier at slaughter than the purebreds, with Nelore steers having the least final weight.

DISCUSSION

Differences in breed additive and heterosis effects help us to explain the differences in the animal performance. The positive and significant effect of maternal breed effect and individual and maternal heterosis explains the greater birth weights from purebreds and crossbreds in relation to N. The lighter birth weights from calves out of N dams are consistent with previous observations that indicine dams suppress birth weight (Roberson *et al*, 1986; Alencar *et al*, 1998; Prayaga, 2003). This reduced birth weight may be favorable because neonatal care is not always feasible in extensive production systems, birth weight is positively correlated with dystocia, and dystocia can result in death of the calf and more rarely its dam (Bellows *et al.*, 1971; Laster *et al.*, 1973).

Weaning weight has a high phenotypic correlation of 0.91 with milk yield (Gregory *et al.*, 1992). Rodrigues *et al.* (2014); using some of the same genetic groups as were evaluated in the present study, we found that NA and CA dams produced more milk over a 210-d lactation than AN and HA dams. Reduced preweaning ADG and consequently lighter weaning weight of calves born to H dams may be due to the lower milk production from H dams (Gregory *et al.*, 1992; Kress and MacNeil, 1999). Teixeira e Albuquerque (2005) report similar results with negative individual (−0.025 kg/d) and maternal (−0.198 kg/d) Hereford additive effect as deviation from Nelore cattle raised in Brazil.

Caracu is a taurine breed adapted to tropical and subtropical environment and performs well in grass-fed systems. The breed was originated from the first Iberian bovines brought to Brazil by the Portuguese settlers and underwent intense natural selection process (Mercadante, 2005). The maternal breed additive effect of C was reflected in performance of calves from CA dams in the G_2 and is consistent with CA cows producing more milk than other taurine crosses with A (Rodrigues *et al.*, 2014). Cow-calf farmers can capture additional revenue from their weaned calves by exploiting maternal heterosis. Here, the magnitude of maternal heterosis expressed by taurine-indicine cross dams was greater than taurine-taurine maternal heterosis, perhaps due to the greater genetic distance between taurine and indicine breeds (Decker *et al.*, 2014).

Calves from taurine-taurine and taurine-indicine crossed dams in the present study confirmed the knowledge that use of crossbred dams improves performance for preweaning traits (Gregory *et al.*, 1966). Kippert *et al.* (2008) reported a positive and significant maternal heterosis effect (16.40 kg, $P < 0,001$) for weaning weight in Angus × Nelore crosses. Moreover, Williams *et al.* (2010) found positive values for individual heterosis when cross British × Zebu (23.02 + 0.54 kg) and Continental

× Zebu (25.93 + 1.20 kg) for weaning weight as deviation from Angus. Those heretosis deviation values have similar magnitude to the ones found in the present study (Table 2).

The positive and significant breed additive effects, relative to N, on ADG during the post-weaning phase and on W18 (Table 3) were expected due to that phase being in part concurrent with the winter season, to which purebred indicine N are not well adapted. Similarly, Arthur *et al.* (1994) found negative Brahman breed additive effect for post-weaning ADG compared with Hereford (−30 ± 17 g/d). Breed effects of A, H, and C contributed to increased initial weight relative to N (Table 3). Thus, steers with a greater proportion of A, H, and C germplasm had greater initial weights than those that were predominately N. Both taurine-taurine and taurine-indicine individual heterosis effects were also positive for initial weight. The magnitude of the taurine-indicine heterosis effect was sufficiently great to offset the reduced N breed additive effect (Table 3) and resulted in the AN and NA crosses having the greatest initial weights (Table 5).

Maternal breed additive effects were occasionally significant for postweaning traits (Table 3). Meyer *et al.* (1994) showed significant maternal effects to yearling weight and final weight to Hereford and Zebu crosses. The author commented that with a direct heritability for Hereford of 22%, the maternal environmental effect was approximately 40% as important as the animal's genotype in determining final weight. Prayaga (2003) also found significant maternal effects on final weight that were attributable to Zebu. Thus, it appears that maternal breed additive effects should not be ignored in interpreting results from crossbreeding studies that are conducted in the environment of southern Brazil, nor in making recommendations to farmers about crossbreeding systems.

Yearling weight (Table 5) serves as an important indicator to identify heavier animals at the beginning of the fattening phase and is considered as a selection criterion in breeding programs (Marcondes *et al.*, 2000). In part, the reduced weight of purebred N may be due to their not being adapted to the winter of southern Brazil which coincides with the postweaning period.

Environmental adaptation may also contribute to the improved performance of purebred taurine breeds (A and H) in relation to the indicine N. Nonetheless, heterosis enabled crossbred animals to outperform straightbred contemporaries raised in the same environment. Both in the present study and in Prayaga (2003), the benefit of interspecies crossbreeding between adapted taurine and indicine breed was illustrated.

Heavier weight at the beginning of the fattening phase is important because it is associated with greater gains, decreased time required to finish the steers for slaughter, and decreased costs in this phase (Pacheco et al., 2006). Purebreds had the lightest weights going into the fattening phase as a result of their poor performance in previous phases. Similarly, Gregory et al. (1991) verified lower initial weights for Angus (233 kg) and Hereford (217 kg) when compared with 3 crossbred composites of different European breeds (MARC I, II, and III).

Final weight represents the accumulation of performance from the previous phases. Crosses among genetically distant breeds (NA and CA) were heaviest at harvest due to maximum heterosis. These results corroborate with Maggioni *et al.* (2010) that reported that F1 Nelore × European steers had greater final weight when compared with Nelore pure breed, 531.6 and 446.4 kg, respectively.

The British breed groups had greater gains in this phase, compared with N likely due to their longer history of selection under intensive production systems (Restle and Vaz, 1999). According to the authors mentioned above, the greater selection pressure in the European breeds compared with indicine cattle allows animals with higher percentage of taurine composition to express a faster growth rate in good feed conditions. However, again, crossbred steers showed better performance in the final phase. Thus, crossbreeding using C, H, and A germplasm may be a good option to exploit heterosis and their increased rate of growth in the fattening phase. It is important to notice that heterosis allowed to decrease age at slaughter while keeping heavy final weight for crossbreds compared with purebreds.

CONCLUSION

Crossbreeding using both taurine and indicine breeds is recommended to increase beef cattle performance from birth to slaughter in southern Brazil, where a level of tropical adaptation is beneficial. Heterosis effects were sufficiently great for use of N to be recommended as a component of such systems, despite their relatively low breed additive effects. Breed additive effects of A and H suggest that they also have important roles. Germplasm from the tropically adapted *B. taurus* C may be particularly useful to explore the positive maternal effect. With the breed and heterosis effects derived in the present study, it is possible to predict the performance and infer which breed and breed crosses will perform better in crossbreeding systems designed for the subtropical conditions of southern Brazil and similar regions.

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LITERATURE CITED

Alencar, M. M. D., R. L. Trematore, J. D. A. L. Oliveira, and M. A. Almeida. 1998. Características de crescimento até a desmama de bovinos da raça Nelore e cruzados Charolês x Nelore. Rev. Bras. Zootec. 27:40–46.

Arthur, P. F., H. Hearnshaw, P. J. Kohun, and R. Barlow. 1994. Evaluation of Bos indicus and Bos taurus straightbreds and crosses. III Direct and maternal genetic effects on growth traits. Aust. J. Agric. Res. 45:807–818. doi:10.1071/AR9940807

Bellows, R. A., R. E. Short, D. C. Anderson, B. W. Knapp, and O. F. Pahnish. 1971. Cause and effect relationships associated with calving difficulty and calf birth weight. J. Anim. Sci. 33:407–415. doi:10.2527/jas1971.332407x

Cundiff, L. V. 1970. Experimental results on crossbreeding cattle for beef production. J. Anim. Sci. 30:694–705. doi:10.2527/jas1970.305694x

Decker, J. E., S. D. McKay, M. M. Rolf, J. Kim, A. Molina Alcalá, T. S. Sonstegard, O. Hanotte, A. Götherström, C. M. Seabury, L. Praharani, et al. 2014. Worldwide patterns of ancestry, divergence, and admixture in domesticated cattle. PLoS Genet. 10:e1004254. doi:10.1371/journal.pgen.1004254

Dickerson, G. E. 1969. Experimental approaches in utilising breed resources. Anim. Breed. Abstr. 37:191–202.

Dickerson, G. E. 1973. Inbreeding and heterosis in animals. In: Proceedings of the Animal Breeding and Genetics Symposium in Honour of Dr. J. L. Lush. Champaign, IL. p. 54–77.

Galukande, E., H. Mulindwa, M. Wurzinger, R. Roschinsky, A. O. Mwai, and J. Sölkner. 2013. Cross-breeding cattle for milk production in the tropics: achievements, challenges and opportunities. Anim. Genet. Resour. 52:111–125. doi:10.1017/S2078633612000471

Gregory, K. E., L. A. Swiger, L. J. Sumption, R. M. Koch, J. E. Ingalls, W. W. Rowden, and J. A. Rothlisberger. 1966. Heterosis effects on growth rate and feed efficiency of beef steers. J. Anim. Sci. 25:299–310. doi:10.2527/jas1966.252299x

Gregory, K. E., and L. V. Cundiff. 1980. Crossbreeding in beef cattle: evaluation of systems. J. Anim. Sci. 51:1224–1242. doi:10.2527/jas1980.5151224x

Gregory, K. E., L. V. Cundiff, and R. M. Koch. 1992. Effects of breed and retained heterosis on milk yield and 200-day weight in advanced generations of composite populations of beef cattle. J. Anim. Sci. 70:2366–2372. doi:10.2527/1992.7082366x

Gregory, K. E., L. V. Cundiff, and R. M. Koch. 1991. Breed effects and heterosis in advanced generations of composite populations for growth traits in both sexes of beef cattle. J. Anim. Sci. 69:3202–3212. doi:10.2527/1991.6983202x

Henderson, C. R. 1977. Prediction of the merits of single crosses. Theor. Appl. Genet. 49:273–282. doi:10.1007/BF00275133

Kippert, C. J., P. R. N. Rorato, J. S. Lopes, T. Weber, and A. A. Boligon. 2008. Efeitos genéticos aditivos diretos e maternos e heterozigóticos sobre os desempenhos pré e pós-desmama em uma população multirracial Aberdeen Angus × Nelore. Rev. Bras. Zootec. 37:1383–1391. doi:10.1590/S1516-35982008000800007

Kress, D. D., and M. D. MacNeil. 1999. Crossbreeding beef cattle for western range environments. WCC-1 Publ. TB-99-1. Samuel Roberts Noble Found., Ardmore, OK.

Laster, D. B., H. A. Glimp, L. V. Cundiff, and K. E. Gregory. 1973. Factors affecting dystocia and the effects of dystocia on subsequent reproduction in beef cattle. J. Anim. Sci. 36:695–705. doi:10.2527/jas1973.364695x

MacNeil, M. D., C. A. Dinkel, and L. D. VanVleck. 1982. Individual and maternal additive and heterotic effects on 205-day weight in beef cattle. J. Anim. Sci. 54:951–956. doi:10.2527/jas1982.545951x

MacNeil, M. D., and T. B. Mott. 2006. Genetic analysis of gain from birth to weaning, milk production, and udder conformation in line 1 hereford cattle. J. Anim. Sci. 84:1639–1645. doi:10.2527/jas.2005-697

Maggioni, D., J. de Araújo Marques, P. P. Rotta, D. Perotto, T. Ducatti, J. V. Visentainer, and I. N. do Prado. 2010. Animal performance and meat quality of crossbred young bulls. Livest. Sci. 127:176–182. doi:10.1016/j.livsci.2009.09.006

Marcondes, C. R., J. A. G. Bergmann, J. P. Eler, J. B. S. Ferraz, J. C. C. Pereira, and V. M. Penna. 2000. Análise de alguns critérios de seleção para características de crescimento na raça Nelore. Arq. Bras. Med. Vet. Zootec. 52:83–89. doi:10.1590/S0102-09352000000100018

Max, K., W. Steve, W. Jed, F. James, and T. Thorn. 2013. Contrast: a collection of contrast methods. R package version 0.19.

Mercadante, M. E. Z. 2005. Caracu, o Bos taurus brasileiro adaptado aos trópicos: experiências de um programa de seleção para o peso ao sobreano. Agrociencia. 9:485–494.

Meyer, K., M. J. Carrick, and B. J. Donnelly. 1994. Genetic parameters for milk production of Australian beef cows and weaning weight of their calves. J. Anim. Sci. 72:1155–1165. doi:10.2527/1994.7251155x

Miller, S. P., and J. W. Wilton. 1999. Genetic relationships among direct and maternal components of milk yield and maternal weaning gain in a multibreed beef herd. J. Anim. Sci. 77:1155–1161. doi:10.2527/1999.7751155x

Pacheco, P. S., J. Restle, F. N. Vaz, A. K. Freitas, J. T. Padua, M. Neumann, and M. Z. Arboitte. 2006. Avaliação econômica da terminação em confinamento de novilhos jovens e superjovens de diferentes grupos genéticos. Rev. Bras. Zootec. 35:309–320. doi:10.1590/S1516-35982006000100039

Prayaga, K. C. 2003. Evaluation of beef cattle genotypes and estimation of direct and maternal genetic effects in a tropical environment. 1. Growth traits. Aust. J. Agric. Res. 54:1013–1025. doi:10.1071/AR03071

R Core Team. 2017. R: A language and environment for statistical computing. R Found. Stat. Comput., Vienna, Austria.

Restle, J., and F. N. Vaz. 1999. Confinamento de bovinos definidos e cruzados. In: Lobatto J. F. P., J. O. J. Barcellos, and A. M. Kessler, editors. Produção de bovinos de corte. EDIPUCRS, Porto Alegre, Brasil; p. 141–167.

Roberson, R. L., J. O. Sanders, and T. C. Cartwright. 1986. Direct and maternal genetic effects on preweaning characters of Brahman, Hereford and Brahman–Hereford crossbred cattle. J. Anim. Sci. 63:438–446. doi:10.2527/jas1986.632438x

Robison, O. W., B. T. McDaniel, and E. J. Rincon. 1981. Estimation of direct and maternal additive and heterotic effects from crossbreeding experiments in animals. J. Anim. Sci. 52:44–50. doi:10.2527/jas1981.52144x

Rodrigues, P. F., L. M. Menezes, R. C. Azambuja, R. W. Suñé, I. D. Barbosa Silveira, and F. F. Cardoso. 2014. Milk yield and composition from angus and angus-cross beef cows raised in southern Brazil. J. Anim. Sci. 92:2668–2676. doi:10.2527/jas.2013-7055

Teixeira, R. A., and L. G. de Albuquerque. 2005. Heteroses materna e individual para ganho de peso pré-desmama em bovinos Nelore× Hereford e Nelore× Angus. Arq. Bras. Med. Vet. Zootec. 57:518–523. doi:10.1590/S0102-09352005000400013

Williams, J. L., I. Aguilar, R. Rekaya, and J. K. Bertrand. 2010. Estimation of breed and heterosis effects for growth and carcass traits in cattle using published crossbreeding studies. J. Anim. Sci. 88:460–466. doi:10.2527/jas.2008-1628