Crossbreeding effects on growth and efficiency in beef cow–calf systems: evaluation of Angus, Caracu, Hereford and Nelore breed direct, maternal and heterosis effects

Fábio S. Mendonça,[†,1] Michael D. MacNeil,[‡,ǁ,©] Willian S. Leal,[†] Rodrigo C. C. Azambuja,[†,$]
Pedro F. Rodrigues,[†,$] and Fernando F. Cardoso[†,¶]

[†]Departamento de Zootecnia, Programa de Pós-Graduação em Zootecnia, Universidade Federal de Pelotas, Pelotas, Brasil; [‡]Delta G, Miles City, MT; [ǁ]Department of Animal Wildlife and Grassland Sciences, University of the Free State, Bloemfontein, South Africa; [$]Serviço de Aprendizagem Rural (SENAR), Porto Alegre, Brazil; and [¶]Embrapa Pecuária Sul, Bagé, Rio Grande do Sul, Brazil

ABSTRACT: The objective of this study was to determine breed additive and heterosis effects on growth curves, total milk yield (TMY), calf weaning weight (WW), predicted energy intake (EI), and cow efficiency (CE) of purebred and crossbred beef cows raised in Southern Brazil. The data were from 175 purebred and crossbred cows representing eight genetic groups: Angus (A), Hereford (H), Nelore (N), A × H (AH), H × A (HA), A × N (AN), N × A (NA), and Caracu (C) × A (CA). Growth of the cows was modeled using the nonlinear Brody function and machine milking was used to assess TMY. WW was linearly adjusted to 210 d. EI was predicted with an equation in which the independent variables were estimates of parameters of the Brody function and TMY. The ratio of WW to EI estimated CE. Taurine–indicine heterosis effects were significant for all traits, and greater than those for taurine breed crosses. In general, crossbred cows were heavier at maturity, matured earlier, produced more milk, weaned heavier calves, and were predicted to consume more energy. Thus, they were more efficient than purebred cows, despite their greater predicted feed intake. Among the purebreds, A cows matured most rapidly, weighed the least at maturity, produced the most milk, weaned the heaviest calves, were predicted to consume the least energy; and were therefore most efficient among the breeds that were evaluated. These results are useful as inputs to bioeconomic models that can be used to predict productive and economic outcomes from crossbreeding and to facilitate recommendations for beef producers of southern Brazil and other similar subtropical climatic regions.

Key words: energy requirement, genetic effects, indicine, maternal ability, taurine

INTRODUCTION

The diversity of breeds and crosses raised in cow–calf production systems results in phenotypic differences related to biological type, weight, growth, and milk yield within and between herds (Calegare et al., 2007, 2009; Kippert et al., 2008, Rodrigues et al., 2014). These differences may produce economically relevant outcomes, such as weaning weight (WW) (Muniz and Queiroz, 1998; Rodrigues et al., 2014; Walmsley et al., 2016). However, they are also indicative of costs to maintain the cow herd (Montaño-Bermudez et al., 1990; Green et al., 1991). Dickerson (1969, 1973) presented models that facilitate describing these

differences as genetic effects that can be used to simulate a variety of crosses and crossbreeding systems.

Currently there is an increasing use of crossbreeding in Brazil due to a new export market for live calves in the Central West region of the Country. Acknowledging that heterosis depends on the genetic distance between the paternal breeds (Kippert et al., 2008; Brandt et al., 2010; Schiermiester et al., 2015), the evaluation of the different crosses between taurine × zebu, taurine × taurine, and taurine × locally adapted taurine can be useful to support informed breeding decisions of the Brazilian cattlemen.

In Brazil, pasture-based production systems predominate and measuring feed consumed by the cows is not feasible. However, energy intake (EI) by cows can be estimated from their body weight mass and milk production (Anderson et al., 1983). Nonlinear equations, characterized by relatively few parameters to which biological interpretations can be straightforwardly ascribed, have been shown to adequately describe the growth of cattle (Bahashwan et al., 2015; Gano et al., 2015). Such equations can be integrated into simulation models that allow for evaluation of trade-offs such as those that exist between feed consumed and WW produced in cow–calf production systems. Therefore, the objective of the present study was to compare growth curve parameters estimated through nonlinear regression, milk production, calf WW, predicted EI, and efficiency for different breed groups of cows raised under extensive grazing conditions of southern Brazil. A second objective was to predict breed-specific genetic effects on these traits in order to facilitate use of the results in simulation modeling.

MATERIAL 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).

The study was conducted at Embrapa South Livestock Center of the Brazilian Agricultural Research Corporation, near the city of Bagé, Rio Grande do Sul, southern Brazil. The region has a subtropical climate, with an average annual temperature of 17.6 °C, ranging between 12.5 °C in June and 24 °C January, and with extremes of −4 °C and 41 °C. Average annual rainfall is 1,350 mm, with approximately 25%, 34%, 25%, and 16% occurring in autumn, winter, spring, and summer, respectively.

The data originated from 175 cows of the following breed groups: 31 Angus (A), 14 Hereford (H), 12 Nelore (N), 16 A × H (AH), 29 H × A (HA), 15 A × N (AN), 24 N × A (NA), and 34 Caracu (C) × A (CA). The crossbred cows correspond to the first generation (F_1) and breed of sire is denoted first in the identification of breed combinations. The cows were born between August and November of 2006 to 2009. Within each breed group, the cows were randomly divided and mated to either Brangus (BN) or Braford (BO) bulls from 2008 to 2012. Only BN bulls were used from 2013 to 2015. Calves were born between September and December each year.

Growth Parameters

The cows had an average of 19.2 body weight records starting at birth, bimonthly thereafter through 2 years of age when they were first exposed, and subsequently when their calves were weaned (Figure 1). The weights were measured using a Tru-Test XR3000 electronic scale (Tru-Test Group, Auckland, New Zealand) with a maximum capacity of 1,500 kg and precision of 100 g.

The Brody (1964) equation 1 describing the nonlinear growth curve of each cow was fit using the Nonlinear Least Squares function of R:

$$W = A\,(1 - Be^{-kt}) \qquad [1]$$

In this equation, W (kg) = weight at age t (days); A (kg) = asymptotic weight as age t tends to infinity; B = integration constant, and k is the maturing rate. The interpretation of the function parameters is as follows (Fitzhugh, 1976; Freetly et al., 2011): Estimates of A are interpreted as mature size. Estimates of k describe the rate that growth occurs with the change in size (parameter B).

Milk Yield

Milk production (MY) was measured using a Fockink ATBVF200 milking machine (Grupo Fockink, Panambi/RS, Brazil) at three different times during lactation: beginning (18–58 d), middle (92–135 d), and end (152–242 d). These measures
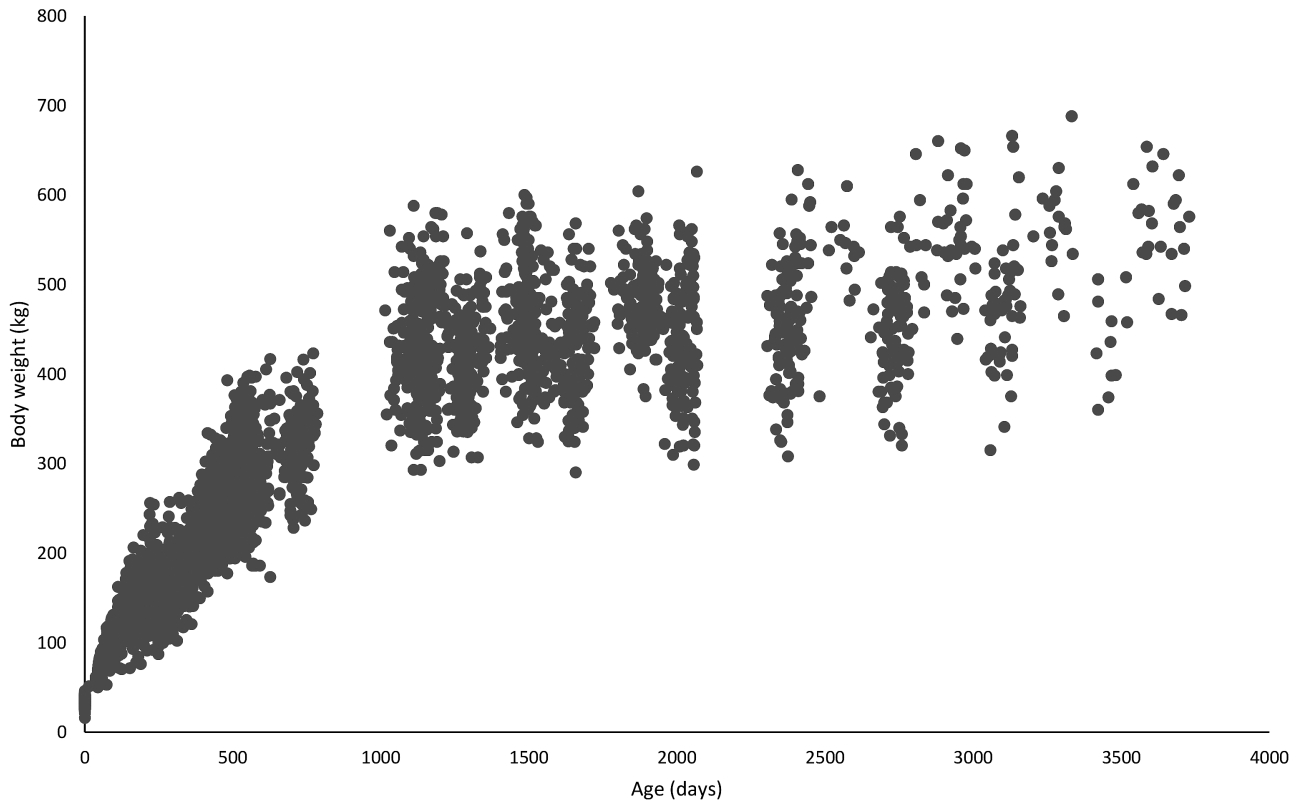
Figure 1. Body weights from birth to maturity of beef animals plotted against their age.

were transformed to estimate the milk yield in 24 h as proposed by Restle et al. (2003):

$$MY = MMY \times \frac{60}{IM} \times 24 \qquad [2.1]$$

where **MY** = estimated 24-h milk yield in kg/day, **MMY** = measured milk yield, kg, and **IM** = time interval in minutes between the last suckling and milking. For all cows, a lactation curve for each lactation was fit to the model proposed by Jenkins and Ferrell (1984):

$$MY_w = \frac{W}{ae^{kw}} \qquad [2.2]$$

where MY_w = milk yield in 24 h corrected to 4% of fat content observed at the wth week after calving, a = curve scale parameter, e = exponential function, k = curve shape parameter, and w = lactation length in weeks.

Estimates of the parameters a and k were used, following Jenkins and Ferrell (1984), to calculate the total production during 210 d (or 30 wk) of lactation (total milk yield [TMY]):

$$TMY = \frac{-7}{ak} \times \left(30e^{-k30} + \frac{1}{ke^{-k30}} - \frac{1}{k} \right) \quad [2.3]$$

Calf WW

At weaning, calves ranged in age from 133 to 249 d and their weights were corrected to 210 d of age using the following equation:

$$WW_{adj} = \left(\frac{WW - BW}{WA} \right) \times 210 + BW \qquad [3]$$

where WW_{adj} = weaning weight in kg corrected to 210 d of age, WW = observed weaning weight, BW = observed birth weight, and WA = age at the weaning day in days.

Energy Intake

Equations for predicting EI in total digestible nutrient (TDN) as a function of body weight and milk were those proposed by Anderson et al. (1983) and validated by Kirkpatrick et al. (1985):

$$Y = 4.6631 + 0.0030W + 0.0010\Delta W + 0.0127 \,(0.022TMY)$$
$$[4.1]$$

$$Y = 4.6631 + 0.0030 \,(W) + 0.0127 \,(0.022TMY)$$
$$[4.2]$$

where Y = TDN consumed/day; W = average weight of the cow in period t, ΔW = the change in weight over that period, and TMY = total milk yield for the 210-d lactation period. Equation 4.1 was used to measure the EI of growing cows (<2,035 d) and equation 4.2 for cows with stabilized mature weight (≥2,035 d). Daily EI in TDN was transformed to annual kilocalorie of metabolizable energy (ME) as follows:

$$ME = TDN \times 3.608 \times 365 \qquad [4.3]$$

Cow efficiency (CE) was estimated as the ratio of WW_{adj} to the EI of the cow (Lin, 1980).

Statistical Models

Parameter estimates for the growth curve of each cow (A and k) were considered dependent variables (Y_{ijkl}) and analyzed with the following model using "R" (R Core Team, 2018):

$$Y_{ijkl} = \mu + BG_i + CS_j + CY_k + e_{ijkl} \qquad [5.1]$$

where Y_{ijkl} = growth parameters (A and k) of the cows, μ = overall mean, BG_i = the fixed effect of the ith breed group, CS_j = the fixed effect of the jth season of birth (early, late), CY_k = the fixed effect of the kth birth year (2006 to 2009) and e_{ijkl} = the random residual effect attributable to the lth cow.

Traits that were recorded from progeny of the cows (TMY, WW, EI, and CE) had repeated measures over time relative to the cows. Thus, additional parameters were introduced into the model:

$$Y_{ijklmnop} = \mu + BG_i + CS_j + CY_k + S_l + CO_m$$
$$+ BS_n + RC_o + e_{ijklmnop} \qquad [5.2]$$

where $Y_{ijklmnop}$ = a dependent variable (TMY, WW, EI, or CE), μ = overall mean, BG_i = the fixed effect of the ith breed group, CS_j = the fixed effect

of the jth calving season (early, late), CY_k = the fixed effect of the kth year of birth (2009 up to 2015), S_l = the fixed effect of the lth sex of calf (male, female), CO_m = the fixed effect of the mth age of cow/calving order combination which was defined as: first calving 3-yr-old cows (3.1), first calving 4-yr-old cows (4.1), second calving 4-yr-old cows (4.2), second calving 4-yr-old cows that were first mated and pregnant at 18 mo (4.18), second calving 5-yr-old cows (5.2), third calving 5-yr-old cows (5.3), second calving 6-yr-old cow (6.2), third calving 6-yr-old cow (6.3), fourth calving 6-yr-old cow (6.4), third calving 7-yr-old (7.3), fourth calving 7-yr-old (7.4), fifth calving 7-yr-old (7.5), fourth calving 8-yr-old (8.4), fifth calving 8-yr-old (8.5), sixth calving 8-yr-old (8.6), sixth calving 9-yr-old (9.6), and seventh calving 9-yr-old (9.7), BS_n = the fixed effect of the nth breed of sire (BO, BN), RC_o = the random effect of the oth cow on time, and $e_{ijklmnop}$ = the random residual effect attributable to the pth calf.

For the analysis of genetic coefficients, the BG effects were replaced by a series of linear regression effects using lm function of the R Software, according to the following statistical model

$$BG_i = b_1 g_A^i + b_2 g_C^i + b_3 g_H^i + b_4 g_A^m$$
$$+ b_5 g_H^m + b_6 h_t^i + b_7 h_z^i \qquad [5.3]$$

In the foregoing equation, g_j^i = the cow individual proportion of jth breed for A = Angus, C = Caracu, and H = Hereford in each ith BG; likewise, g_j^m = the breed proportion of the dams of cows in each BG; h^i = the individual heterosis effects which were assumed to be proportional to expected individual heterozygosity (Gregory and Cundiff, 1980). The heterosis effects were further partitioned into whether the heterozygosity resulted from the combination of alleles from a

Table 1. Genetic effects coefficients for breed groups in the study

Breed group[1]	Genetic effects								
	g_A^i	g_C^i	g_H^i	g_N^i	g_A^m	g_H^m	g_N^m	h_z^i	h_t^i
A	1	0	0	0	1	0	0	0	0
H	0	0	1	0	0	1	0	0	0
N	0	0	0	1	0	0	1	0	0
AH	0.5	0	0.5	0	0	1	0	0	1
HA	0.5	0	0.5	0	1	0	0	0	1
NA	0.5	0	0	0.5	1	0	0	1	0
AN	0.5	0	0	0.5	0	0	1	1	0
CA	0.5	0.5	0	0	1	0	0	0	1

g_j^i = individual additive effect, g_j^m = maternal additive effect, h_j^i = individual heterosis; with subscripts A = Angus, C = Caracu, H = Hereford, N = Nelore, t = taurine breed crosses, and z = taurine–indicine crosses.

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

Translate basic science to industry innovation

taurine breed and an indicine breed (subscript z) or from two taurine breeds (subscript t). This formulation for model parameters identification required restrictions that were imposed by setting the Nelore breed direct and maternal additive effects to zero in order to obtain a unique solution. The genetic expectations of each BG are shown in Table 1. Finally, b_1, b_2, b_3 = individual additive breed effects of Angus, Caracu and Hereford coefficients, respectively; b_4, b_5 = maternal additive breed effects of Angus and Hereford coefficients, respectively; b_6, b_7 = individual heterosis coefficients as expressed by crosses of taurine breeds and of taurine and indicine breeds, respectively. Predicted means were estimated and compared applying the R/base contrast function to direct and maternal additive and individual heterosis effects, and fractional coefficients (Max et al., 2013) that are appropriate to the BGs.

RESULTS

Greater values of the A parameter were observed for the AN, HA, and CA crossbred cows compared to the purebred A cows, whereas the AN and CA cows had a greater maturing rate (k) compared to N and H cows (Table 2). Despite, an overall trend for larger crossbred cows, except for H that also had a large mature weight, there was great variability in body weight and growth within breed group, such that most of the comparisons were not significant ($P > 0.10$). Individual additive effects were positive for A, but only the H breed effect was significant indicating a 63.9 kg increase relative to g_N^i (Table 3). Estimates of maternal effects for A were negative, but no significant differences were identified. The h_z^i effect significantly increased mature weight by 34.8 kg. And, likewise, the parameter k increased by 0.00025 kg due to the h_z^i effect, resulting from earlier maturation of taurine × indicine crossbred cows (Table 3).

Greater TMY was observed for AH, AN, and CA cows compared to HA, A, H, and N cows (Table 2). This was mostly due to significant h_z^i and h_t^i effects of 207 and 194 kg of milk in a 210-day lactation (Table 3). The H breed had negative individual and positive maternal effect on TMY. This resulted in the surprising greater milk production of AH cows (i.e., daughters of H dams) than their HA contemporaries (Table 2). Crossbred AN and CA cows produced heavier calves than purebreds A, N, and H and also the crossbred HA cows (Table 2). The h_z^i effect was positive on WW (Table 3) increasing milk production by 9.7%. The g_H^i and g_C^i also affected WW, respectively, with differences of −11.1% and +12.1% in comparison to g_N^i.

Purebred N cows consumed on average less energy than the crossbreds, but were less efficient at transforming energy consumed in calf production, except that HA breed group was similar in efficiency to the N breed (Table 2). The AN, AH, and CA cows despite larger consumption of energy had the greatest efficiency in converting this EI into WW. When the data were partitioned into genetic coefficients, significant effects were observed of the g_C^i, g_H^i, and h_z^i coefficients for annual EI (Table 3). Regarding CE, unfavorable g_H^i and favorable h_z^i effects were observed (Table 3). The g_H^i effect increased kilocalorie intake by 2.9% compared to g_N^i. This result combined with negative g_H^i effect on WW explains the observed 11.1% decrease in CE that was attributed to g_H^i. Despite increasing EI, the positive effect of h_z^i on WW resulted in a favorable increase in CE of 7.4%.

DISCUSSION

The main objective of the use of the genetic resources is to exploit genetic differences between breeds, heterosis, and complementarity to improve

Table 2. Estimated breed group means for mature weight (A), maturing rate (k), total milk yield (TMY), 210-day weight (WW), predicted energy intake (EI), and cow efficiency (CE)

Breed group	A	k (× 10⁻³)	TMY	WW	EI	CE (× 10⁻²)
Angus (A)	433.7 ± 11.5 b	1.54 ± 0.06 ab	1098. ± 78 b	201.9 ± 8.9 bc	8238. ± 57 c	2.46 ± 0.11 b
Hereford (H)	467.7 ± 16.2 ab	1.44 ± 0.08 bc	1060. ± 91 b	186.8 ± 10.4 c	8283. ± 71 bc	2.26 ± 0.12 c
Nelore (N)	445.9 ± 18.2 ab	1.30 ± 0.09 c	1012. ± 98 b	194.1 ± 11.2 bc	8150. ± 79 c	2.40 ± 0.13 bc
AH	465.0 ± 28.3 ab	1.62 ± 0.14 abc	1427. ± 127 a	221.6 ± 14.5 ab	8435. ± 116 abc	2.64 ± 0.17 ab
HA	472.1 ± 11.5 a	1.60 ± 0.12 ab	1120. ± 80 b	196.3 ± 9.1 bc	8343. ± 56 b	2.37 ± 0.11 bc
AN	492.1 ± 15.8 a	1.72 ± 0.06 a	1356. ± 88 a	224.3 ± 9.9 a	8516. ± 68 a	2.66 ± 0.12 a
NA	457.0 ± 24.7 ab	1.62 ± 0.12 ab	1168. ± 112 ab	215.6 ± 12.7 ab	8318. ± 98 abc	2.61 ± 0.14 ab
Caracu × A	466.4 ± 10.2 a	1.62 ± 0.12 a	1312. ± 78 a	221.5 ± 8.7 a	8405. ± 53 ab	2.65 ± 0.11 a

Breed of sire is identified by the first symbol in crossbred groups. Means within column not sharing a common suffix are significantly different ($P < 0.05$) by contrast t test.

Table 3. Estimates and standard errors of breed additive and heterosis effects on for mature weight (A), maturing rate (k), total milk yield (TMY), 210-day weight (WW), predicted energy intake (EI), and cow efficiency (CE)

Genetic effect	A	k ($\times 10^{-4}$)	TMY	WW	EI	CE ($\times 10^{-3}$)
g_A^i	22.8 ± 40.6	3.4 ± 2.0	275. ± 221.	16.6 ± 16.4	286. ± 129	1.16 ± 1.94
g_C^i	54.4 ± 32.1	2.7 ± 1.6	314. ± 115**	26.4 ± 13.1*	363. ± 118**	2.18 ± 1.54
g_H^i	63.9 ± 28.1*	2.2 ± 1.4	−70. ± 101	−23.9 ± 11.5*	240. ± 103*	−3.60 ± 1.36**
g_A^m	−35.1 ± 31.6	−1.0 ± 1.6	−189. ± 110.	−8.7 ± 12.6	−198. ± 115	−0.54 ± 1.48
g_H^m	−42.1 ± 25.0	−0.8 ± 1.3	118. ± 88.	16.6 ± 10.1	−106. ± 91.	2.24 ± 1.18
h_z^i	34.8 ± 14.7*	2.5 ± 0.7***	207. ± 52***	21.9 ± 5.9***	223. ± 53***	2.06 ± 0.69**
h_t^i	17.9 ± 19.0	1.2 ± 1.0***	194. ± 68**	14.6 ± 7.7	128. ± 69	1.40 ± 0.91

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

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

the performance of animals raised in different environmental conditions (Perotto et al., 2000; Prayaga, 2003). Therefore, we measured cow performance and estimated EI to identify crosses that are characterized by a favorable balance of outputs and inputs; an essential feature of successful crossbreeding systems (Trematore et al., 1998). Measured genetic variation in components of biological efficiency is intended to provide benchmarks for improving economic return to production systems in southern Brazil.

Growth Parameters

Growth traits have a direct relationship with the productive life of animals (Araújo et al., 2012; Espigolan et al., 2013; Bahashwan et al., 2015). Therefore, they have been long recognized as important to all animal scientists, regardless of specialization, who are concerned with the effects of their research and recommendations on lifetime production efficiency (Fitzhugh, 1976). Herein body weights were related to age using a nonlinear model, since these models have the advantage of summarizing several measurements taken during the life of the animal in few parameters with straightforward interpretations (Marinho et al., 2013; Bahashwan et al., 2015).

In extensive systems of beef production, in which food is exclusively based on natural resources (pasture), animals usually reach mature weight relatively late in life with a consequent reduction in maturing rate. This trend is evident when comparing the growth curve of the cows in the present study with those raised in more intensive production systems (Kaps et al., 2000; Freetly et al., 2011; Gano et al., 2015).

In the present study, the Brody (1964) model was used because it has been shown to successfully describe the growth of beef cattle (Brown et al., 1976 De Lima Silva et al., 2011; Marinho et al.,

2013; Lopes et al., 2016). Here cow growth was modeled using mature weight and maturing rate parameters indicating trends for greater size and earlier maturation of crossbreds (except the asymptotic weight of H) compared to purebred cows (Table 2). Similar results have been found previously (Muniz and Queiroz, 1998; Trematore et al., 1998; Kippert et al., 2008). Nevertheless, there was also substantial variation in mature weight (cv = 13.3%) and maturing rate (cv = 19.7%) within breed groups and just the most extreme differences could be declared significant. Evidence clearly points to taurine × indicine crossbred cows attaining greater mature size and maturing earlier than their purebred counterparts as h_z^i effects on mature weight and maturing rate were positive 7.8% and 19.2%, respectively (Table 3), Likewise, Nelsen et al. (1982) found positive individual heterosis effects on mature weight in crosses between Angus, Brahman, Hereford, Holstein, and Jersey. However, contrary to the present results, Nelsen et al. (1982) did not find evidence of heterosis for maturing rate.

The fact that h_z^i was greater than h_t^i for growth parameters (A and k) may be related to the dominance theory, assuming that the genetic distance between the parental breeds is proportional to the magnitude of heterosis (Kippert et al., 2008; Brandt et al., 2010; Schiermiester et al., 2015) and that the distance between taurine and zebu breeds is greater than the distance between taurine breeds (Roso and Fries, 2000; Decker et al., 2014).

The g_H^i effect was significant and increased weight at maturity by 14.3% relative to N and thus the greater predicted mature weight of H among purebred cows (Table 3). These results suggest use of H in systems that target larger cows. Although the presence of maternal effects, mainly due to the uterine environment and milk production (Muniz and Queiroz,

1998), are well established, their effects on parameters of the Brody growth curve were not detected (Table 3). However, most of the weights were recorded after weaning when maternal effects are no longer expected (Meyer, 1992). Thus, when evaluating the variance components for birth, weaning, yearling, and final weight, Meyer (1992) observed significant maternal effects on all weights except for final weight.

The primary purpose of including TMY and WW in the present work was to assess EI and CE. Therefore, only key results for these traits are discussed here with a more detailed assessment of the studied population found elsewhere (Rodrigues et al., 2014; Leal et al., 2018). Greater TMY and WW observed in the crossbred (AH, AN, and CA) relative to purebred cows (except AH vs. A and N for WW) were mainly due to heterosis effects; with h_z^i slightly greater than h_t^i for both traits (Tables 2 and 3). These results agree with previous studies in which cows with greater milk yield had heavier calves at weaning (Miller and Wilton, 1999; MacNeil and Mott, 2006; Rodrigues et al., 2014). This also confirms the positive effect of crossbreeding on productive traits of economic importance, such as WW for cow and calf systems.

The success of the beef production depends on an appropriate matching of the genetic resources with the particular nutritional environment (Kress and MacNeil, 1999; Calegare et al., 2009; Walmsley et al., 2016). Under extensive conditions, adapted animals, feeding exclusively on pasture, may generate not only productive advantages but also economic benefits for the beef cattle production system. Here, EI was predicted as a function of cow weight, weight change, and milk production. Thus, genetic effects that affected these traits also had some impact on EI. Jenkins and Ferrell (1983) established that although heterosis and complementarity potentially increased productive traits, crossbreeding also had the potential to increase herd energy requirements. Calegare et al. (2007) also observed that crossbred cows (Nelore × Angus or Nelore × Simmental) were 46 kg heavier and presented a 10% increase in EI in relation to N cows.

Adaptation of the N breed to restricted nutritional environments in tropical climate may be advantageous to reduce the energetic requirements of the herd (Calegare et al., 2009). However, the Nelore breed is not well adapted to the southern Brazilian conditions, mainly due to the low temperatures that occur in the winter and may not have had an adaptive advantage in this environment where more of their nutrient intake make have been directed toward maintenance. In fact, another benefit of crossbreeding is that heterosis has potentially larger effect in poor environments with feed restrictions (Cunningham, 1982), such as the case of the present study in which cows were reared in extensive native pasture grazing systems.

Cow Efficiency

According to MacNeil et al. (2017) CE can be measured in a number of ways including by the ratio between the mass of calf produced and the feed inputs required to maintain the cow and allow her to provide for her calf. Thus, CE was measured in the present study as the ratio of WW and predicted EI. This allowed an estimation of productive efficiency in an environment where it was not feasible to directly measure feed intake.

Considering that the main energy demands of cows are due to weight, growth and milk production, Anderson et al. (1983) developed equations to predict the EI based on these parameters, which presented a reasonable approximation of NRC (1976).

One might expect that larger animals with greater energy requirements could be less efficient in an extensive environment, based exclusively on natural grazing (Lopez de Torre et al., 1992). According Dickerson (1982), the higher maintenance requirements of heavier breeding females reduce the efficiency at the herd level. On the other hand, Pang et al. (1999) evaluating through simulations the effects of cows size (mature cow weights of 450, 550, and 650 kg) concluded that when comparisons of cow size were made at a constant calf weaning age (200 d), the small size cows were least efficient.

In the present study, even though there significant differences observed in parameter A among the breed groups, mature size was not the single cause of breed differences in cow performance and efficiency. A broader interpretation is necessary, considering the different selection histories of breeds and selection intensities for WW, milk yield, and reproductive performance (Morris and Wilton, 1976). Probably because we did not have continental breeds in our breed groups, there were no major differences between cow weights (Table 2), as was the case of other similar studies (Laster et al., 1976; Nadarajah et al., 1984). In our case, AN cows were the heaviest, produced more milk, and had greater predicted EI, but were also more efficient (Table 2), as result of a positive effect of h_z^i (Table 3). Thus, the extra WW was more than sufficient to offset the higher EI of AN cows.

Although the H had a large mature size, it had moderate EI, as a result of producing less milk,

which in turn negatively affected WW. The negative value of the g_H^i effect to CE indicates less efficient production as the proportion of H increased. Although A cows weighed less at maturity, they produced calves with intermediate WW and thus were more efficient than H cows.

The results presented in this study are useful to parameterize bioeconomic models in terms of expected means and variability of designed crossbreeding systems (MacNeil et al., 1994) and to predict their productive and economical benefits. Because estimates were derived from genetic coefficients (equation 5.3), model predictions could be generalized to evaluate systems including breed groups other than the ones in the present study as long as the coefficients are within the evaluated range. The development of such predictions tools would be instrumental to make reliable crossbreeding recommendations for beef producers of southern Brazil and other similar subtropical climate regions.

CONCLUSION

Crossbred cows on average have greater mature weight and maturing rate due to heterotic effects that may depend on the distance between the parental breeds. However, purebred H cows were similar in mature weight to crossbreds.

Crossbred cows produced a greater amount of milk and heavier calves, and these traits also influenced by heterosis. However, they were less dependent on the distance between the breeds involved in the crossing. Among purebreds, the A cows produced heavier calves at weaning than H, N being intermediate.

The effect of taurine–indicine heterosis increased EI (input) and calf weight at weaning (output). The greater relative importance of increases in outputs resulted in greater efficiency of the crossbred cows.

ACKNOWLEDGMENTS

LITERATURE CITED

Anderson, V. L., L. Jost, C. A. Dinkel, and M. A. Brown. 1983. Prediction of daily total digestible nutrient requirement of beef cows in northern climates. J. Anim. Sci. 56:271–279. doi:10.2527/jas1983.562271x.

Araújo, R. O., C. R. Marcondes, M. C. F. Damé, A. D. V. Garnero, R. J. Gunsk, D. M. Everlingi, and P. R. N. Rorato. 2012. Classical nonlinear models to describe the growth curve for Murrah buffalo breed. Cienc. Rural. 42:520–525. doi:10.1590/S0103-84782012000300022.

Bahashwan, S., A. S. Alrawas, S. Alfadli, and E. S. Johnson. 2015. Dhofari cattle growth curve prediction by different non-linear model functions. Livestock. Res. Rural. Dev. 27:1–10.

Brandt, H., A. Müllenhoff, C. Lambertz, G. Erhardt, and M. Gauly. 2010. Estimation of genetic and crossbreeding parameters for preweaning traits in German Angus and Simmental beef cattle and the reciprocal crosses. J. Anim. Sci. 88:80–86. doi:10.2527/jas.2008-1742.

Brody, S. 1964. Bioenergetics and growth. New York (NY): Hafner Publishing Company Inc.

Brown, J. E., H. A. Fitzhugh, and T. C. Cartwright. 1976. A comparison of nonlinear models for describing weight-age relationships in cattle. J. Anim. Sci. 42:810–818. doi:10.2527/jas1976.424810x.

Calegare, L., M. M. Alencar, I. U. Packer, C. L. Ferrell, and D. P. Lanna. 2009. Cow/calf preweaning efficiency of Nellore and Bos taurus × Bos indicus crosses. J. Anim. Sci. 87:740–747. doi:10.2527/jas.2007-0759.

Calegare, L., M. M. Alencar, I. U. Packer, and D. P. Lanna. 2007. Energy requirements and cow/calf efficiency of Nellore and Continental and British Bos taurus × Nellore crosses. J. Anim. Sci. 85:2413–2422. doi:10.2527/jas.2006-448.

Cunningham, E. P. 1982. The genetic basis of heterosis. In Proc. of the 2nd World Congress on Genetics Applied to Livestock Production. 6:190–205.

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.

De Lima Silva, F., M. M. De Alencar, A. R. De Freitas, I. U. Packer, and G. B. Mourão. 2011. Curvas de crescimento em vacas de corte de diferentes tipos biológicos. Pesq. Agropec. Bras. 46:262–271.

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.

Dickerson, G. E. 1982. Principles in establishing breeding objectives. In: R.A. Barton and W.C. Smith, editor, Proc. Wld. Congr. on Sheep and Cattle Breed. 1 p. 9.

Espigolan, R., F. Baldi, A. A. Boligon, G. Banchero, G. Brito, A. La Manna, F. Montossi, E. Fernandez, and L. G. Albuquerque. 2013. Aplicação de modelos não-lineares para descrever a evolução de características de crescimento e carcaça em bovinos da raça Hereford. Cienc. Rural. 43:513–519.

Fitzhugh, H. A., Jr. 1976. Analysis of growth curves and strategies for altering their shape. J. Anim. Sci. 42:1036–1051. doi:10.2527/jas1976.4241036x.

Freetly, H. C., L. A. Kuehn, and L. V. Cundiff. 2011. Growth curves of crossbred cows sired by Hereford, Angus, Belgian Blue, Brahman, Boran, and Tuli bulls, and the fraction of mature body weight and height at puberty. J. Anim. Sci. 89:2373–2379. doi:10.2527/

jas.2011-3847.

Gano, G., M. Blanco, I. Casasús, X. Cortés-Lacruz, and D. Villalba. 2015. Comparison of B-splines and non-linear functions to describe growth patterns and predict mature weight of female beef cattle. Animal Prod. Sci. 56:1787–1796. doi:10.1071/AN15089.

Green, R. D., L. V. Cundiff, G. E. Dickerson, and T. G. Jenkins. 1991. Output/input differences among nonpregnant, lactating Bos *indicus-Bos taurus and Bos taurus-bos taurus* F$_1$ cross cows. J. Anim. Sci. 69:3156–3166. doi:10.2527/1991.6983156x.

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.

Jenkins, T. G., and C. L. Ferrell. 1983. Nutrient requirements to maintain weight of mature, nonlactating, nonpregnant cows of four diverse breed types. J. Anim. Sci. 56:761–770. doi:10.2527/jas1983.564761x.

Jenkins, T. G., and C. L. Ferrell. 1984. A note on lactation curves of crossbred cows. Anim. Sci. 39:479–482. doi:10.1017/S0003356100032232.

Kaps, M., W. O. Herring, and W. R. Lamberson. 2000. Genetic and environmental parameters for traits derived from the Brody growth curve and their relationships with weaning weight in Angus cattle. J. Anim. Sci. 78:1436–1442. doi:10.2527/2000.7861436x.

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.

Kirkpatrick, B. W., C. A. Dinkel, J. J. Rutledge, and E. R. Hauser. 1985. Prediction equations of beef cow efficiency. J Anim Sci., 60:964–969. doi:10.2527/jas1985.604964x.

Kress, D. D., and M. D. MacNeil. 1999. Crossbreeding for beef cattle for western range environments. WCC-1 Committee Publications p. 1–21.

Laster, D. B., G. M. Smith, and K. E. Gregory. 1976. Characterization of biological types of cattle IV. Postweaning growth and puberty of heifers. J. Anim. Sci. 43:63–70. doi:10.2527/jas1976.43163x.

Leal, W. S., M. D. MacNeil, H. G. Carvalho, R. Z. Vaz, and F. F. Cardoso. 2018. Direct and maternal breed additive and heterosis effects on growth traits of beef cattle raised in southern Brazil. J. Anim. Sci. 96:2536–2544. doi:10.1093/jas/sky160.

Lin, C. I. 1980. Relative efficiency of selection methods for improvement of feed efficiency. J. Dairy Sci. 63:491–494. doi:10.3168/jds.S0022-0302(80)82960-2.

Lopes, F. B., C. U. Magnabosco, F. M. De Souza, A. S. De Assis, L. C. Brunes, E. Cerrados, and C. P. D. Brasil. 2016. Análises de dados longitudinais em bovinos Nelore Mocho por meio de modelos não lineares. Arch. Zootec. 65:123–129. doi:10.21071/az.v65i250.478.

Lopez de Torre, G., J. J. Candotti, A. Reverter, M. M. Bellido, P. Vasco, J. J. Gorciao, and J. S. Brinks. 1992. Effects of growth curve parameters on calf efficiency. J. Anim. Sci., 70:2668–2672. doi:10.2527/1992.7092668x.

MacNeil, M. D., M. C. Mokolobate, M. M. Scholtz, F. J. Jordaan, and F. W. C. Neser. 2017. Alternative approaches to evaluation of cow efficiency. S. Afr. J. Anim. Sci. 47:118–123. doi:10.4314/sajas.v47i2.2.

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.

MacNeil, M. D., S. Newman, R. M. Enns, and J. Stewart-Smith. 1994. Relative economic values for Canadian beef production using specialized sire and dam lines. Can. J. Anim. Sci. 74:411–417. doi:10.4141/cjas94-059.

Marinho, K. N. D. S., A. R. D. Freitas, A. J. D. S. Falcão, and F. E. F. Dias. 2013. Nonlinear models for fitting growth curves of Nellore cows reared in the Amazon Biome. Rev. Bras. Zootec. 42:645–650. doi:10.1590/S1516-35982013000900006.

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

Meyer, K. 1992. Variance components due to direct and maternal effects for growth traits of Australian beef cattle. Livest. Prod. Sci. 31:179–204. doi:10.1016/0301-6226(92)90017-X.

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.

Montaño-Bermudez, M., M. K. Nielsen, and G. H. Deutscher. 1990. Energy requirements for maintenance of crossbred beef cattle with different genetic potential for milk. J. Anim. Sci. 68:2279–2288. doi:10.2527/1990.6882279x.

Morris, C. A. and J. W. Wilton. 1976. Influence of body size on the biological efficiency of cows: a review. Can. J. Anim. Sci. 56:613–617. doi:10.4141/cjas76-076.

Muniz, C. A. D. S. D., and S. A. D. Queiroz. 1998. Avaliação do peso à desmama e do ganho médio de peso de bezerros cruzados, no Estado do Mato Grosso do Sul. Rev. Bras. Zootec. 27:504–512.

Nadarajah, K., T. J. Marlowe, and D. R. Notter. 1984. Growth patterns of Angus, Charolais, Charolais × Angus and Hholstein × Angus cows from birth to maturity. J. Anim. Sci. 59:957–966. doi:10.2527/jas1984.594957x.

Nelsen, T., C. R. Long and T. C. Cartwright. 1982. Postinflection growth in straightbred and crossbred cattle. I. Heterosis for weight, height and maturing rate. J. Anim. Sci. 55:280–292. doi:10.2527/jas1982.552280x.

NRC. 1976. Nutrient requirements of domestic animals, No. 4. Nutrient Requirements of Beef Cattle. 5th revised ed. Washington (DC): National Academy of Sciences-National Research Council.

Pang, H., M. H. Makarechian, and J. A. Basarab. 1999. A simulation study on the effects of cow size and milk production on bioeconomic efficiency of range beef cattle. J. Appl. Anim. Res. 16:119–128. doi:10.1080/09712119.1999.9706273.

Perotto, D., A. C. Cubas, J. L. Moletta, and C. Lesskiu. 2000. Heterose sobre os pesos de bovinos Canchim e Aberdeen Angus e de seus cruzamentos recíprocos. Pesq. Agropec. Bras. 35:2511–2520.

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. 2018. R: a language and environment for statistical computing. Vienna: R Foundation for Statistical Computing. Available from https://www.R-project.org/ [Verified April 2018].

Restle, J., P. S. Pacheco, J. L. Moletta, I. L. Brondani, and L. Cerdótes. 2003. Genetic group and postpartum nutritional level on the milk yield and composition of beef cows. Rev. Bras. Zootec. 32:585–597. doi:10.1590/

S1516-35982003000300010.

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.

Roso, V. N., and L. A. Fries. 2000. Avaliação das Heteroses Materna e Individual sobre o Ganho de Peso do Nascimento ao Desmame em Bovinos Angus × Nelore. Rev. Bras. Zootec. 29:732–737.

Schiermiester, L. N., R. M. Thallman, L. A. Kuehn, S. D. Kachman, and M. L. Spangler. 2015. Estimation of breed-specific heterosis effects for birth, weaning, and yearling weight in cattle. J. Anim. Sci. 93:46–52. doi:10.2527/jas.2014-8493.

Trematore, R. L., M. D. Alencar, P. F. Barbosa, J. D. A. L. Oliveira, and M. A. D. Almeida. 1998. Estimativas de efeitos aditivos e heteróticos para características de crescimento pré-desmama em bovinos Charolês-Nelore. Rev. Bras. Zootec. 27:87–94.

Walmsley, B. J., S. J. Lee, P. F. Parnell, and W. S. Pitchford. 2016. A review of factors influencing key biological components of maternal productivity in temperate beef cattle. Anim. Prod. Sci. 58:1–19. doi:10.1071/AN12428.