


Genetic and environmental effects on weaning weight in crossbred beef cattle (*Bos taurus* × *Bos indicus*)

P. Dominguez-Castaño^{1,2} , A. M. Maiorano¹, M.H.V. de Oliveira¹,
L.E.C. dos Santos Correia¹ and J.A.II.V. Silva³

Animal Research Paper

Cite this article: Dominguez-Castaño P, Maiorano AM, de Oliveira MHV, dos Santos Correia LEC, Silva JAIIV (2021). Genetic and environmental effects on weaning weight in crossbred beef cattle (*Bos taurus* × *Bos indicus*). *The Journal of Agricultural Science* **159**, 139–146. <https://doi.org/10.1017/S0021859621000344>

Received: 21 May 2020

Revised: 17 February 2021

Accepted: 5 April 2021

First published online: 28 April 2021

Key words:

Crossbreeding; heterozygosis; maternal ability; pre-weaning growth

Author for correspondence:

P. Dominguez-Castaño, E-mail:
pablodomca11@gmail.com

¹Departamento de Zootecnia, Faculdade de Ciências Agrárias e Veterinárias, Universidade Estadual Paulista, Jaboticabal, SP 14884-900, Brazil; ²Facultad de Medicina Veterinaria, Fundación Universitaria Agraria de Colombia, Bogotá D.C. 111166, Colombia and ³Departamento de Melhoramento e Nutrição Animal, Faculdade de Medicina Veterinária e Zootecnia, Universidade Estadual Paulista, Botucatu, SP 18618-000, Brazil

Abstract

This work aimed to evaluate the effects of sire's and dam's biological type, dam's age class at calving and individual heterozygosis, and to estimate variance components for weaning weight adjusted to 210 days (WW210) in beef cattle of different breed groups. Records of 13 687 animals, obtained from 2000 to 2007, were used. Bulls from the biological types Zebu (N), Adapted (A), British (B), Continental (C) and $\frac{1}{4}N|\frac{1}{4}A|\frac{1}{4}B|\frac{1}{4}C$ were mated with purebred zebu (N) and crossbred females ($\frac{1}{2}C|\frac{1}{2}N$ and $\frac{1}{2}B|\frac{1}{2}N$). Dam age at calving was 3–12 years. The influence of several effects on WW210 was tested using the least square method. Variance component analysis was performed using a Bayesian approach. The model included contemporary group, dam's age class at calving, sire's and dam's biological types as systematic effects, animal's age and individual heterozygosis as linear covariates, and direct and maternal additive genetic, maternal permanent environmental and residual effects as random effects. The progeny of bulls from biological type B and the crossbred cows showed higher WW210 means. Cows at 6–7 years old weaned heavier calves. Direct and maternal heritability estimates for WW210 were 0.5 ± 0.04 and 0.1 ± 0.02 , respectively. Calves with 100% individual heterozygosis weighed on average 25.98 kg more at weaning compared to progenies from pure breeds. Sire's and dam's biological types influence the WW210 of the crossed progenies. Crossbred cows produce heavier calves compared to biological type N cows. These results and the obtained direct and maternal heritabilities suggest it is possible to choose the lines of sires and dams that could be used to make the crosses to obtain progenies with better performance for WW210.

Introduction

The interest in genetically improving crossbred zebu cattle populations and better understanding the phenotypic and genetic variations of economically important traits has been increasing throughout the world during the last decade (Sørensen *et al.*, 2008; Grigoletto *et al.*, 2019). The use of artificial insemination along with accurate genetic evaluations offers confidence in using pure breeds or composite breeds to explore the advantages of crossbreeding in production traits (Teixeira and Albuquerque, 2005).

Crossbreeding and genetic selection allow obtaining more efficient animals in adverse climates such as tropical climates, with low-quality forages and high presence of parasites. The increase in production is due in part to heterosis; however, caution should be taken because the non-additive effect of genes can also contribute to this increment. To maintain this gain in production constant, it is necessary to keep high levels of heterozygosis.

The superiority of crossbred animals is due to the combination of traits from complementary breeds, the additive effect and heterosis (Leal *et al.*, 2018). The potential growth and adaptability of crossed animals may increase the total cattle production index by up to 50% in *Bos taurus* and *Bos indicus* crossbreds when compared to purebred herds under tropical conditions, types of climates Aw (Tropical Savannah) and Cfa (Humid Subtropical) according to the Köppen–Geiger classification (Teixeira and Albuquerque, 2005). This increase in production indicates that crossbreeding can be a strategy to promote efficiency in beef cattle production.

In addition to the heterosis effect on individual performance, maternal heterosis results in maternal environmental benefit and higher milk yield, which allows for higher calf growth during the lactation (Leal *et al.*, 2018). Some studies have reported the influence of cows (Meyer *et al.*, 1994; Leal *et al.*, 2018; Mendonça *et al.*, 2019) and bulls (Baker *et al.*, 2001; Schatz *et al.*, 2014; Cardoso *et al.*, 2018) breed compositions on the calf performance, assessing mainly the weaning weight. However, environmental factors such as the nutritional and health

management of the herd, body condition and age of the dam at calving may impact calf growth, being the latter factor of great relevance as it affects the maternal-offspring behaviour and milk production (Silva *et al.*, 2015). Identifying independent effects that impact weaning weight in crossbred animals may benefit the production index as well as the design of optimal breeding programmes.

The objectives of this study were defined in two steps: (I) to investigate whether sire's and dam's biological types, dam's age class at calving and individual heterozygosity influence the weaning weight in crossbred beef animals raised under Tropical Savannah conditions; and (II) to estimate variance components and direct and maternal heritabilities for weaning weight in the studied population.

Material and methods

Data description

The data set comprised 13 687 phenotypic records of animals born between 2000 and 2007. The weaning weight was adjusted to 210 days (WW210), as follows:

$$WW210 = \left(\left(\frac{WW - BW}{WA} \right) \times 210 \right) + BW$$

where WW210 is the phenotype adjusted to 210 days of age; BW is the birth weight; WW is the weaning weight and WA is the weaning age.

All the animals were raised in the State of Goiás, Midwest region of Brazil. This region is characterized by an average annual rainfall of 1663 mm and temperatures ranging from 20 to 35°C; the climate type is classified as tropical savannah according to Köppen and Geiger (1936); with a predominance of grasses of genus *Brachiaria*. Regardless of the breed, the calves were supplemented in a creep feeding system (18% of crude protein, at 500 g/animal/day) until approximately 7 months of age, when they were weaned and weighed. Creep feeding is a common practice in farms that make use of technology to improve production in Brazil (Ferraz and Felício, 2010), where the main objectives are to obtain increased weaning weights, greater weight gains after weaning and reduced the time to finish calves. After weaning, the animal's nutritional management consisted of pastures, and the animals were supplemented with mineral salt *ad libitum*. The herd's health management followed the technical standards for this region, including vaccinations and treatments for endo and ectoparasites.

Crossbred calves were produced with artificial insemination of mating purebred zebu cow (N; including Nelore, Brahman and Tabapua breeds) and crossbred ($\frac{1}{2}B|\frac{1}{2}N$ and $\frac{1}{2}C|\frac{1}{2}N$) cows to bulls from four different biological type compositions being used 58 Zebu bulls (N), 14 Adapted bulls (A), 23 British bulls (B) and seven Continental bulls (C), following the so-called NABC system, and three crossbred bulls ($\frac{1}{4}N|\frac{1}{4}A|\frac{1}{4}B|\frac{1}{4}C$) (Table 1). The breed classification by biological types, the so-called NABC system, was described in details by Ferraz *et al.* (1999), which aimed to associate breeds to four different groups according to their geographic origins, attributing N to zebu breeds, A to Adapted taurine breeds, C to Continental breeds and B to British breeds. Considering the four different biological types previously described, our data set was composed of the following breeds followed by the number of bulls used per breed: *B. indicus* animals such as Nelore [46], Brahman [10] and Tabapua

[2] breeds are classified as type N; *B. taurus* animals adapted to the tropics by natural or artificial selection, including Bonsmara [3], Caracu [2], Romo-Sinuano [1], Senepol [5] and Santa Gertrudis [3] breeds; *B. taurus* animals from British origin such as Aberdeen Angus [12], Red Angus [7], Devon [1] and Hereford [3]; *B. taurus* animals from Continental Europe, including Simmental [2], Limousin [3] and Brown-Swiss [2] breeds. These breeds were used in the crossbreeding that originated the progenies assessed in this study.

The farm that provided the access to the data set raises in general Nelore beef cattle and started a crossbreeding programme in 2000, inseminating cows with semen from bulls of biological type B. Later, bulls from other biological types described above were considered. Therefore, there was no design in the use of bulls and cows in the crossings. Consequently, there is an imbalance in the number of calves, mainly of biological types N and B compared to other types. This imbalance can also be seen in the number of cows per biological type. For instance, Nelore cows are most representative of the biological type N, 80%, being the remaining portion composed of Brahman and Tabapua cows (Table 1).

The choice of biological types to be used in the crosses was made trying to prioritize the maximum exploration of heterozygosity; therefore, direct matings were conducted in a way that the composition of the parents was genetically distant from each other, i.e. parents composed by totally different biological types (Table 1). The genetic distance among cattle breeds was described as a triangle where each vertex is represented by European taurine, West African taurine and indicine populations (Mastrangelo *et al.*, 2020). The representation of the genetic segregation of European populations grouped breeds from biological types B and C in different clusters, indicating the existence of genetic distances among them (Mastrangelo *et al.*, 2020). In the case of biological type A, the breeds that compose this type are formed by the mating of European taurine and African taurine breeds (i.e. Senepol and Bonsmara), European taurine and Indian zebuine breeds (i.e. Santa Gertrudis), and matings within European breeds (i.e. Romosinuano and Caracu). The last combinations of European breeds were introduced in South America during the Colonization period and, nowadays, they form what is known as Creole cattle. These adapted breeds composing type A exhibit a lower genomic distance when compared to zebu and taurine breeds (Bovine HapMap Consortium, 2009).

Statistical analysis

Testing variables

The effects and interactions that could influence the WW210 trait were tested using the least square method with the PROC GLM procedure available in the SAS software (SAS, 2011). If the effects of its interactions were significant at a level of significance equal to 1% ($P < 0.01$), they were included in the mixed model to evaluate WW210.

The evaluated effects were: birth year (animals born from March to year 'x' to February to year 'x + 1', where x ranged from 2000 to 2007), birth season (dry season refers to births concentrated from March to August, and rainy season refers to births concentrated from September to February), sex, management lot at weaning (paddock grazing), dam's age class at calving (evaluated in ten classes: 1st = less and equal than 3 years of age, 2nd = 4 years, 3rd = 5 years of age, ..., until 10th = 12 years or older), sire's biological type (evaluated in five classes: N, A, B, C, $\frac{1}{4}N|\frac{1}{4}A|\frac{1}{4}B|\frac{1}{4}C$), cow's biological type (evaluated in three

Table 1. Number of animals grouped according to the sire's and cow's biological type considering the NABC system (Ferraz *et al.*, 1999)

		Cow biological type ^a			Total
		N	½B ½N	½C ½N	
Sire biological type ^a	N_obs	7454	159	957	8570
N	59	10 854	53	148	11 055
A	15	127	116	712	955
B	21	1324	–	103	1427
C	7	140	–	–	140
¼N ¼A ¼B ¼C	3	33	–	77	110
Total	105	12 478	169	1040	13 687

^aBiological type: N = Zebu; A = Adapted taurine; B = British; C = Continental.

classes: N, ½C|½N, ½B|½N) and individual heterozygosis. Because the interaction of birth year, birth season, sex and paddock grazing was statistically significant ($P < 0.01$), these effects were considered to generate the contemporary groups (CGs). It is important to note that each CG presented animals from different biological types. Individuals with records above or below 3.5 standard deviations from its CG mean were removed. After editing the data, crossbreed cows were more prevalent at ages under 9 years old.

The effects of dam's age class at calving, the sire's biological type and the cow's biological type also influenced the WW210 trait ($P < 0.01$). Although WW210 was preadjusted, the effect of animal's age in the measurement of weaning weight was still significant in our previous analysis, then it was included as a linear covariable in the final model.

Total individual heterozygosis (TH) is the sum of the direct heterozygoses considering the percentages of the biological types N × A; N × B; N × C; A × B; A × C; and B × C, existing in the racial composition of the animal. TH was calculated as follows: $H_{ij} = \sum_{i \neq j} r_i r_j$, where H_{ij} is the direct heterozygosis between

the biological type (NABC) i and (NABC) j in the progeny, r_i and r_j are the percentage of biological type contribution based on the NABC system for sire i and cow j (Mourão *et al.*, 2007). Maternal heterozygosis was not significant in the previous analysis probably due to the distribution of the number of observations in relation to the cows' biological types, therefore it was not included in the model. The pedigree file contained 21 784 animals from six generations, including records of 13 687 progenies from 105 bulls and 8570 dams, distributed in 61 CGs. The reduced amount of bulls is due to the large use of artificial insemination technology. The distribution of the number of bulls and cows and their progenies classified by sire's and dam's biological type was described in Table 1.

Genetic parameters estimation

The estimation of variance components was performed by the Bayesian approach, using a single-trait animal model and the software GIBBS1F90 (Misztal *et al.*, 2002). The model was composed of CG, dam's age class at calving, sire and dam biological types as systematic effects, animal's age and individual heterozygosis as linear covariates, and direct and maternal additive genetic, maternal permanent environmental and residual effects as random effects. The average of calves per dam was 1.6. Due to the structure of the data, it was possible to include the maternal effect in

the model, but the estimation of this effect can be biased. The mixed model adopted can be written in matrix notation as:

$$y = X\beta + Z_1a + Z_2m + Wp + e$$

where y is the vector of the observed phenotypic records for WW210; X is the incidence matrix of systematic effects; β is the vector of the systematic effects; Z_1 is the incidence matrix of direct genetic effects; a is the vector of direct genetic effects; Z_2 is the incidence matrix of maternal genetic effects; m is the vector of maternal genetic effects; W is the incidence matrix of permanent maternal environmental effects; p is the vector of permanent maternal environmental effects; and e is the vector of random residual effects. The data structure from commercial herds is inadequate to estimate the covariance for direct and maternal genetic effects (Teixeira and Albuquerque, 2005). Thus, following the recommendation of these authors, covariance between these effects was assumed to be null.

A uniform *a priori* distribution was defined for the systematic effects (β). Gaussian and inverted Wishart distributions were adopted as *a priori* distributions for random effects and (co)variance components, respectively (Van Tassel and Van Vleck, 1996). The marginal distributions are represented as follows:

β, α constant;

$$\begin{pmatrix} a \\ m \end{pmatrix} | G_a, G_m, G_{am} \sim MVN \left(\begin{pmatrix} 0 \\ 0 \end{pmatrix}, \begin{pmatrix} A \otimes G_a & A \otimes G_{am} \\ A \otimes G'_{am} & A \otimes G_m \end{pmatrix} \right)$$

$$p | P \sim MVN[0, (I_n P)]$$

$$G_a | S_a, v_a \sim IW[S_a v_a, v_a]$$

$$G_m | S_m, v_m \sim IW[S_m v_m, v_m]$$

$$P | S_p, v_p \sim IW[S_p v_p, v_p]$$

$$R | S_r, v_r \sim IW[S_r v_r, v_r]$$

where A is the relationship matrix; G, P and R are the (co)variances matrices of direct and maternal genetics effects, permanent

environmental effects and residual effects, respectively; I_n is the identity matrix; \otimes is the Kronecker product; S_a and v_a , S_v and v_m , S_p and v_p , and S_r and v_r are the *a priori* values and degrees of freedom for direct additive genetic, maternal additive genetic, permanent environmental and residual (co)variances, respectively (Van Tassel and Van Vleck, 1996). Genetic (co)variance estimates reported in the literature were used as *a priori* values in the analyses.

A single chain with a length of 11 000 000 samples was defined for Gibbs sampling, discarding the first 1 000 000 samples and collecting samples at every 20 cycles, resulting in 50 000 samples for inference.

The convergence was verified by assessing the effective chain size and the test proposed by Geweke (1991). The convergence diagnosis by the effective chain size is based on means and variances, and its efficiency is confirmed if the evaluated components present posterior Gaussian distribution (Gelman *et al.*, 2013).

The posterior (co)variances were used to estimate the measures of central tendency of direct and maternal additive heritabilities (h_a^2 and h_m^2 , respectively), as well as the posterior standard deviation and higher density intervals to 95%.

A new analysis was performed in the GIBBS1F90 programme (Misztal *et al.*, 2002) using the same mixed model described above but assuming that (co)variances were known. The (co)variances estimates obtained in the previous analysis (Table 2) were defined as known values by the addition of the command line 'OPTION fixed_var all' in the parameter file used in GIBBS1F90. This command uses fixed (co)variances and estimates solutions for all effects in the model. Based on this parameter file, a new Markov chain of 1 000 000 cycles was established, with a burn-in of 10 000 cycles and a thin interval of ten cycles, resulting in 9000 solutions for each level of systematic effects. After obtaining the final solutions, mean comparisons were performed using the *t* test statistic to compare groups at the 5% significance level.

Results

Sire's and dam's biological type

The adjusted means for WW210 were statistically different ($P < 0.05$) for four sires' biological types. While progenies from type B sires had the greatest WW210 mean value, progenies from type A sires had the worst WW210 mean value (Table 3).

The superiority in WW210 was noted in crossbred cows in relation to purebred cows. The greatest WW210 mean was observed in progenies of cows $\frac{1}{2}B|\frac{1}{2}N$, followed by progenies of cows $\frac{1}{2}C|\frac{1}{2}N$, with an increment of 10.4 and 7.8%, respectively, in relation to the mean obtained in the progenies of type N cows (Table 3).

Dam age classes

The WW210 means observed for each dam's age class at calving are shown in Fig. 1(a). Cows ageing 6 and 7 years at calving weaned the heaviest progenies, with an improvement of up to 11.47 kg over the other classes.

Individual heterozygosis effect

Results showed that the higher the calf individual heterozygosis, the higher the WW210, indicating the positive effect of crossbreeding between genetically distant breeds (Fig. 1(b)). Calves

with 100% heterozygosis weighed on average 25.98 kg more at weaning in comparison to the progenies from pure breeders.

Variance components and heritability

According to the samples of variance posterior densities, the central tendency measures such as mean, mode and median of the later marginal densities of heritability estimates showed similarity for the majority of the components, demonstrating symmetry and convergence (Table 2). The exception was for maternal permanent environmental variance (V_{ep}^2), where the mode was smaller than the mean and median. The effective sample size (ESS) for V_{ep}^2 was 94.4 samples (Table 2), which suggested convergence since the minimum ESS expected to reach convergence should be ten samples (Misztal *et al.*, 2002). Therefore, the ESS obtained indicates that the total chain samples stipulated (11 000 000 cycles with the 1 000 000 initial samples discarded as burn-in) were adequate to obtain the ESS and convergence for all variance components estimates.

The values obtained by the Geweke test were lower than 1. In other words, the difference between the first and last halves was lower than 1, indicating convergence (Table 2). The posterior mean estimate of h_a^2 obtained for WW210 was 0.5 ± 0.04 , while the posterior mean estimate obtained for h_m^2 was 0.1 ± 0.02 .

Discussion

Identifying the genetic and environmental effects that influence WW210 in different beef cattle breed groups allows breeders to learn about the determining factors in calf growth during the pre-weaning. The obtained results showed that sire's and cow's biological type, dam's age at calving and individual heterozygosis are factors that influence the WW210 in the crossbred studied population. Our results suggested that favourable influence on the progenies growth is achieved with the use of type B sires and crossed cows ($\frac{1}{2}C|\frac{1}{2}N$ and $\frac{1}{2}B|\frac{1}{2}N$). Besides that, cows in adult age (6–7 years old) demonstrated a positive influence on the calves' weaning weight.

Regarding the sire's biological type, the results showed that there are statistical differences among progenies of bulls from the four biological types. The proximity between the WW210 averages of progenies originated from N, B and C sires was not expected, since previous studies showed breeds within B and C groups to have a higher potential of growth (Fialho *et al.*, 2015). Our hypothesis is that crossed cows $\frac{1}{2}B|\frac{1}{2}N$ and $\frac{1}{2}C|\frac{1}{2}N$, when mated with type N sires (Table 1), contributed positively to increase the WW210 average, due to the maternal heterosis that these cows offer which can increase the potential gain in weaning weight (Table 3). A contrary outcome would be observed in the WW210 average of progenies from type C sires with type N cows, because no gain derived from the maternal heterosis would be expected. Following this reasoning, it is important to note that the WW210 average of progenies from type N cows presented up to 21.98 kg less than obtained in case of crossed cows.

The greater number of animals in type N is due to the Brazilian breeders' preference for *B. indicus* animals, specifically, Nelore animals as the breed represent approximately 80% of the national beef cattle herds (IBGE, 2016). The preference for the Nelore breed is due to its rusticity and resistance to tropical parasites, which benefits the production and management of Nelore animals under tropical environments.

Table 2. Descriptive statistics of the posterior estimates of variance components and direct and maternal heritabilities for weaning weight

Parameter	Mean	Median	Mode	HPD 95%	ESS	Geweke diagnosis
Va ²	186 ± 15.1	185.9	183.2	156.5–215.7	2317.9	0.00
Vm ²	42 ± 8.1	41.9	42.76	25.1–56.7	190.7	−0.11
Vep ²	9 ± 6.1	7.5	3.26	0.31–20.1	94.4	0.20
Ve ²	174 ± 11.2	174.4	173.0	152.80–196.7	3555.5	−0.02
h ² a	0.5 ± 0.04	0.45	0.50	0.39–0.52	–	–
h ² m	0.1 ± 0.02	0.10	0.05	0.06–0.14	–	–

HPD 95%, 95% highest density intervals; ESS, effective sample size; Va², direct additive genetic variance; Vm², maternal additive genetic variance; Vep², permanent environment maternal variance; Ve², residual variance; h²a, direct additive heritability; h²m, maternal additive heritability.

Similar results regarding the sire's biological type were reported by Baker *et al.* (2001) in crossbred cattle originated from the mating of type B cows or crossbred cows (½N|½B and 3/4B|1/4N) with type B, type N and type A sires. These authors observed that progenies of type B and type N sires were weaned heavier than progenies of type A sires. Fialho *et al.* (2015) observed no significant difference for adjusted weaning weight between Nelore and Aberdeen Angus progenies; however, superiority was observed for progenies from British (Red Angus) and Brangus sires, a composite breed, when compared to progenies from the crosses of Nelore sires with females Nelore, Brangus, Wayu and ½Brangus|½Nelore.

Although most sires from the Adapted group were crossed with ½C|½N females (Table 1) to generate heterosis retention, progenies from this cross presented low WW210 average, 20 kg below the average found in progenies of the British sires. The results indicated that using biological type A sires has no positive impact on the WW210 in calves of this population. Similar results were reported in a crossbred population descendant of a taurine adapted breed (Senepol) and females of biological type N, which is considered a viable cross for improving meat quality traits; however, no significant difference was observed for growth traits (Schatz *et al.*, 2014). Higher weaning weight was reported in progenies of sires of biological type N or B in comparison to type A sires, when they were mated with type B cows or crossed cows, 1/2N1/2B and 3/4B1/4N (Baker *et al.*, 2001). The authors observed a low growth rate for progenies from Senepol bulls until weaning.

The pre-weaning weight gain of calves is associated with their genetic potential and the environment in which they are raised. Differently from the sire contribution, the cow has an environmental contribution to the progeny. Considering the calf is monogastric in the early stages of life, its feeding depends only on the milk provided by the cow, i.e. the maternal ability of the cow, which is responsible for the calf development. Therefore, the cow is the major environmental factor especially during the pre-weaning period (Cerdótes *et al.*, 2004). However, since the animals were raised in tropical savannah conditions, after 3 months of age, milk is not sufficient to meet the calves requirements to support the potential growth (Carvalho *et al.*, 2019), thus they were supplemented in creep feeding system in order to obtain calves with greater weights at weaning. According to Carvalho *et al.* (2019), creep feeding systems can increase weaning weight up to 30 kg on average. The results for dam's biological type showed that progenies from females crossed with British breeds (½B|½N) presented higher WW210 means (Table 3). This

superiority found in crossbred cows may be associated with the lower frame of the British breeds compared to the Continental breeds, reflecting a lower energy requirement for body maintenance, which could be available for milk production. Studies showed that crossbred cows produce more milk than purebred cows (Williams *et al.*, 2010; Leal *et al.*, 2018; Mendonça *et al.*, 2019), evidencing the positive effect of crossbreeding on milk production and consequently on the calf development.

Progenies from crossbred cows gained on average 8.7% more weight from birth to weaning compared to progenies from purebred cows. The increase in WW210 justifies the maintenance of F1 crossbred cows in the herds to improve production. Williams *et al.* (2010) and Leal *et al.* (2018) also observed that crossbred cows B × N and C × N had a positive effect on WW210. Similarly, Teixeira and Albuquerque (2005) reported an average 11.2% higher in daily gain from birth to weaning in progenies of crossbred cows Nelore × Angus and Nelore × Hereford compared to progenies of pure female Nelore, Angus and Hereford. Therefore, our findings demonstrated additional gains in weaned calves being interesting in breeding programmes to explore the sire's biological type together with the maternal heterosis. The cow's maximum heterosis will be obtained by taurine and zebu crossbreeding and will bring great gains for the progeny due to the genetic distancing between the breeds.

Another important factor to be considered is the dam's age class at calving as it influences milk yield (Euclides Filho *et al.*, 1998; Cerdótes *et al.*, 2004). The results showed that the highest WW210 means were obtained for adult cows, at 6 and 7 years of age at calving (Fig. 1(a)). These ages coincide with the physiological maturity of the cow, favouring the calves weights. Younger cows (between 3 and 4 years old) usually are primiparous and need to mobilize energy for both their own growth and milk production, reflecting in lower values of WW210 of their calves. The obtained results agree with other findings in Tabapuã and Nelore cows (Sakaguti *et al.*, 2002; Júnior *et al.*, 2004, respectively). Both studies suggested that cow age at calving influences calf growth and development, and adult cows at ages of 6–8 years weaned heavier calves.

According to Cerdótes *et al.* (2004), the ideal age of the dam for calving is around 7 years, and progenies born from cows before or after this age do not perform well at the weaning period due to cow's physiological condition. Cow age should then be considered in the selection of animals. In crossbred cattle populations raised in Tropical Savanna climate in the Midwest region of Brazil, the decision to discard cows while selecting future dams must consider other economically important traits such as

Table 3. Adjusted means and standard deviations for weaning weight (WW210) of progenies according to the sire's and dam's biological type [left], and differences between adjusted means according to biological types for sires and dams, with 95% confidence interval (95% CI) for WW210 [right]

	Biological type ^a	WW210 ± s.d.	Biological types contrast ^b	Differences with 95% CI for WW210	
Sire			B v. C	11.10	11.35
			B v. A	20.35	20.50
	N	205 ± 13.3	B v. N	0.74	0.94
	A	185 ± 13.3	B v. ¼N ¼A ¼B ¼C	6.51	6.72
	B	206 ± 13.3	N v. C	10.23	10.55
	C	195 ± 13.5	N v. A	19.47	19.70
			N v. ¼N ¼A ¼B ¼C	5.66	5.90
			¼N ¼A ¼B ¼C v. C	4.46	4.76
		¼N ¼A ¼B ¼C v. A	13.71	13.90	
		C v. A	9.07	9.32	
Dam	N	206 ± 11.7	1/2B1/2N v. N	21.79	21.98
	½B ½N	228 ± 11.9	1/2B1/2N v. 1/2C1/2N	4.43	4.59
	½C ½N	223 ± 11.7	1/2C1/2N v. N	17.32	17.43

^aFor abbreviations, see Table 1.

^bAll the comparisons were statistically significant at the 5% significance level (*t* test, $P < 0.05$).

longevity and fitness. However, for cows over 7 years old, if they do not provide a satisfactory milk yield, their possible discard should be evaluated.

The sire's and dam's biological type directly influence the progeny heterozygosity, as previously discussed. These factors have a positive effect on the individual performances for WW210. Mating breeds with greater genetic distance should provide maximum heterozygosity expression in the progeny (Mourão *et al.*, 2007; Williams *et al.*, 2010; Leal *et al.*, 2018). Maximum heterozygosity also makes it possible to explore the complementarity between breeds. In Tropical Savannah conditions, crossbreeding enables the obtention of animals that are productive and still resilient to climate challenges. The estimated individual heterozygosity effect was 25.98 kg in the studied crossed population (Fig. 1 (b)); considering that the mean value for WW210 was equal to 227.49 kg in this population, the estimate of heterozygosity represents an increase of 11.42% in WW210 for F1 calves.

The use of bulls N and ¼N|¼A|¼B|¼C in crosses implies the loss of heterozygosity and lower WW210 values compared to animals with heterozygosity equal to 1 because mated cows also have a proportion of N in their composition. For this reason, the mentioned biological types should be avoided in sires. Kippert *et al.* (2008) observed a positive effect on individual heterozygosity in terms of weaning weight in crossings between the biological types B × N (13.29 kg). The values of the heterozygosity observed in the present study showed that maintaining high levels of direct heterozygosity is desirable, since it provides benefits in the weaning weight of calves.

The posterior mean estimate of h_a^2 was high, indicating that genetic progress is expected by the selection of WW210 in this crossbred cattle population. The h_a^2 for weaning weight was higher in the presented study when compared to that found by Montaldo and Kinghorn (2003) (0.38), Mourão *et al.* (2007) (0.36) and Grigoletto *et al.* (2019) (0.30) in crossbred and composite populations.

The high magnitude of direct heritability obtained in the current study can be explained in part by the animals' management

since we considered the paddock's management group until weaning in the formation of CGs. The paddock's management group until weaning was considered due to the possibility of differences in the quality of pastures from different paddocks in the studied farm. According to Bourdon (2000), one important way to increase heritability estimates is to make the environment as similar as possible. The same author described that environmental differences in weaning weight in beef cattle can be minimized by offering the animals pastures of similar quality and providing the same health management. Demeke *et al.* (2003) explained that the high standard of calf management as well as environmental stress highly affects the magnitude of additive genetic variance for traits in crossbred cattle populations. Other factors that can affect the identification of genetic variation in a given trait are the animals' management criteria, the statistical model, the methodology adopted to obtain variance components, and the additive genetic differences between the breeds considered in the crosses.

The posterior mean estimate of the heritability of maternal genetic effect was low (0.10) (Table 2). In multibreed beef cattle populations, Mourão *et al.* (2007), Vergara *et al.* (2009) and Grigoletto *et al.* (2019) reported h_m^2 close to the value obtained in our population, with the values of 0.14, 0.11 and 0.12, respectively. Direct and maternal heritability estimates are influenced by the data set structure, mainly by the proportion of dams with known phenotypic information and the number of progenies per dam. Boligon *et al.* (2012) mentioned the inclusion of dams with phenotypic performance in data sets with few progenies per dam (1–3) can result in the increase of direct heritability for weaning weight. Therefore, the structure of our data may have influenced the observed heritability estimates.

The heritability estimates for the direct and maternal effect on WW210 indicate that a large portion of the genotypic variance of this trait must be from direct additive genetic origin, with a slightly maternal contribution. This confirms that WW210 should respond to selection and can be used as selection criteria in animal breeding programmes for the selection of heavier animals.

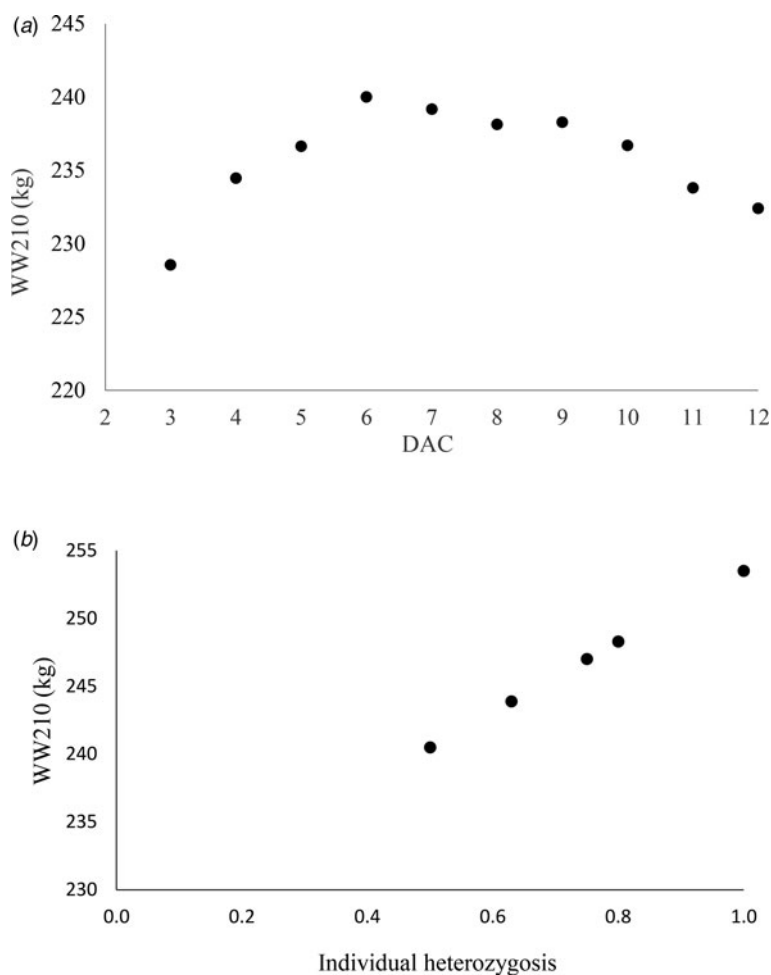


Fig. 1. (a) Estimated dam's age class effect (DAC) at the weaning weight; (b) Estimated individual heterozygosity effect on weaning weight (WW210).

Conclusions

Sire's and dam's biological types influence the WW210 of the crossed progenies. Crossbred cows $\frac{1}{2}B|\frac{1}{2}N$ and $\frac{1}{2}C|\frac{1}{2}N$ produce heavier calves when compared to biological type N cows. Better performance of the progeny at weaning was observed for cows at the ages of 6 and 7 years due to their physiological conditions.

Direct and maternal heritability estimates confirmed the possibility of selection for WW210 in crossbred cattle, allowing to choose the lines of sires and dams that could be used to make the crosses, with the intention to obtain progenies with better performance for weaning weight. It is important to prioritize the matings of genetically distant parents in order to explore the maximum heterozygosity.

Financial support. The Coordenação de Aperfeiçoamento de Pessoal de Nível Superior – Brasil (CAPES) – Finance Code 001.

Conflict of interest. None.

Ethical standards. Animal Care and Use Committee approval was not necessary for this study because the data were obtained from an existing database.

References

- Baker JF, Tucker SV and Vann RC** (2001) Effects of Tuli, Senepol, Brahman, Angus, and Polled Hereford sire breeds on birth and weaning traits of offspring. *The Professional Animal Scientist* **17**, 160–165.
- Boligon AA, Pereira RJ, Ayres DR and Albuquerque LGD** (2012) Influence of data structure on the estimation of the additive genetic direct and maternal covariance for early growth traits in Nelore cattle. *Livestock Science* **145**, 212–218.
- Bourdon RM** (2000) *Understanding Animal Breeding*, 2nd Edn. Upper Saddle River, New Jersey: Prentice-Hall Inc.
- Bovine HapMap Consortium** (2009) Genome-wide survey of SNP variation uncovers the genetic structure of cattle breeds. *Science (New York, N.Y.)* **324**, 528–532.
- Cardoso LL, Leal JJB, Nunes MHG, Teixeira BBM, Sollero BP, Silveira IDB and Cardoso FF** (2018) Sire breed effect on carcass and temperament traits. *Semina: Ciência Agrária* **39**, 2717–2726.
- Carvalho VV, Paulino MF, Detmann E, Valadares Filho SC, Lopes AS, Rennó LN, Sampaio CB and Silva AG** (2019) A meta-analysis of the effects of creep-feeding supplementation on performance and nutritional characteristics by beef calves grazing on tropical pastures. *Livestock Science* **227**, 175–182.
- Cerdótes L, Restle J, Alves Filho DC, Nörnberg MDFBL, Nörnberg JL, Heck I and Silveira MFD** (2004) Produção e Composição do Leite de Vacas de Quatro Grupos Genéticos Submetidas a Dois Manejos Alimentares no Período de Lactação. *Revista Brasileira de Zootecnia* **33**, 610–622.
- Demeke SFWC, Naser FWC and Schoeman SJ** (2003) Variance components and genetic parameters for early growth traits in a mixed population of purebred *Bos indicus* and crossbred cattle. *Livestock Production Science* **84**, 11–21.
- Euclides Filho K, Figueiredo GR, Da Silva LO and Alves RGO** (1998) Idade aos 165kg de peso vivo para progênies de Nelore, Fleckvieh, Chianina, Charolês, F1's e retrocruzadas. *Revista Brasileira de Zootecnia*, **27**, 899–905.
- Ferraz JBS and Felício PE** (2010) Production systems – an example from Brazil. *Meat Science* **84**, 238–243.

- Ferraz JBS, Eler JP and Golden BL (1999) Análise genética do composto Montana Tropical. *Revista Brasileira de Reprodução Animal* **23**, 111–113.
- Fialho FRL, Rezende MPGD, Souza JCD, Silva RMD, Oliveira NMD and Silveira MVD (2015) Performance in preweaning pure and crossbred calves in the Mato Grosso do Sul Pantanal region, Aquidauana, Mato Grosso do Sul State, Brazil. *Acta Scientiarum. Animal Sciences* **37**, 437–442.
- Gelman A, Carlin JB, Stern HS, Dunson DB, Vehtari A and Rubin DB (2013) *Bayesian Data Analysis*, 3rd Edn. Boca Raton, FL: CRC Press.
- Geweke J (1991) *Evaluating the Accuracy of Sampling-Based Approaches to the Calculation of Posterior Moments*. Minneapolis, MN: Federal Reserve Bank of Minneapolis, Research Department.
- Grigoletto L, Brito LF, Mattos EC, Eler JP, Bussiman FO, Silva BDCA, Silva RPDS, Carvalho FE, Berton MP, Baldi F and Ferraz JBS (2019) Genome-wide associations and detection of candidate genes for direct and maternal genetic effects influencing growth traits in the Montana Tropical* Composite population. *Livestock Science* **229**, 64–76.
- IBGE (2016) Instituto Brasileiro de Geografia e Estatística – IBGE. Estatísticas. Available at <https://www.ibge.gov.br/> (Accessed 1 April 2020).
- Júnior JJ, Dias LT and Albuquerque LG (2004) Fatores de Correção de Escores Visuais de Conformação, Precocidade e Musculatura, à Desmama, para Idade da Vaca ao Parto, Data Juliana de Nascimento e Idade à Desmama em Bovinos da Raça Nelore. *Revista Brasileira de Zootecnia* **33**, 2044–2053.
- Kippert CJ, Borato PRN, Lopes JS, Weber T and Boligon AA (2008) Efeitos genéticos aditivos diretos e maternos e heterozigóticos sobre os desempenhos pré e pós-desmama em uma população multirracial Aberdeen Angus x Nelore. *Revista Brasileira de Zootecnia* **37**, 1383–1391.
- Köppen W and Geiger R (1936) *Handbuch der Klimatologie*. Berlin, Gebr. Borntraeger.
- Leal WS, MacNeil MD, Carvalho HG, Vaz RZ and Cardoso FF (2018) Direct and maternal breed additive and heterosis effects on growth traits of beef cattle raised in southern Brazil. *Journal of Animal Science* **96**, 2536–2544.
- Mastrangelo S, Tolone M, Ben Jemaa S, Sottile G, Gerlando RD, Cortés O, Senczuk G, Portolano B, Pilla F and Ciani E (2020) Refining the genetic structure and relationships of European cattle breeds through meta-analysis of world-wide genomic SNP data, focusing on Italian cattle. *Scientific Reports* **10**, 14522.
- Mendonça FS, MacNeil MD, Leal WS, Azambuja RC, Rodrigues PF and Cardoso FF (2019) Crossbreeding effects on growth and efficiency in beef cow-calf systems: evaluation of Angus, Caracu, Hereford and Nelore breed direct, maternal and heterosis effects. *Translational Animal Science* **3**, 1286–1295.
- Meyer K, Carrick MJ and Donnelly BJP (1994) Genetic parameters for milk production of Australian beef cows and weaning weight of their calves. *Journal of Animal Science* **72**, 1155–1165.
- Misztal I, Tsuruta S, Strabel T, Auvray B, Druet T and Lee DH (2002) BLUPF90 and related programs. In *Proceedings of the 7th World Congress on Genetics Applied to Livestock Production*, Montpellier, France. **33**, 743–744.
- Montaldo HH and Kinghorn BP (2003) Additive and non-additive, direct and maternal genetic effects for growth traits in multibreed population of beef cattle. *Archivos de Medicina Veterinaria* **35**, 1–7.
- Mourão GB, Ferraz JBS, Eler JP, Balieiro JCDC, Bueno RS, Mattos EC and Figueiredo LGG (2007) Genetic parameters for growth traits of a Brazilian *Bos taurus* x *Bos indicus* beef composite. *Genetics and Molecular Research* **6**, 1190–1200.
- Sakaguti ES, Silva MA, Martins EN, Lopes PS, Silva LOC, Quaes RL, Regazzi AJ, Euclides RF and Duarte RG (2002) Trajetória de crescimento e efeito da idade da vaca nos modelos de regressão aleatória de bovinos jovens da raça Tabapuã. *Arquivos Brasileiros de Medicina Veterinária e Zootecnia* **54**, 414–423.
- SAS (2011) *SAS/STAT guide for personal computers*, version 9.3. SAS Institute, Inc, Cary, NC, USA.
- Schatz TJ, Thomas S and Geesink G (2014) Comparison of the growth and meat tenderness of Brahman and F1 Senepol x Brahman steers. *Animal Production Science* **54**, 1867–1870.
- Silva JAII, Ribeiro CB, Maiorano AM, Hadlich JC, Curi RA, Oliveira HN, Lamare M and Meirelles PRDL (2015) Influência de fatores ambientais sobre pesos pré-desmama de bovinos cruzados Aberdeen Angus x Nelore. *Revista Brasileira de Saúde e Produção Animal* **16**, 278–289.
- Sørensen MK, Norberg E, Pedersen J and Christensen LG (2008) Invited review: crossbreeding in dairy cattle: a Danish perspective. *Journal of Dairy Science* **91**, 4116–4128.
- Teixeira RA and Albuquerque MLG (2005) Heteroses materna e individual para ganho de peso pré-desmama em bovinos Nelore x Hereford e Nelore x Angus. *Arquivos Brasileiros de Medicina Veterinária e Zootecnia* **57**, 518–523.
- Van Tassell CP and Van Vleck LD (1996) Multiple-trait Gibbs sampler for animal models: flexible programs for Bayesian and likelihood-based (co) variance component inference. *Journal of Animal Science* **74**, 2586–2597.
- Vergara OD, Elzo MA, Ceron-Munõs MF and Arboleda EM (2009) Weaning weight and post-weaning gain genetic parameters and genetic trends in a Blanco Orejinegro-Romosinuano-Angus-Zebu multibreed cattle population in Colombia. *Livestock Science* **124**, 156–162.
- Williams JL, Aguilar I, Rekaya R and Bertrand JK (2010) Estimation of breed and heterosis effects for growth and carcass traits in cattle using published crossbreeding studies. *Journal of Animal Science* **88**, 460–466.