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Technical note

Genetic analysis of live weight and pregnancy rate at first calving in Brahman cattle from Venezuela

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Abstract:

The live weight (LW) of 2,777 animals (1,377 females and 1,400 males with 53,258 individual data between 30 and 600 days of age), born between February 2000 and June 2011, was analyzed using a random regression (RR) model to estimate the genetic components of (co)variance throughout the age-sex scale. The pregnancy rate (PR) and the LW adjusted to 548 days of age (WA548) were studied using a multitrait (MT) model, an increase in the heritability (h^2) estimates for PR compared to the classical univariate model (0.08 ± 0.03 *vs.* 0.11 ± 0.02) was observed, increasing the accuracy of the genetic value (GV) for PR in 15.7 %. The genetic correlation (r_g) between the PR and the WA548 was 0.31 ± 0.11. The RR showed that, through time, the LW could not be considered as an expression of the same trait in both sexes, as the r_g were less than 0.60. The principal component analysis showed that there are important changes in the animal growth on the age scale represented in these data. A prominent dimorphism of genetic origin manifested, estimated as the difference between the male and female GVs in LW, which shows a positive relationship with the GVs of PR.

Key words: Heritability, Genetic correlations, Multitrait model, Random regression model, Sexual dimorphism.

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A general breeding program for the reproductive traits of the Brahman breed is carried out in the experimental station "La Cumaca", Facultad de Ciencias Veterinarias of the Universidad Central de Venezuela, this represents a valuable source of genes for this population(1).

The methodology used for genetic evaluations has different crucial elements. First, the WA548, used to estimate the genetic values (GVs), may be biased, since it assumes growth is linear. The results published (2,3,4,5) for *B. indicus* show growth variations throughout the behavioral tests. Furthermore, the sex of the animal is generally considered a fixed effect in the model, which implicitly assumes that the (co)variance components are the same in both sexes. This approach can incorporate another biased source for the GVs estimation, decreasing their accuracy and thus, affecting the breeding program development(6,7,8). The exposed elements can affect the genetic correlations of the same trait between both sexes (r_{FM}), which could manifest genotype-sex interaction effects.

The LW has been generally expressed at a fixed point, although it seems quite reasonable to examine these relationships throughout the age. If the information is available, the (co)variance components can be estimated using multitrait (MT) models, or, preferably, random regression (RR) models. Previous studies have compared the MT and RR models for the LW in *Bos indicus* cattle(2,4); their results show the advantages of RR. However, this longitudinal approach has not examined the relationships between the sex of the animals. Therefore, more evidence is required, particularly when considering possible relationships between LW and female reproductive behavior (RB).

The importance of RB in the beef cattle economy is well known. However, the seemingly low h^2 of most of the reproductive traits(9,10,11) has been a limiting factor for its use as a direct selection criterion. As an alternative, previous studies have reported the scrotal circumference (SC) or the measured LW in young males, and its response correlated with the RB of females measured by services per pregnancy, days to calving, and the PR at the first service. These encouraging results(12,13) correspond to a fixed age, but the evolution of these trends throughout the age and until first calving remains unknown.

This study aimed to estimate the heritabilities and genetic correlations between the WA548 and the PR of heifers in their first breeding season using a MT model; as well as the genetic (co)variance components of the LW of both sexes regarding age using a RR model; and to compare the genetic values for each i^{th} age (GVi), based on the RR, with the MT-based GVs.

The experimental station "La Cumaca", located at 472 m asl., near San Felipe City, Yaracuy State, Venezuela, has an extension of 433 ha, with 300 ha cultivated with Guinea, Star, Swazzi, Pará, and Wire grasses. The annual mean precipitation is 1,650 mm, with a mean temperature of 24 to 31.9 °C, and a mean relative humidity of 84 %(14). It has a herd of pure, registered Brahman cattle, with approximately 180 cows in production.

The LW adjusted to 548 d of age (WA548) of 3,120 animals, born between February 2000 and June 2011, was modified, eliminating records with pedigree inconsistencies, absence, or problems in the date of birth. Finally, there were 2,777 animal records available (1,377 females and 1,400 males). These animals were born from 984 mothers (729 in the data vector) and 107 sires (48 in the data vector). The pedigree file included 3,977 animals. A total of 94,752 individual LW records from 1,776 females and 1,864 males, born between February 1978 and June 2011, were used. These animals were born from 1,291 mothers (929 in the data vector) and 128 sires (58 in the data vector), and the pedigree file included 4,070 animals. These data were edited, eliminating those records with pedigree inconsistencies, absence or problems in the date of birth, and data recorded less than 30 or more than 570 d of age. Data outside the range of ± 3.2 standard deviations within a 30-d range age classes were removed. Finally, a total of 53,258 individual data were available from 1,737 females and 1,803 males.

Several models were analyzed using the SAS GLM procedure(15). Table 1 shows some indicators of the studied data.

Table 1: Live weight indicators of Brahman animals in the experimental station "La Cumaca", Venezuela

Trait	Female sample size	Females	Male sample size	Males
Birth weight	1,776	29.5 ± 4.5	1864	31.9 ± 4.9
Weaning weight	1,639	165.8 ± 26.2	1630	177.3 ± 28.3
Weight at 365 d	1,396	209.9 ± 29.8	1410	231.8 ± 34.9
Weight at 450 d	1,378	235.6 ± 32.0	1392	271.2 ± 38.9
Weight at 548 d	1,340	290.0 ± 34.1	1385	326.3 ± 42.2
Number of live weight records	25,781	25781	27477	27477
Pregnancy rate	1,377	0.67 ± 0.37		

There were completed three block analyses using the ASReml3 program(16):

Block 0. Multivariate (MU) model for WA548 and PR.

$$\begin{bmatrix}\mathbf{y}_1\\ \mathbf{y}_2\end{bmatrix}=\begin{bmatrix}\mathbf{X}_1 & \mathbf{0}\\ \mathbf{0} & \mathbf{X}_2\end{bmatrix}\begin{bmatrix}\mathbf{b}_1\\ \mathbf{b}_2\end{bmatrix}+\begin{bmatrix}\mathbf{Z}_1 & \mathbf{0}\\ \mathbf{0} & \mathbf{Z}_2\end{bmatrix}\begin{bmatrix}\mathbf{a}_1\\ \mathbf{a}_2\end{bmatrix}+\begin{bmatrix}\mathbf{e}_1\\ \mathbf{e}_2\end{bmatrix}$$

Where:

$\mathbf{y}_i$ is a vector that corresponds to the WA_{548} and the PR analyzed at the same time;

$\mathbf{b}_i$ is a fixed-effects vector of the jk^{th} combination of sex-year-month (with 275 levels for WA_{548} and 124 for PR);

$\mathbf{a}_i$ is a random correlated vector due to the genetic additive effect of the i^{th} animal with data and its predecessors without records (4,070 levels) for WA_{548} and PR;

$\mathbf{e}_{il}$ is a random residual vector correlated between trait 1 and 2;

X and Z are incidence matrices that connect the fixed and random effects with the vector of observations.

This model assumes that:

$$\mathrm{Var}\begin{bmatrix}\mathbf{a_i}\\ \mathbf{e_i}\end{bmatrix}=\begin{bmatrix}\mathbf{G_i} & \mathbf{0}\\ \mathbf{0} & \mathbf{R_i}\end{bmatrix}$$

In which $\mathbf{G_i}=\begin{bmatrix}\sigma^2_{a_1} & \sigma_{a_{12}}\\ \sigma_{a_{21}} & \sigma^2_{a_2}\end{bmatrix}\otimes \mathbf{A}$, where $\sigma^2_{a_1}$ and $\sigma^2_{a_2}$ represent the genetic variances for both traits, and $\sigma_{a_{12}}$ their covariance. The residual (co)variance $\mathbf{R_i}=\begin{bmatrix}\sigma^2_{e_1} & \sigma_{e_{12}}\\ \sigma_{e_{21}} & \sigma^2_{e_2}\end{bmatrix}$ includes $\sigma^2_{e_1}$ and $\sigma^2_{e_2}$, which represent the variances for both traits and $\sigma_{e_{12}}$ their covariance. **A** is the relationship matrix between all the animals and $\otimes$ is the product symbol. With these parameters, it was estimated the h^2 for each trait ($\mathbf{h^2_{a_i}}$) and the genetic correlations ($\mathbf{r}_{gi}$) between both traits, using linear functions of the corresponding components and classical equations(17). The GVs for each trait were estimated as a solution of the described model, and the accuracy (Acc_{ij}) of such estimates according to:

$$\mathbf{Acc_{ij}}=\sqrt{1-\frac{\mathbf{Pev}}{\boldsymbol{\sigma}^2_{\mathbf{i}}}}*100$$

Where: Pev is the prediction error variance (individual value for each animal and study trait), and $\boldsymbol{\sigma}^2_{\mathbf{i}}$: is the genetic variance of the trait in the studied population. It was applied this same model in its univariate form in order to present similar parameters to the original program in the experimental station.

To analyze the LW at different ages, it was applied RR, using different models and without considering the maternal effects, which variated in the fitting order of the polynomial for random effects, as well as the estimates of the total or intrasexual (co)variance components of the animal. In total, two model blocks were made:

Block 1 - Assumes that the (co)variance components are the same in both sexes.

$$y_{ijkl}=\mathrm{fixed}_i+\mathrm{sex}_j+\sum_{r=0}^{3}\Phi_r b_{1r}+\sum_{r=0}^{1}\Phi_r a_{kr}+\sum_{r=0}^{1}\Phi_r p_{ir}+Z_1 q_m+R\rightarrow \text{Model } 1$$

$$y_{ijkl}=\mathrm{fixed}_i+\mathrm{sex}_j+\sum_{r=0}^{3}\Phi_r b_{1r}+\sum_{r=0}^{2}\Phi_r a_{kr}+\sum_{r=0}^{1}\Phi_r p_{ir}+Z_1 q_m+R\rightarrow \text{Model } 2$$

$$y_{ijkl}=\mathrm{fixed}_i+\mathrm{sex}_j+\sum_{r=0}^{3}\Phi_r b_{lr}+\sum_{r=0}^{3}\Phi_r a_{kr}+\sum_{r=0}^{1}\Phi_r p_{ir}+Z_1 q_m+R\rightarrow \text{Model } 3$$

Block 2 - Assumes that the (co)variance components are not the same in both sexes.

$$\mathbf{y_{ijkl} = fixed_i + sex_j + \left[\sum_{r=0}^{3} \Phi_r b_{1r} + \right]_{:j} + \left[\sum_{r=0}^{1} \Phi_r a_{kr}\right]_{:j} + \left[\sum_{r=0}^{1} \Phi_r p_{ir}\right]_{:j} + Z_1 q_m + R_{:j} \rightarrow model\ \ 4}$$

$$\mathbf{y_{ijkl} = fixed_i + sex_j + \left[\sum_{r=0}^{3} \Phi_r b_{1r} + \right]_{:j} + \left[\sum_{r=0}^{2} \Phi_r a_{kr}\right]_{:j} + \left[\sum_{r=0}^{1} \Phi_r p_{ir}\right]_{:j} + Z_1 q_m + R_{:j} \rightarrow model\ \ 5}$$

$$\mathbf{y_{ijkl} = fixed_i + sex_j + \left[\sum_{r=0}^{3} \Phi_r b_{1r} + \right]_{:j} + \left[\sum_{r=0}^{3} \Phi_r a_{kr}\right]_{:j} + \left[\sum_{r=0}^{1} \Phi_r p_{ir}\right]_{:j} + Z_1 q_m + R_{:j} \rightarrow model\ \ 6}$$

In both blocks, Y_{ijkl} represents the different LW estimates in the l akth animal, of the jth sex. The fixed effects ($fixed_i$) were year-month of control with 674 levels: sex-age at calving with 18 levels, represented in all the models, so that the results can be compared by applying the LogL information criteria; BIC and AIC. The six models only differ in the fitting order of the Legendre polynomial ($\mathbf{\Phi_i}$) for random effects and the residual variance (R), considered homogeneous for block 1 and intra jth sex in block 2. The strategy applied in block 2 consisted in estimating the inter- and intrasexual (co)variance components of the animal. The Z_1 incidence matrix contains the elements 1 or 0 to connect each observation with the random effects of maternal permanent environment (q_m) with 91 levels. For both blocks, the population growth curve was modeled by a regression coefficient (b_1) dividing the age by the live weight, using the $\mathbf{\Phi_i}$ coefficients of third-order, the random genetic effects of **r** =1, 2, 3 orders, and the individual permanent effect (p_i) of first-order, due to the repetitions of the same trait in the animals throughout the age scale. The expected variance components in both blocks were:

$$\mathbf{y \sim N\ [0,(\sigma_y^2 = \Phi_i * [G_0 = (A \otimes K_G)] * \Phi' + I_p \sigma_i^2 + I_q \sigma_m^2 + I_n \sigma_e^2]} \quad \text{Block 1}$$

$$\mathbf{y \sim N\ [0,(\sigma_y^2 = \Phi_i * [G_0 = (A \otimes K_{G:j})] * \Phi' + \Phi_i * [P_0 = (Ip \otimes K_{P:j})] * \Phi' + I_q \sigma_m^2 + I_n \sigma_{e:j}^2]} \quad \text{Block 2}$$

Where A is the numerator of the relationship matrix between the animals with data and their ancestors without records (n= 4,070 total animals). I_p is the identity matrix for the random effects of the individual permanent environment (**p**=3540 dimension for block 1 with $\boldsymbol{\sigma_i^2}$ variance, p_h= 1,737, and p_m=1,803 levels for females and males, respectively in block 2, with variances included in the random regression matrix of individual permanent effect intra jth sex of the animal ($\mathbf{K_{P:j}}$). I_q is the incidence matrix for the maternal permanent environment (**q** dimension=1,291 mothers and $\boldsymbol{\sigma_m^2}$ variance). R is the residual error with I_n as incidence matrix (n=53,258 records in block 1 and $\boldsymbol{\sigma_e^2}$ variance, and n_h= 25,781 and n_m=27,477 for females and males in block 2 with $\boldsymbol{\sigma_{e:j}^2}$variance, respectively). G_0 have a random regression matrix (K_G) of (r+1)*(r+1) dimension, in the most complex models of block 2 the elements will be:

$$\mathbf{K_G} = \begin{bmatrix} \mathbf{K_h} = \begin{pmatrix} \sigma^2_{ho} & \sigma_{hos} \\ \sigma_{hso} & \sigma^2_{hs} \end{pmatrix} & \mathbf{K_{hm}} = \begin{pmatrix} \sigma_{hmo} & \sigma_{hmos} \\ \sigma_{hmso} & \sigma h_{dms} \end{pmatrix} \\ \mathbf{K_{mh}} = \begin{pmatrix} \sigma_{mho} & \sigma_{mhso} \\ \sigma_{mhos} & \sigma_{mhs} \end{pmatrix} & \mathbf{K_m} = \begin{pmatrix} \sigma^2_{mo} & \sigma_{mos} \\ \sigma_{mso} & \sigma^2_{ms} \end{pmatrix} \end{bmatrix}$$

ASReml automatically produces the principal component analysis of this matrix, which facilitates the interpretation of the estimated (co)variances trajectories. Herein, K_G is a symmetrical matrix that consists of four submatrices with the same (co)variance components for the genetic effects in females (K_h); males (K_m), and their covariances (K_{hm}), with their corresponding variances of the intercept (σ^2_{ho} and σ^2_{mo}); slope (σ^2_{hs} and σ^2_{ms}), and covariances (σ^2_{hso} , σ^2_{mso}, σ^2_{mhs}, and σ^2_{hmos}). In these cases, the subscripts *o* and *s* indicate intercept and slope, respectively. The described matrix applies to a fitting order of r=1. Therefore, each submatrix has a 2x2 dimension; for r = 2 it will be 3x3, and for r = 3 it will be 4x4, and the additional components will be the quadratic and cubic terms, respectively. For block 1, the K_G matrix does not represent the estimates for each sex. For both blocks, manipulating the elements of these matrices, as well as the r-order Legendre polynomial coefficients (Φ_i), it is possible to estimate the (co)variance components throughout the age and for each sex$^{(18)}$:

$\sigma^2_{hi} = \Phi_i K_h \Phi_i'$; $\sigma^2_{mi} = \Phi_i K_m \Phi_i'$, **and** $\sigma_{hm_{ij}} = \Phi_i K_{hm} \Phi_j'$.

Generally, the genetic parameters of h^2 and r_g can be determined using classical equations$^{(17)}$. The GVs of LW are determined for each sex using the best model solution where, for the kth animal it will have:

$$VG_k^i = a_k \Phi_i'$$

and where Φ_i are the corresponding Legendre polynomial coefficients for each ith point on the age scale. In this model, each animal (total; female or male) will be assigned a genetic function (a_k) linked to the effects of the intercept, slope, and other terms according to the fitting order of the chosen polynomial.

Table 2 shows the genetic parameters obtained from block 0, where the correlations between the estimated GVs determined by MU and MT were incorporated.

Table 2: (Co)variance components and heritability of live weight adjusted to 548 d and the pregnancy rate at first calving (Block 0 models)

Genetic parameter	Live weight (kg)	Pregnancy rate (d)
Genetic variance-MU	369.9	0.017588
Genetic variance-MT	375.3	0.02335
Heritability-MU	0.337±0.11	0.084±0.03
Heritability-MT	0.349±0.10	0.109±0.02
Genetic correlation- Weight and pregnancy rate	0.309±0.11	
Accuracy, % of the MU genetic value (GV)	63.5±12.1	34.2±8.9
Accuracy, % of the MT genetic value	64.1±12.1	39.6±9.8
Correlation between MU x MT genetic values	0.996	0.8971
Correlation between MU pregnancy rate GV x MU weight GV	0.286	
Correlation between MU pregnancy rate GV x MT weight GV	0.570	

For the WA548 there were no differences between MU and MT. For the PR, the MT increased the h^2, improving the accuracy of the GVs. The r_g between both traits was positive (r_g =0.309), which indicates the absence of antagonism in the improvement of both traits. The correlations between the GVs, based on the models, were higher than 0.897, from which it is inferred that there will be no changes in the order of merit for both procedures. The MT model has additional advantages, manifested in a higher correlation with the GV for PR, as well as greater accuracy in the GV estimates for this last trait, whose h^2 value was low.

The fitness of the six models in blocks 1 and 2 was determined using the LogL, AIC, and BIC criteria, all three agreed that the third-order polynomial for the genetic effect is the best fit to the data. Block 2 models present better results, which demonstrate that there is a significant variation between sexes for the (co)variance genetic components.

The LW h^2 throughout the age in both sexes, as well as the genetic correlation between them is showed in Figure 1. The h^2 trends show slight increases as age progresses, being higher for females. The r_g reflect an inverse pattern with values ranging from 0.25 to 0.35. In contrast, the frequency distribution of the GVs for WA548, estimated according to block 0 models and RR, in Figure 2 shows an overlap of the three GVs estimates. The principal component analysis of the KG matrix for the chosen model 6 demonstrates that the first (vp1) and second (vp2) eigenvectors explained the 57 and 31 % of the genetic variation, respectively. The GVs of the best 200 animals in the MU (official current method) and the

RR throughout age and for each sex are shown in Figure 3. This figure shows that in males the trend is positive, while in females we can find animals with negative GVs.

Figure 1: Heritability and genetic correlation estimates for live weight in females and males throughout the age scale in Brahman animals (model 6)

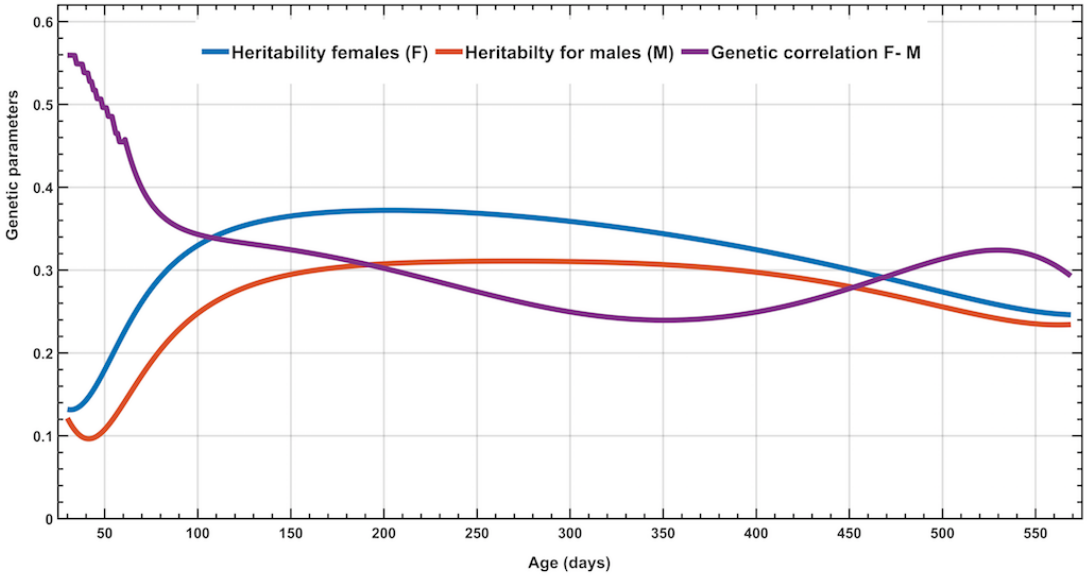


Figure 2: Frequency distribution of genetic values for weight at 548 days of age according to the current model and by means of random regression (model 6)

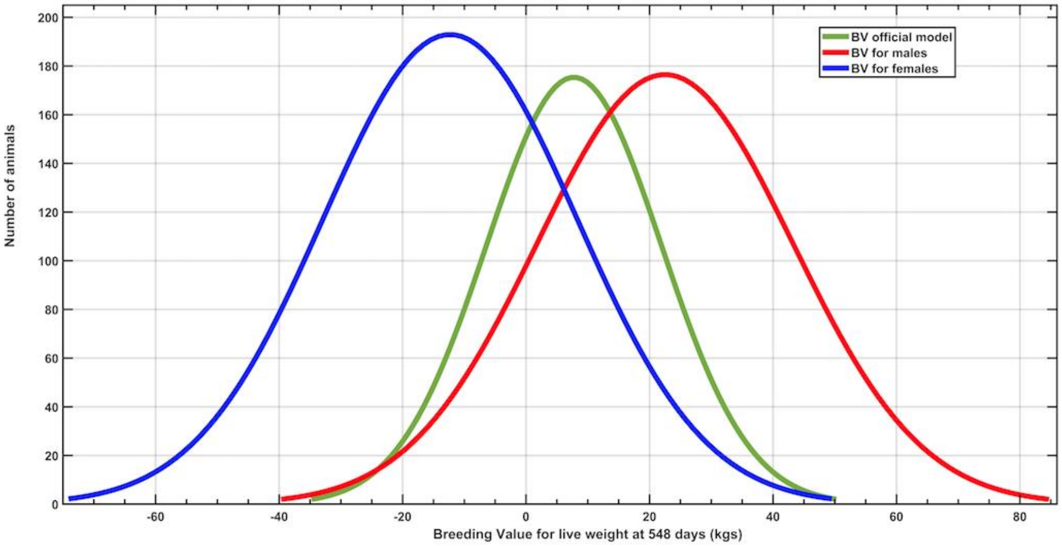
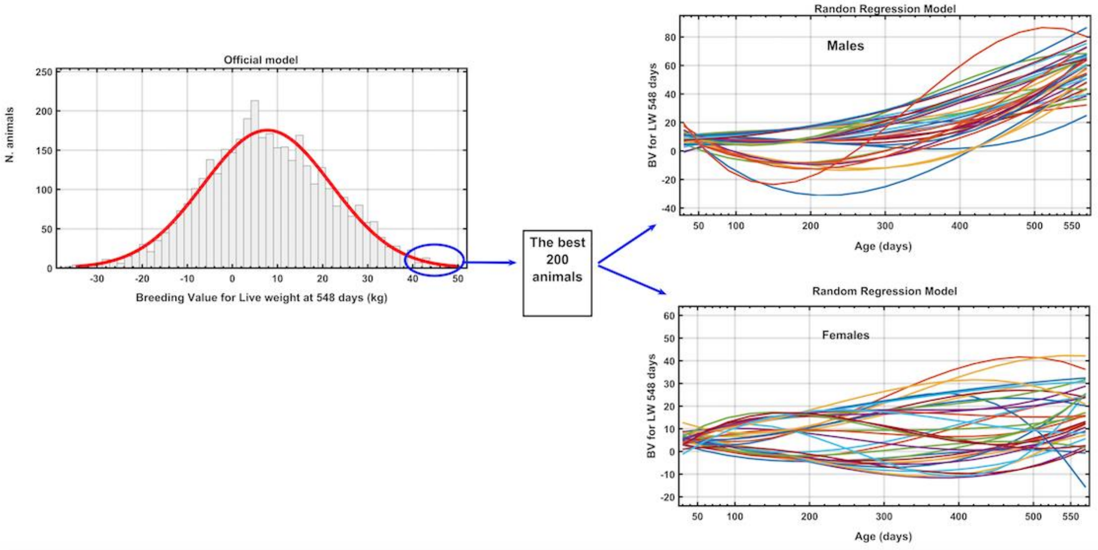
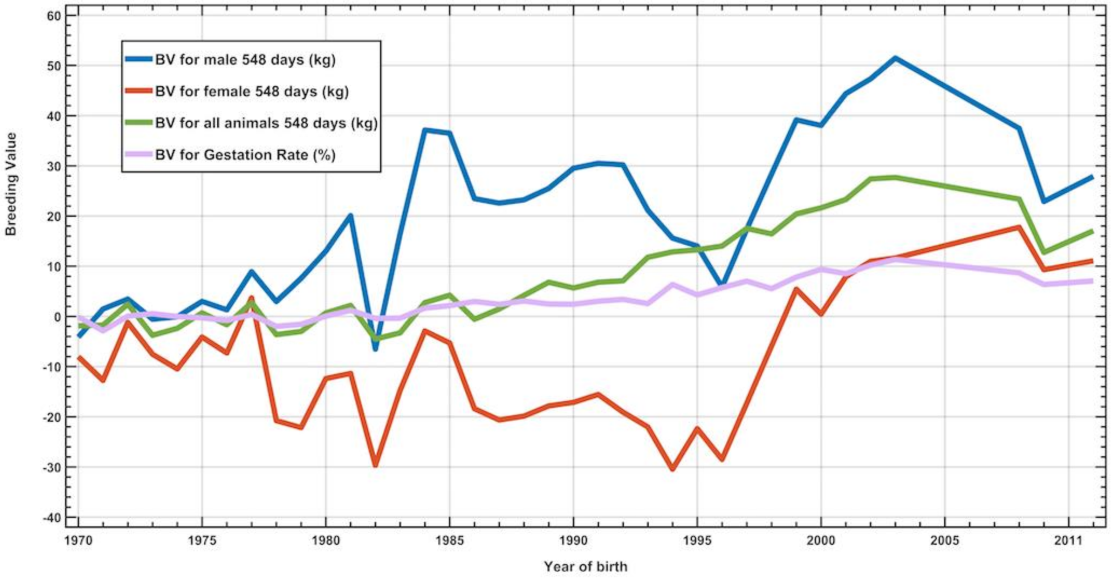


Figure 3: Evolution of the genetic values of Brahman animals of each sex and throughout the age scale, chosen based on the current evaluation model



The merit evolution based on the year of birth of the animals is shown in Figure 4. The annual genetic progress was of 0.933 ± 0.021 kg/yr for the WA548, the principal trait in the applied breeding program; for the PR it was of 0.354 ± 0.010 %/yr.

Figure 4: Evolution of the genetic merit for live weight and pregnancy rate in Brahman animals in the experimental station "La Cumaca"



The h^2 values for the WA548 are similar to several references published in Venezuela for this type of animal(19,20), as well as with the results published for *B. indicus* in different Latin American countries(21). Genetic progress for the WA548 was lower than that published by other authors(20,22).

The h^2 estimates with the MU for PR were low, which is similar to most of the publications about reproductive traits(10,23). However, the h^2 levels for PR with the MT increased, (h^2=0.109 *vs* 0.087), which boosts the average accuracy of the GVs in 15.7 %. The r_g levels between both traits suggest the absence of antagonism, which means that a selection process for LW and PR is possible, this approach has already been suggested in other studies(11,12,24). The greatest genetic variability (Figure 2) and different h^2 and r_g levels for the WA548 throughout the age-sex scales (Figure 1) indicate that the expression of this trait should not be considered as an expression of the same trait in both sexes. The latter agrees with other published results(7,8).

The sexual dimorphism (SD), evident in these data, has been studied in detail in the evolutionary context of the populations, creating a debate about the importance of the heterogeneous variance between sexes and its effects in the specialization and adaptability of the populations(25), while there are previous statements about changes in SD as a correlated response to fertility selection. In relation to this last point of view, these results present a new approach, this study presents the GVs in each sex for the WA548M and WA548F (model 6 solution results, block 2), which makes possible to estimate a SD of genetic origin like SDg=GVWA548M - GVWPA548F, and these estimates of SDg can be related with the GVs of the same animals for the PR (MT model solution, block 0). The analysis results indicate that a quadratic equation ($TG= 0.574 + 0.1045*SDg + 0.000765*SDg^2 - 0 .0000244*SDg^3$, and R^2= 96.1 **%**) was the best fit for the data, with an order increase of +1.2 % in PR for each 10 kg of SDg, with a maximum point when 40>SDg<60 with PR= +4.4 %. However, when -10>SDg<0, the PR was -1.4 %. These results are encouraging, but more research is required on this topic, which may have an important practical application in beef cattle production systems.

This study detected a wide genetic variety in the LW and PR of Brahman animals. It is suggested to use MT models, which allow substantial increases in h^2 values and the accuracy of the estimated GVs, particularly in the PR. The RR analysis indicated that the h^2 and r_g levels between the LW of females and males vary throughout the age scale, which means that they should not be considered as expressions of the same trait. Finally, this study identified an important genetic variability in sexual dimorphism, which is related to the PR, although this suggestion requires further investigation with a larger number of animals.

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