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Tiago Albandes Fernandes⁽¹⁾ 
Liliane Cerdótes⁽²⁾ 
Ricardo Zambarda Vaz⁽³⁾ 
João Restle⁽⁴⁾  and
Otoniel Geter Lauz Ferreira⁽¹⁾ 

⁽¹⁾ Universidade Federal de Pelotas, Faculdade de Agronomia Eliseu Maciel, Departamento de Zootecnia, Campus Capão do Leão, s/nº, CEP 96160-000 Pelotas, RS, Brazil. E-mail: tiago.albandes.fernandes@zootecnista.com.br, ogferreira@gmail.com

⁽²⁾ Instituto Federal Catarinense, Departamento de Zootecnia, Campus de Santa Rosa do Sul, Avenida Nascimento José da Rosa, Vila Nova, CEP 88965-000 Santa Rosa do Sul, SC, Brazil. E-mail: liliane.cerdotes@ifc.edu.br

⁽³⁾ Universidade Federal de Santa Maria, Departamento de Ciências Biológicas e Zootecnia, Campus Palmeira das Missões, Avenida Independência, nº 3.751, Vista Alegre, CEP 98300-000 Palmeira das Missões, RS, Brazil. E-mail: rvaz@terra.com.br

⁽⁴⁾ Universidade Federal de Goiás, Faculdade de Veterinária e Zootecnia, Departamento de Zootecnia, Campus Samambaia, Avenida Esperança, s/nº, Chácaras de Recreio Samambaia, CEP 74690-900 Goiânia, GO, Brazil. E-mail: jorestle@terra.com.br

✉ Corresponding author

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Relationship between heterosis, weight gain, and body measurements of Nellore and Charolais calves

Abstract – The objective of this work was to assess the effect of genetic group and heterosis on the relationship between body weight and morphometric measurements, in purebred and crossbred animals from the second (G2) and third (G3) generations of Nellore and Charolais calves. Body weight (BW), average daily weight gain (ADG), foreleg circumference (FC), thoracic girth (TG), body length (BL), and croup height (CH) were measured at birth and at 63, 210, and 365 days of age in animals from G2 and G3. Charolais animals were superior to Nellore ones for gains BW, ADG, BL, and TG, as well as for the ratio between BW gain and CH gain; Nellore animals were superior for CH gains. Crossbred animals of both generations were superior to the purebred animals for gains of BW, BL, and CH. In G2, the predominance of Charolais genes resulted in greater gains of BW, ADG, FC, and TG. The G3 animals were superior to the purebred animals for ADG, FC, and TG. No differences were found for the ratio between gains of weight and morphometric measurements. Heterosis and complementarity are apparent for weight and body measurements of crossbred calves from rotational crossings.

Index terms: biometry, beef calves, complementarity, crossbred, growth.

Relação entre heterose, ganho de peso e medidas corporais de bezerros Nelore e Charolês

Resumo – O objetivo deste trabalho foi avaliar o efeito do grupo genético e da heterose na relação entre peso corporal e medidas morfométricas, em bezerros puros e mestiços das raças Nelore e Charolesa de segunda (G2) e terceira (G3) gerações. Peso corporal (PC), ganho de peso médio diário (GMD), circunferência da perna dianteira (CPD), circunferência torácica (CT), comprimento corporal (CC) e altura da garupa (AG) foram medidos ao nascimento e aos 63, 210 e 365 dias de idade, nos animais de G2 e G3. Os animais da raça Charolesa foram superiores aos da Nelore quanto aos ganhos de PC, GMD, CC e CT, e para a razão entre o ganho de PC e o de AG; os animais Nelore foram superiores quanto aos ganhos de AG. Animais mestiços de ambas as gerações foram superiores aos animais puros quanto aos ganhos de PC, CC e AG. Na G2, a predominância dos genes da raça Charolesa resultou em maiores ganhos de PC, GMD, CPD e CT. Os animais da G3 foram superiores aos puros quanto a GMD, CPD e CT. Não se encontraram diferenças na proporção entre os ganhos nas medidas de peso e morfometria. Heterose e complementaridade são aparentes para as medidas de peso e corporais de bezerros mestiços de cruzamentos rotacionais.

Termos para indexação: biometria, bezerros de corte, complementaridade, mestiço, crescimento.



Introduction

Body weight is the main criterion of the selection and management (feeding and health) of animals (Lucila Sobrinho et al., 2013). However, morphometric measurements can also be reliable, as they are less subject to temporary effects – such as the filling out of the gastrointestinal tract, when measuring body weight –, and they are more accurate than subjective methods, such as visual scores (Lesosky et al., 2013). However, there is a large variation of performance and body growth among breeds of beef cattle (Menezes et al., 2005). The crossing of Taurine breeds with Zebu cattle is widely used to increase the production of bovine herds by the exploration of the generated heteroses, with variations of performance between the generations of crossbreeds (Pacheco et al., 2014; Vaz et al., 2016).

Morphometric measurements can be taken with the aid of a tape measure, at low cost, good precision, consistency and high repeatability, with a low-standard deviation for the average values (Choy et al., 2017).

Morphometric measurements can be used as a selection criterion based on animal growth (Lesosky et al., 2013) and are useful to understand this growth (Choy et al., 2017), when associating them with body weight. The result is a better description of individuals and populations, indicating bodily changes over time. Further, these measurements are indirect predictors of performance and productive longevity (Lee & Kim, 2010) and can be used to estimate animal weight and conformation (Fernandes et al., 2010; Wangchuk et al., 2018).

Thoracic girth and croup height are positively correlated with body weight (Vanvanhossou et al., 2018). Methods to estimate the weight of cattle were developed using equations derived from morphometric body measurements (Gunawan & Jakaria, 2010). However, due to growth variations between races, there may be differences of precision of the models for the relationship between weight gain and increases of body measurements. As similar behavior occurs between the increase of measurements and the increase of body weight of *Bos taurus* and *Bos indicus* cattle and their crosses, it is possible to work on the creation of a weight-determination model through the increase of body measurements. The heterosis generated by crossing Charolais and Nellore animals increases the productivity of the herds (Favero et al.,

2019). However, all measured heteroses generally originate in characteristics that are very dependent on the breeding conditions of the animals, differently from body measurements which are less susceptible to variations in the environment (Mendonça et al., 2019).

The combination of body measurements and weight are of interest as predictors to the beef industry, as it allow of the determination of more productive animals (Vaz et al., 2016), with a higher proportion of heavier prime cuts in the carcass (Cardoso et al., 2020) and even a greater degree of fat (Sakamoto et al., 2014; Huerta-Leidenz et al., 2018).

The objective of this work was to evaluate the effect of genetic group and heterosis on the relationship between weight and morphometric measurements, in purebred and crossbred Nellore and Charolais calves from second and third generations, in continuous alternating crossing.

Materials and methods

The study was carried out at the Universidade Federal de Santa Maria, located in the Depressão Central region (at 29°43'S and 53°42'W, at 95 m altitude), in the state of Rio Grande do Sul, Brazil. According to the classification of Köppen-Geiger, the climate in the region is humid subtropical (cfa) (Moreno, 1961).

A total of 159 calves was used, from which 29 Charolais (C), 22 Nellore (N), and animals from the second generation (G2) (21 – 3/4C 1/4N, and 9 – 3/4N 1/4C), and third generation (G3) (44 – 5/8C 3/8N, and 34 – 5/8N 3/8C). All births occurred during the same calving season, and the animals were kept under the same conditions of health and nutritional management for 365 days. The C and N bulls used to father the purebred animals were the same ones used to father the crossbred animals.

From birth to early weaning (63 days of age), the calves and cows remained in areas of natural pasture at 0.9 AU ha⁻¹ (AU=animal unit) stocking density. After weaning, all calves were kept in a pen for 5 days, where they received concentrate with 22% crude protein. For the following 30 days, the diet was based on corn silage and concentrate at 1% body weight (BW) containing 18% crude protein. After this period, the calves were transferred to an area of millet pasture (*Penisetum americanum* Leeke), receiving the same concentrate at the same proportion. From five to 12 months of age,

the animals remained in areas of natural pasture, with a supplement of corn silage and concentrate (1% BW).

The calves were weighed at birth, at early weaning, and at 210 and 365 days of age. The increase of weight was calculated from the difference between each weighing divided by the number of days. Morphometric body measurements were taken together with each weighing: foreleg circumference (FC), thoracic girth (TG), body length (BL) and croup height (CH). During the different growth phases, calves up to 12 months of age were evaluated to verify whether the development in measurement and weight remained unchanged between the different genetic groups and mating systems under study. Foreleg circumference, thoracic girth, and body length were measured with a tape, and croup height was measured using a square. The foreleg circumference was measured halfway between the radiocarpal joint and the olecranon. Thoracic girth included the complete thoracic circumference of the animal, passing through the upper withers and lower sternum. Body length was measured between the scapulohumeral and coxofemoral joints, and croup height was taken as the distance between the upper part of the sacrum and the ground.

The effects of genetic group and heterosis on body weight, average daily weight gain, morphometric measurements and their increase, and the relationship between weight and measurements (kg m^{-1}) were evaluated for the different intervals. The heterosis was obtained by dividing the average value of the crossbred animals from each generation (G2 and G3) by the average value of the purebred animals, and the result was subtracted from 1 and multiplied by 100 (Menezes et al., 2005; Pacheco et al., 2010). The retained heterosis was calculated by dividing the average of all crossbred animals by the average of the purebred animals, subtracting the result from 1 and multiplying by 100 (Menezes et al., 2005; Pacheco et al., 2010).

The adopted experimental design was completely randomized, with different number of replicates per genetic group. Data of the different intervals were subjected to the analysis of variance, and the means were compared by t-test, with the aid of the SAS 9.0 statistical software SAS (SAS Institute Inc., Cary, NC, USA), using the following mathematical model:

$$Y_{ijklm} = \mu + P_i + SA_j + P \times SA_{ij} + GGk(SA_j) + P \times GG(SA)_{ijk} + AM I + OP_m + E_{ijklm},$$

where: Y_{ijklm} are the dependent variables (body measurements); μ is the average value of all observations of the characteristic; P_i is the effect of the i^{th} age for the measurements equal to 1 (birth), 2 (63 days), 3 (210 days), and 4 (365 days); SA_j is the effect of the j^{th} breeding system equal to 1 (purebred), 2 (crossbreds from G2), and 3 (crossbreds from G3); $P \times SA_{ij}$ is the effect of the interaction between the i^{th} interval and j^{th} breeding systems; $GGk(SA_j)$ is the effect of the genetic group with index k equal to 1 (Charolais) and 2 (Nellore), within SA_j ; 1 (3/4C 1/4N) and 2 (3/4N 1/4C) within SA_j 2, and 1 (5/8C 3/8N) and 2 (5/8N 3/8C) within SA_j 3; $P_i \times GGk(SA_j)$ is the effect of the interaction between the i^{th} P and k^{th} genetic group within the j^{th} breeding system; AM I is the covariate age of the mother, for animals of index 1 ($\beta \times s$ are regression coefficients associated with age of mother in years (AM, $3 \leq AM \leq 12$)); OP_m is the covariate calves birth order m ; and E_{ijklm} is the residual effect.

The covariables AM and OP were tested with the quadratic model and, as they were not significant, they were removed from the model.

Results and Discussion

The Charolais animals were superior to the Nellore ones for total weight gain and total average daily gain, from birth to 365 days of age (Table 1). The superiority within each breeding generation of the purebred Charolais animals, or those with a predominance of Charolais genes over the purebred Nellore animals, or with a predominance of Nellore genes, is due to the different characteristics of the selection process and the respective fitness of each breed. The Charolais animals were selected for their weight gain and greater body weight at maturity, in comparison to Nellore animals, since they are more adapted to meat production and traction strength, both of which require great musculature (Pacheco et al., 2010). The Natural selection of *indicus* breeds such as Nellore, included a tolerance to high-temperature climates, thus resulting in animals with a thinner, lighter body structure, with less bone and muscle mass, a thinner but larger hide with greater skinfolds, and better fat deposition than the Charolais (Calegare et al., 2009). Menezes et al. (2005) found additive genetic effect for muscle deposition in the carcass of predominant Charolais animals, in comparison to the predominant Nellore and

these showed a greater potential for the deposition of adipose tissue than the predominant Charolais (24.69 vs 21.61%).

Heterosis for weight gain was positive for each interval, except between 210 and 365 days of age in G2. Animals from G2 and G3 showed a significant heterosis for total weight gain and daily weight gain. To corroborate this, from 63 to 210, and from 210 to 365 days of age, the Charolais animals in the present study showed a greater average daily weight gain and a greater absolute daily weight gain than the Nellore animals. The G2 animals with a predominance of Charolais showed a greater average daily weight gain from 210 to 365 days of age than animals with a predominance of Nellore breed, whereas for G3, no significant differences were observed. The results for average daily weight gain showed that G2 animals may have benefitted from maternal heterozygosity, as their mothers came from the first generation of crossbreeds (F1), showing 100% heterozygosity (Leal et al., 2018). Due to this heterozygosity, the cows produce more milk with a higher level of total dry extract than those of pure breeds (Rodrigues et al., 2014; Mendonça et al., 2019). The heterosis of G3 animals for weight gain and average daily gain are influenced by individual

heterozygosity, which was significant in all age ranges, except for the period from birth to weaning (1-63 days of age). This lack of development in G3 animals of similar weight shows, by their heterozygosity, a greater homogeneity in the animals that comprise the generation, regardless of whether the animal genes are predominantly Charolais or Nellore.

Greater increases of total body length were observed for the Charolais animals in relation to the Nellore ones, while the Nellore animals were superior to Charolais for the total increase of croup height (Table 2). As to structure and conformation, it is expected that the purebred animals, or predominantly Charolais animals have longer carcasses, while the purebred animals or predominantly Nellore animals have longer hind and forelegs (Menezes et al., 2005). The increase of Nellore genes in crossings with European breeds reduces the length of the carcasses and increases the length of the limbs, highlighting the morphological differences and additive genetic effect between *Bos indicus* and *Bos Taurus*, as well as the additive genetic effect of the two breeds as being responsible for the variation (Mendonça et al., 2019); these results are reversed when Charolais genes are added (Menezes et al., 2005). The superiority in croup height of the Nellore animals is a

Table 1. Mean values, standard errors, and heterosis, for weight gain and average daily gain in beef cattle under development from 1 to 365 days of age, for genetic group and breeding system⁽¹⁾.

Genetic composition			Weight gain (kg) according to age				SEM	Average daily gain (kg) according to age				SEM
Bull	Cow	Calf	1-63	63-210	210-365	1-365		1-63	63-210	210-365	1-365	
C	C	C	27.02a	66.08a	66.23a	162.60a	4.61	0.45b	0.45a	0.46a	0.44a	0.03
N	N	N	37.77a	55.43a	33.99b	118.66b	5.26	0.55a	0.37b	0.23b	0.34b	0.03
Mean purebred			32.39A	60.76B	50.11A	140.63B	3.49	0.50B	0.41B	0.34B	0.39B	0.02
C	1/2N 1/2C	3/4C 1/4N	38.68a	67.26a	63.34a	174.58a	5.87	0.64a	0.46a	0.44a	0.47a	0.03
N	1/2C 1/2N	3/4N 1/4C	43.31a	65.44a	31.74b	144.31b	8.28	0.71 ^a	0.45 ^a	0.22b	0.39a	0.05
Mean G2			40.99A	66.35AB	47.54A	159.45A	5.22	0.67A	0.45AB	0.33B	0.43AB	0.03
C	3/4N 1/4C	5/8C 3/8N	37.20a	75.41a	64.08a	171.34a	3.73	0.56a	0.51a	0.44a	0.48a	0.02
N	3/4C 1/4N	5/8N 3/8C	31.00a	73.16a	53.54a	164.95a	4.29	0.52a	0.50a	0.37a	0.44a	0.02
Mean G3			34.10A	74.29A	58.81A	168.14A	2.87	0.54B	0.51A	0.41A	0.46A	0.02
Heterosis ⁽²⁾ (%)		G2	26.55	9.20	-5.13	13.38*		34.00*	9.76	-2.94	10.26	
		G3	5.28	22.27*	17.36	19.56*		8.00	24.39*	20.59*	17.95*	
Retained heterosis ⁽³⁾			15.92	15.73	6.12	16.47		21.00	17.07	8.82	14.10	
Differences crossbred vs ⁽⁴⁾		C (%)	38.95	6.42	-19.71	0.73		34.44	6.67	-19.57	1.14	
		N (%)	-0.60	26.86	56.44	38.04		10.00	29.73	60.87	30.88	

⁽¹⁾Means with equal, lowercase letters in the same column differ within the breeding system, by the t-test, at 5% probability. Means with equal, uppercase letters in the same column differ between breeding systems, by the t-test, at 5% probability. *Statistical difference at 5% probability in the comparison between crossbred and purebred animals. C, Charolais; N, Nellore; G2, second generation; G3, third generation. ⁽²⁾[(Mean of the crossbred generation / overall mean of the purebred generations) - 1]×100. ⁽³⁾[(Mean of the crossbred generations / overall mean of the purebred generations) - 1]×100. ⁽⁴⁾[(Overall mean of the crossbred generations / individual mean of the purebred generations) - 1]×100.

result of the evolutionary process of natural selection in environments with high temperatures (Randhawa et al., 2014). Under such conditions, a greater distance between the ground and the animal's body results in body temperature being more efficiently maintained on warmer days (Vaz et al., 2016). The croup height has a heritability equal to 0.28, a value considered moderate (Silveira et al., 2017). In addition, the mothers of calves from the two generations of crossbred animals were also crossbreeds, affording possible benefits from maternal heterosis (Wakchaure et al., 2015; Leal et al., 2018) through an increase of milk production and nutrient density (Mendonça et al., 2019), providing the calves with a greater input of energy, and relating positively to croup height (Rodrigues et al., 2014).

Purebred animals did not differ for the increase in foreleg circumference in any of the time intervals (Table 3). Charolais animals showed a greater total increase of thoracic girth from birth to 365 days. Foreleg circumference and thoracic girth are important, as they are positively related to the muscular development of the animals (Menezes et al., 2005), as well as to the size and conformation of the carcass (Pacheco et al., 2014), and to its cut yield (Choy et al., 2017). Cardoso et al. (2020) developed equations to determine the weight of

commercial cuts and the degree of carcass fat, using morphometric measurements and ultrasound, and they found that carcass measurements were responsible for explaining 44 to 94% of the final cut weight of meat. Charolais animals were superior due to the intensive selection for musculature, weight gain, and adult weight (Vaz et al., 2016).

For the total increase of measurements, a significant heterosis was found in both generations for body length and height in G3, in relation to G2, as well as in the purebred animals, for foreleg circumference, and in G3, for thoracic girth compared to the purebred animals (Tables 2 and 3).

No differences were found between the genetic groups within the breeding systems for increases of weight in relation to increases in foreleg circumference, thoracic girth, or body length, for the different stages under evaluation (Tables 4 and 5).

The Charolais animals gained more weight per unit of measurement for croup height from 63 to 365 days of age than the Nelore animals. Comparing the generations, a difference was only observed in those variables that relate weight gain to increases in foreleg circumference and thoracic girth from 210 to 365 days of age, for which the G3 animals superior to the

Table 2. Mean values, standard errors, and heterosis, for gains of body length and croup height in beef cattle under development from 1 to 365 days of age, for genetic group and breeding system⁽¹⁾.

Genetic composition			Body length (cm) according to age				SEM	Croup height (cm) according to age				SEM
Bull	Cow	Calf	1-63	63-210	210-365	1-365		1-63	63-210	210-365	1-365	
C	C	C	15.90a	20.04a	13.25a	49.52a	1.25	8.68b	12.58a	10.13a	31.82b	0.84
N	N	N	18.66a	18.94a	8.80b	45.07b	1.42	12.40a	13.45a	10.36a	35.22a	0.96
Mean purebred			17.28A	19.49A	11.02A	47.30B	0.94	10.54A	13.01A	10.24B	33.52B	0.63
C	1/2N 1/2C	3/4C 1/4N	19.69a	18.59a	11.92a	52.16a	1.56	12.47a	13.80a	10.52a	37.37a	1.05
N	1/2C 1/2N	3/4N 1/4C	20.87a	18.65a	8.98a	49.42a	2.24	12.37a	15.48a	7.48a	35.70a	1.50
Mean G2			20.28A	18.62A	10.45A	50.79A	1.40	12.42A	14.64A	9.00B	36.54A	0.94
C	3/4N 1/4C	5/8C 3/8N	18.05a	22.11a	12.91a	51.98a	1.01	11.90a	14.58a	12.08a	37.94a	0.68
N	3/4C 1/4N	5/8N 3/8C	17.29a	19.62a	12.29a	49.73a	1.16	10.85a	13.79a	12.61a	37.85a	0.78
Mean G3			17.67A	20.87A	12.60A	50.86A	0.77	11.37A	14.18A	12.34A	37.89A	0.52
Heterosis ⁽²⁾ (%)		G2	17.36	-4.46	5.17	7.38*		17.84	12.53	-12.11	9.01*	
		G3	2.26	7.08	14.34	7.53*		7.87	8.99	20.51*	13.04*	
Retained heterosis ⁽³⁾			9.81	1.31	4.58	7.45		12.86	10.76	4.20	11.02	
Differences crossbred vs ⁽⁴⁾		C (%)	19.34	-1.47	-13.02	2.64		37.04	14.55	5.33	16.95	
		N (%)	1.69	4.25	30.97	12.77		-4.07	7.14	2.99	5.66	

⁽¹⁾Means with equal, lowercase letters in the same column differ within the breeding system, by the t-test, at 5% probability. Means with equal, uppercase letters in the same column differ between breeding systems, by the t-test, at 5% probability. *Statistical difference at 5% probability comparing crossbred vs purebred animals. C, Charolais; N, Nelore; G2, second generation; G3, third generation. ⁽²⁾[(Mean of the crossbred generations / overall mean of the purebred generations) - 1]×100. ⁽³⁾[(Mean of the crossbred generations / overall mean of the purebred generations) - 1]×100. ⁽⁴⁾[(Overall mean of the crossbred generations / individual mean of the purebred generations) - 1]×100.

Table 3. Mean values, standard errors, and heterosis for gains of foreleg circumference and thoracic girth in beef cattle under development from 1 to 365 days of age, for genetic group and breeding system⁽¹⁾.

Genetic composition			Foreleg circumference (cm) according to age				SEM	Thoracic girth (cm) according to age				SEM
Bull	Cow	Calf	1-63	63-210	210-365	1-365		1-63	63-210	210-365	1-365	
C	C	C	3.43a	4.95a	2.14a	10.59a	0.43	18.60b	23.46a	22.43a	65.08a	1.36
N	N	N	4.67a	4.27a	1.52a	9.70a	0.49	23.20a	21.56a	16.11b	58.38b	1.55
Mean purebred			4.05A	4.61A	1.83B	10.14B	0.32	20.90A	22.51B	19.27AB	61.73B	1.03
C	1/2N 1/2C	3/4C 1/4N	3.38a	4.81a	3.08a	11.88a	0.53	21.83a	22.12a	20.83a	66.83a	1.71
N	1/2C 1/2N	3/4N 1/4C	3.94a	4.50a	0.61b	9.39b	0.76	23.72a	21.39a	12.72b	59.06b	2.43
Mean G2			3.66A	4.66A	1.84AB	10.64B	0.47	22.78A	21.75B	16.78B	62.94AB	1.53
C	3/4N 1/4C	5/8C 3/8N	4.69a	4.92a	2.53a	11.76a	0.34	21.60a	25.31a	21.81a	67.24a	1.10
N	3/4C 1/4N	5/8N 3/8C	3.14b	5.55a	2.80a	11.95a	0.39	19.41a	25.44a	19.32a	65.59a	1.26
Mean G3			3.91A	5.23A	2.67A	11.85A	0.26	20.50A	25.37A	20.56A	66.41A	0.84
Heterosis ⁽²⁾ (%)			G2	-9.63	1.08	0.55	4.93	9.00	-3.38	-12.92	1.96	
			G3	-3.46	13.45	45.90*	16.86*	-1.91	12.71*	6.69	7.58*	
Retained heterosis ⁽³⁾				-6.54	7.27	23.22	10.90	3.54	4.66	-3.11	4.77	
Differences crossbred vs ⁽⁴⁾			C (%)	10.35	-0.10	5.37	6.19	16.34	0.43	-16.76	-0.62	
			N (%)	-18.95	15.81	48.36	15.93	-6.72	9.28	15.89	10.78	

⁽¹⁾Means with equal, lowercase letters in the same column differ within the breeding system, by the t-test, at 5% probability. Means with equal, uppercase letters in the same column differ between breeding systems, by the t-test, at 5% probability. *Statistical difference at 5% probability comparing crossbred vs purebred animals. C, Charolais; N, Nellore; G2, second generation; G3, third generation. ⁽²⁾ $[(\text{Mean of the crossbred generations} / \text{overall mean of the purebred generations}) - 1] \times 100$. ⁽³⁾ $[(\text{Mean of the crossbred generations} / \text{overall mean of the purebred generations}) - 1] \times 100$. ⁽⁴⁾ $[(\text{Overall mean of the crossbred generations} / \text{individual mean of the purebred generations}) - 1] \times 100$.

Table 4. Mean values, standard errors, and heterosis for gain of body weight (GBW) / gain of foreleg circumference (GFC), and GBW / gain of thoracic girth (GTG) in beef cattle under development from 1 to 365 days of age, for genetic group and breeding system⁽¹⁾.

Genetic composition			GBW / GFC (kg cm ⁻¹) according to age				SEM	GBW / GTG (kg cm ⁻¹) according to age				SEM
Bull	Cow	Calf	1-63	63-210	210-365	1-365		1-63	63-210	210-365	1-365	
C	C	C	10.17a	15.44a	14.11a	16.16a	2.52	1.55a	2.83a	1.93a	2.46a	0.24
N	N	N	8.39a	14.57a	11.68a	12.39a	2.88	1.56a	2.57a	2.14a	2.06a	0.27
Mean purebred			9.28A	15.01A	12.89B	14.28A	1.91	1.56A	2.69A	2.04B	2.26A	0.18
C	1/2N 1/2C	3/4C 1/4N	13.73a	15.59a	16.25a	13.81a	3.13	1.80a	3.01a	2.99a	2.54a	0.29
N	1/2C 1/2N	3/4N 1/4C	11.83a	18.42a	14.15a	15.57a	4.53	1.81a	3.11a	2.64a	2.39a	0.42
Mean G2			12.78A	17.00A	15.20AB	14.69A	2.81	1.80A	3.06A	2.81A	2.46A	0.26
C	3/4N 1/4C	5/8C 3/8N	9.63a	19.60a	18.51a	15.05a	2.05	1.74a	2.97a	2.95a	2.54a	0.19
N	3/4C 1/4N	5/8N 3/8C	12.28a	14.21a	20.09a	13.89a	2.37	1.57a	2.88a	2.92a	2.48a	0.22
Mean G3			10.96A	16.90A	19.30A	14.47A	1.56	1.66A	2.93A	2.94A	2.51A	0.15
Heterosis ⁽²⁾ (%)			G2	37.72	13.26	17.92	2.87	15.38	13.75	37.75*	8.85	
			G3	18.10	12.59	49.73*	1.33	6.41	8.92	44.12*	11.06	
Retained heterosis ⁽³⁾				27.91	12.92	33.82	2.10	10.90	11.34	40.93	9.96	
Differences crossbred vs ⁽⁴⁾			C (%)	16.72	9.78	22.25	-9.78	11.61	5.83	48.96	1.02	
			N (%)	41.48	16.33	47.69	17.68	10.90	16.54	34.35	20.63	

⁽¹⁾Means with equal, lowercase letters in the same column differ within the breeding system, by the t-test, at 5% probability. Means with equal, uppercase letters in the same column differ between breeding systems, by the t-test, at 5% probability. *Statistical difference at 5% probability comparing crossbred vs purebred animals. C, Charolais; N, Nellore; G2, second generation; G3, third generation. ⁽²⁾ $[(\text{Mean of the crossbred generations} / \text{overall mean of the purebred generations}) - 1] \times 100$. ⁽³⁾ $[(\text{Mean of the crossbred generations} / \text{overall mean of the purebred generations}) - 1] \times 100$. ⁽⁴⁾ $[(\text{Overall mean of the crossbred generations} / \text{individual mean of the purebred generations}) - 1] \times 100$.

purebred ones, and were not different from the G2 animals. The crossbred animals showed superiority for absolute weight gain, average daily gain, body length, croup height, foreleg circumference and thoracic girth, and for the relationship between the increase of weight and the increase of morphometric body measurements. The higher performance of the crossbred animals is probably the result of maternal heterozygosity up to weaning, and direct heterozygosity after that (Leal et al., 2018). In addition, the increases of the crossbred animals were positive in relation to the average value of these characteristics in the purebred animals (Mendonça et al., 2019). The purebred or predominantly Charolais animals showed not only a greater weight gain than the purebred or predominantly Nellore animals, but they showed also a greater body length that directly affected the relationship between weight gain and gain of body length, balancing the greater weight gain of the Charolais animals by their greater body length. Heterosis in these relationships was not significant. The differences for the average increases of the crossbred animals were positive in the comparison to those of the purebred Nellore

animals; however, they were negative, when compared to those of the purebred Charolais animals. For the relationship between weight gain and croup height, the superiority of the purebred or predominantly Charolais G2 animals, in comparison to the purebred or predominantly Nellore G2 animals, is attributed to the fact that Charolais animals showed greater weight gains and smaller croup height gains than Nellore animals, for the different time intervals.

In the comparison of the breeding systems, no differences were observed between the average values of the purebred, G2, or G3 animals. This lack of difference is due to the heterosis in this relationship, which is evident, but not significant; it is also due to the positive differences for the average increase of the crossbred animals, in comparison to the purebred Nellore animals, and to the negative differences for this parameter, when comparing the crossbred animals to the purebred Charolais animals.

The complementarity of the breeds is found when the differences of the crossbred animals from both generations are evaluated separately, in relation to the purebred animals. In the present work, for

Table 5. Mean values, standard errors, and heterosis for gain of body weight (GBW) / gain of body length (GBL), and gain of body weight (GBW) / gain of croup height (GCH) in beef cattle under development from 1 to 365 days of age, for genetic group and breeding system⁽¹⁾.

Genetic composition			GBW / GBL (kg cm ⁻¹) according to age				SEM	GBW / GCH (kg cm ⁻¹) according to age				SEM
Bull	Cow	Calf	1-63	63-210	210-365	1-365		1-63	63-210	210-365	1-365	
C	C	C	2.66a	3.91a	5.29a	3.16a	0.67	3.44a	5.54a	6.85a	5.16a	0.46
N	N	N	1.35a	2.96a	4.07a	2.50a	0.77	2.99a	4.17b	3.58b	3.39b	0.51
Mean purebred generation			2.01A	3.44A	4.68A	2.83A	0.51	3.22A	4.86A	4.22A	4.28A	0.34
C	1/2N 1/2C	3/4C 1/4N	2.59a	2.28a	5.77a	3.55a	0.83	3.20a	4.87a	6.27a	4.51a	0.56
N	1/2C 1/2N	3/4N 1/4C	2.21a	3.58a	4.63a	3.01a	1.21	3.54a	4.12a	3.64b	3.93a	0.80
Mean of G2			2.40A	2.93A	5.20A	3.28A	0.75	3.37A	4.49A	4.95A	4.22A	0.50
C	3/4N 1/4C	5/8C 3/8N	2.06a	3.42a	4.35a	3.23a	0.55	3.20a	5.29a	5.62a	4.50a	0.36
N	3/4C 1/4N	5/8N 3/8C	1.64a	4.12a	5.30a	3.38a	0.63	4.07a	5.73a	4.92a	4.43a	0.42
Mean of G3			1.85A	3.77A	4.82A	3.30A	0.43	3.63A	5.51A	5.27A	4.47A	0.28
Heterosis ⁽²⁾ (%)		G2	19.46	-14.83	11.11	15.90		4.66	-7.61	17.30	-1.40	
		G3	-7.96	9.59	2.99	16.61		12.73	13.37	24.88	4.44	
Retained heterosis ⁽³⁾			5.72	-2.62	7.05	16.25		8.70	2.88	21.09	1.52	
Differences crossbred vs ⁽⁴⁾		C (%)	-20.11	-14.32	-5.29	4.11		1.74	-9.75	-25.40	-15.79	
		N (%)	57.41	13.18	23.10	31.60		17.06	19.90	42.74	28.17	

⁽¹⁾Means with equal, lowercase letters in the same column differ within the breeding system, by the t-test, at 5% probability. Means with equal, uppercase letters in the same column differ between breeding systems, by the t-test, at 5% probability. *Statistical difference at 5% probability comparing crossbred vs purebred animals. C, Charolais; N, Nellore; G2, second generation; G3, third generation. ⁽²⁾ $[(\text{Mean of the crossbred generations} / \text{overall mean of the purebred generations}) - 1] \times 100$. ⁽³⁾ $[(\text{Mean of the crossbred generations} / \text{overall mean of the purebred generations}) - 1] \times 100$. ⁽⁴⁾ $[(\text{Overall mean of the crossbred generations} / \text{individual mean of the purebred generations}) - 1] \times 100$.

all characteristics analyzed, the complementarity was evidenced in almost all evaluations of weight and measurements, as well as in the relationship between both, when the increase of weight per unit of measurement was analyzed, and the differences resulted positive for the predominance of *Bos Taurus*, or *Bos indicus*, according to the selection process (Calegare et al., 2009; Pacheco et al., 2010).

The results showed characteristics of complementarity for the crosses between breeds. Due to the additive genetic merit of the Charolais and Nellore breeds, absolute weight gain, average daily gain, body length, croup height, foreleg circumference, and especially thoracic girth, were all optimized. The same fact was observed in the absolute relationships between weight gain and gains for thoracic girth, body length, and particularly croup height and foreleg circumference. The inclusion of Nellore genes afforded increased gains of croup height, a product of crossbreeding, in comparison to the Charolais breed. The addition of Charolais genes resulted in an increase of weight gain, in the morphometric measurements linked to the muscularity of the animals, as well as in the relationship between weight gain and the gains of morphometric measurements, in comparison to the Nellore breed, which is mainly due to the increase of weight gain.

The effect of complementarity between these two breeds is mainly due to their significant genetic distance (Schiermiester et al., 2015; Mendonça et al., 2019). The characteristics of croup height and withers height are more susceptible to additive genetic gain, since they have moderate heritability value (Silveira et al., 2017). However, for the characteristics of muscularity, such as foreleg circumference and thoracic girth, the expression of complementarity is less pronounced, due to its average heritability (Silveira et al., 2017), furthermore, these characteristics together with weight are highly susceptible to environmental effects such as variations of climate and nutrition (Walmsley et al., 2016). The increase of weight gain is highly correlated with increased gains of morphometric body measurements. Certain body measurements are limited by the physiological maturity of the animal (Sakamoto et al., 2014), in which measurements such as body length and croup height are directly related to, and limited by, the development of bone tissue, while thoracic girth, foreleg circumference, and body weight

are mainly related to the development of muscle and adipose tissue, and follow their variation curves (Lee & Kim, 2010). As such, high, positively correlated responses between thoracic girth and body weight are to be expected (Rezende et al., 2014).

Conclusions

1. Purebred or second-generation predominantly Charolais crossbred animals are more efficient for gaining weight and have greater muscularity than purebred or predominantly Nellore animals.

2. Nellore animals gain more croup height, but their genetic inclusion does not affect this characteristic in crossed genotypes.

3. The third generation from alternating crossbreeding between Charolais and Nellore produces animals which are homogeneous for both weight gain and morphometric measurements.

4. Crossbred animals are superior to purebred ones in increasing body weight and morphometric measurements, especially third-generation animals, except for the relationship between gain of body weight and gain of croup height.

5. There is no difference for the relationship between weight gain and the gains of morphometric measurements for genotype within the generations of alternating crosses, which shows a strong and homogeneous relationship between increased body weight and skeletal, muscular and adipose development in the animals; this fact suggests that these measurements can be taken and used as good indicators of weight gain and body development of the animal.

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