R. Bras. Zootec., 51:e20210175, 2022
https://doi.org/10.37496/rbz5120210175

Breeding and genetics
Full-length research article

Revista Brasileira de Zootecnia

Brazilian Journal of Animal Science
e-ISSN 1806-9290
www.rbz.org.br

The impact of heterogeneity of variances on the genetic evaluation of performance traits in Nellore cattle

Flávio Luiz de Menezes[1]*, **Cláudio Vieira de Araújo**[1], **Larissa Carolina Novo**[2], **Monyka Marianna Massolini Laureano**[1], **Simone Inoe Araújo**[1], **Raysildo Barbosa Lôbo**[3], **Letícia Mendes de Castro**[3], **Lílian Roberta Matimoto Nakabashi**[3], **Fernando Baldi**[4]

[1] Universidade Federal de Mato Grosso, Sinop, MT, Brasil.
[2] University of Wisconsin, Department of Animal and Dairy Sciences, Madison, WI, USA.
[3] Associação Nacional de Criadores e Pesquisadores, Ribeirão Preto, SP, Brasil.
[4] Universidade Estadual Paulista, Faculdade de Ciências Agrárias e Veterinárias, Jaboticabal, SP, Brasil.

***Corresponding author:**
flm.zootecnista@gmail.com

Received: September 17, 2021
Accepted: August 20, 2022

How to cite: Menezes, F. L.; Araújo, C. V.; Novo, L. C.; Laureano, M. M. M.; Araújo, S. I.; Lôbo, R. B.; Castro, L. M.; Nakabashi, L. R. M. and Baldi, F. 2022. The impact of heterogeneity of variances on the genetic evaluation of performance traits in Nellore cattle. Revista Brasileira de Zootecnia 51:e20210175.
https://doi.org/10.37496/rbz5120210175

ABSTRACT - The objective was to evaluate the existence of heterogeneity of variances and its impact on the genetic evaluation of ponderal performance in sires of the Nellore breed. We used records of adjusted body weights at 210 (W210), 365 (W365), and 450 (W450) days of age. Both W365 and W450 were combined by principal component analyses using the first component (PC). Average daily gain (ADG) was obtained by difference between W450 and W210. The classes of standard deviations (SD) for W210, PC, and ADG were obtained by the standardization of means of herd-year means subclasses, with positive values composing the high SD and values equal and less than zero composing the SD. The model included the fixed effects of contemporary group and age at calving as a covariate, random genetic additive, and maternal genetic (except for PC) effects, and the permanent maternal environment. Variance components were obtained by Gibbs sampling. Posterior means of heritability in analyses without considering heterogeneity of variances ranged from 0.15±0.01 to 0.31±0.01. Posterior means of genetic correlations between the two classes of SD for W210, PC, and ADG were equal to 0.85±0.04, 0.83±0.03, and 0.71±0.08, respectively. Spearman correlation to breeding values of sires for ADG as the selection intensity increased in them, and the correlations between breeding values in general analyses were more correlated with those predicted in the high DP. Therefore, when there is a higher selection intensity on the sires only for the ADG criterion, there is a significant presence of the heterogeneity of variances and impact on the genetic evaluation of the sires. Thus, for ADG, the predictions of breeding values obtained by the genetic evaluation model in which the heterogeneity of variances are not considered are more weighted by the class of greater heterogeneity.

Keywords: animal breeding, beef cattle, genetic correlation, heritability

1. Introduction

The cattle raising shows up as a relevant activity at the national agribusiness and, in this context, Brazil assumes a prominent position in the production of beef worldwide. However, the Brazilian production systems are very diversified and come from different regions, cultures, genetic groups, and different availability of resources, which may lead to the presence of genotype by environment interaction (GEI).

The GEI is characterized by differences obtained in the responses of the genotypes in different environments that, when present, can lead to error on genetic evaluation, changing the order of the genotypes when created in different environments (Falconer, 1952).

As a form of GEI, the heterogeneity of variances consists of differences in expression of the same genotype in different production strata. If there is a heterogeneity of variance by environmental sources, then the selection process can be biased.

Since, in most cases, the environment in which the sires are selected is not the same for the exploitation of their offspring, the sires may present different performances, thus leading to the need to carry out studies on the GEI in the performance of animals raised in different locations. In this sense, Carneiro et al. (2006) found that in the presence of heterogeneity of variances, the selection intensity used is important in the evaluation of cows and bulls with accuracy in the prediction of breeding values impaired by the means of standard deviations between herds, leading to errors when the classification of superior animals is performed.

Assessing the effect of heterogeneity of variance on weaning weight in Nellore animals in the Amazon biome, Ferreira et al. (2014) verified heritability estimates equal to 0.27, 0.33, and 0.26, for classes high, medium, and low standard deviations, respectively. On the other hand, Araújo et al. (2011) evaluated Nellore animals for yearling weight and found heritability estimates for the classes of low and high standard deviation equal to 0.34 and 0.36, respectively, showing no GEI.

This study aimed to evaluate the presence of the effects of heterogeneity of variance and its impact on genetic evaluation of Nellore cattle to traits of body weight at 210 days, for a linear combination between body weights at 365 and 450 days, as well as on weight gain from 210 to 450 days of age.

2. Material and Methods

We used information from 40,306, 35,024, and 31,697 records of adjusted body weights at 210 (W210), 365 (W365), and 450 (W450) days of age, respectively, of individuals participants in the Genetic Improvement Program of Nellore Brazil from Associação Nacional de Criadores e Pesquisadores (ANPC), from herds located in the states of Mato Grosso, Mato Grosso do Sul, and Goiás, born between 1990 and 2014. The relationship matrix presented 57,664 animals.

For the information referring to the records of W365 and W450, we used the Principal Component (PC) analysis. Average daily gain (ADG) was obtained from the initial standardized weight at 210 and the final one at 450 days of age. This analysis was conducted using SAS software (Statistical Analysis System, OnDemand for Academics).

The months of calving were grouped into seasons 1 and 2, which corresponded to the months of lowest and highest rainfall (from April to September and from October to March, respectively). The contemporary group was composed by combining the effects of herd, year, and season of birth and sex of the animal. Contemporary group information with less than four observations were not considered. The age at calving of cow was used as covariate, with a mean of 76.00±37.36 months.

For the establishment of SD classes at each trait, we standardized the means of herd-year classes to scale normal distribution standardized. Thus, positive values composed the high SD class, and values equal to and less than zero composed the low SD class.

For genetic connectivity, only information from sires with at least three progenies in each class of SD and with progenies in both classes of SD was considered.

The analyses were divided by the unitrait for each variable (general analyses), disregarding the heterogeneity of variances, and bitrait, considering the value in each class of SD as distinct traits.

The mixed linear animal model was represented as $y = X\beta + Za + Wm + Ppm + e$, in which y is a vector of observations, β is a vector of fixed effects (contemporary group and linear and quadratic effect of age at calving of cow, as covariate), a is the vector of additive genetic effect, m is the vector referring to the maternal genetic effect, *pm* is the vector associated with the effect of the maternal permanent environment, *e* is the residual effect vector, *X* is the incidence matrix that associates β with y, *Z* is the incidence matrix of the additive genetic effect, *W* is the incidence matrix of the maternal genetic effect, and *P* is the incidence matrix of the effect of the maternal permanent environment. In the analyses of PC and ADG, models disregarded the maternal genetic effect.

The variance components, heritability, and genetic correlations were estimated by Bayesian inference, using the Gibbs sampling through the GIBBS1F90 program (Misztal et al., 2014). To obtain the posterior means, chains of 300,000 cycles were used, saving every 10 cycles, with burn-in period of 30,000 cycles. To diagnose the chains, the Geweke criterion (Geweke, 1991) was used at the level of 5% probability of significance. The means and respective SD for W210, ADG, and PC in general analyses and in each class of SD, and also the coefficient of variation in each trait, are shown in Table 1.

To assess the consistency of the ordering of the sires, whether or not the presence of heterogeneity of variances was considered, the Spearman correlation was used between the additive breeding values of the sires with progenies in each trait. The values were obtained for the same sires in general analyses and in the classes of low and high SD, as well as the correlations between these predictions considering samples of top 90, 80, 70, 60, 50, 40, 30, 20, and 10% sires better classified in the situation in which heterogeneity of variance was disregarded, in other words, in general analyses.

Table 1 - Descriptive statistics for standardized weight at 210 days of age (W210), principal component (PC), and average daily gain (ADG) from 210 to 450 days of age in different classes of phenotypic standard deviations

Variable	N	Class	NCG	NR	Mean (kg)	SD	CV
		Low	315	21206	173.96	24.81	14.26
W210	387	High	276	19100	195.83	26.95	13.76
		General	591	40306	184.32	28.06	15.22
		Low	316	25709	321.33	44.34	13.80
PC	1835	High	274	26055	395.01	60.38	15.28
		General	590	51764	358.42	64.56	18.01
		Low	270	15797	0.31	0.11	34.37
ADG	300	High	237	14254	0.45	0.14	31.04
		General	507	30051	0.38	0.14	37.79

N - number of sires; NCG - number of contemporary groups; NR - number of records; SD - standard deviation; CV - coefficient of variation.

3. Results

The PC obtained through the orthogonal transformation of the first eigenvalue, which generated the first orthogonalized eigenvector and which converted the set of observations from W365 and W450 into a linear combination of them, was equal to PC = 0.634 * (W365) + 0.773 * (W450). It retained 96.5% of the total variation of the original variables (W365 and W450). Thus, the PC technique was efficient in reducing the parametric space.

This result is explained by the high value of the posterior mean of genetic correlation between W365 and W450, equal to 0.85, indicating similarity between gene groups in the expression of both traits.

To assess the size adequacy of Markov chains, it was verified by the estimates obtained for the Geweke diagnostic (Table 2) that the sizes were satisfactory to obtain the posterior averages of all the variance components (P>0.05). In this sense, the estimates of genetic additive and residual variance components for W210 and ADG, both between the standard deviation classes and in general analyses, were found in the same credibility interval, indicating that there are no differences between the posterior medians.

Table 2 - Posterior means of components of variances and their standard deviations (SD) by the Gibbs Sampling method for standardized weight at 210 days of age (W210), principal component (PC), and average daily gain (ADG) from 210 to 450 days of age in the different classes of phenotypic standard deviations

	W210			PC			ADG		
	Class								
	Low	High	General	Low	High	General	Low	High	General
σ^2_a	110.54±11.96	153.81±15.29	118.55±9.48	322.98±24.15	595.69±33.84	396.27±19.94	0.01±0.01	0.01±0.01	0.01±0.01
HPD (95%)	(87.27-133.8)	(124.7-184.7)	(100.8-137.7)	(276.8-370.4)	(530.9-663.6)	(358.4-436.4)	(0.01-0.01)	(0.01-0.01)	(0.01-0.01)
Geweke	0.16(0.87)	0.07(0.94)	0.08(0.94)	0.1(0.92)	0.15(0.88)	0.03(0.98)	0.11(0.91)	0.13(0.90)	0.06(0.95)
σ^2_{pm}	52.91±6.65	78±7.73	87±4.95	115±10.45	145.73±12.23	138.25±7.47	0.01±0.01	0.01±0.01	0.01±0.01
HPD (95%)	(39.63-65.81)	(63.02-93.42)	(77.35-96.79)	(93.91-135.1)	(121.4-169.7)	(123.8-153)	(0.01-0.01)	(0.01-0.01)	(0.01-0.01)
Geweke	0.1(0.92)	0.16(0.87)	0.03(0.98)	0.07(0.94)	0.03(0.98)	0.02(0.98)	0.01(0.99)	0(1)	0.04(0.97)
σ^2_m	53.86±6.51	67.16±8.09	29.91±4.77	-	-	-	-	-	-
HPD (95%)	(41.38-66.57)	(51.9-83.42)	(20.94-39.58)	-	-	-	-	-	-
Geweke	0.08(0.94)	0.27(0.79)	0.07(0.94)	-	-	-	-	-	-
σ^2_e	281.65±8.1	271.42±9.6	290.34±5.98	619.05±16.45	762.03±21.63	735.61±12.87	0.01±0.00	0.01±0.00	0.01±0.00
HPD (95%)	(266-297.9)	(252.6-290.4)	(278.8-302.3)	(587.5-651.4)	(720.5-805.3)	(710.7-760.9)	(0.01-0.00)	(0.01-0.00)	(0.01-0.00)
Geweke	0.02(0.98)	0.04(0.97)	0.07(0.94)	0.13(0.90)	0.13(0.90)	0.02(0.98)	0.1(0.92)	0.09(0.93)	0.02(0.98)
h^2	0.22±0.02	0.27±0.02	0.23±0.02	0.31±0.02	0.40±0.02	0.31±0.01	0.17±0.02	0.17±0.02	0.15±0.01
HPD (95%)	(0.18-0.27)	(0.22-0.32)	(0.19-0.26)	(0.27-0.35)	(0.36-0.43)	(0.28-0.34)	(0.13-0.21)	(0.14-0.21)	(0.12-0.18)
r_g	0.85±0.04			0.83±0.03			0.71±0.08		

σ^2_a - additive genetic effect; HPD (95%) - higher density intervals posteriori; σ^2_{pm} - effect of the maternal permanent environment; σ^2_m - maternal genetic effect; σ^2_e - residual variance; r_g - genetic correlation.

On the other hand, for PC, there was a higher posterior mean of additive genetic variance in the high deviation class in relation to those obtained in the low standard deviation class and in general analyses and with no differences between the last ones. Also, the posterior mean of residual variance in the high deviation class was higher in relation to those obtained in the low standard deviation class, but equal to that obtained in general analyses.

In this sense, the posterior heritability means obtained in general analyses were equal to 0.23±0.02, 0.31±0.01, and 0.15±0.01 for W210, PC and ADG, respectively, indicating better response efficiency to the selection in the post-weaning period.

4. Discussion

As observed in this work, Muniz et al. (2014) and Souza et al. (2010), evaluating growth traits in cattle through the PC analyses, also observed the efficiency of this technique in reducing the parametric space and simplifying the developed analyses.

Values of posterior heritability means obtained in this study are consistent with values observed by other authors. Heritability estimates in cattle for weaning weight ranged from 0.11 to 0.25 (Moreira et al., 2015; Santos et al., 2019; Barbosa et al., 2017), from 0.16 to 0.44 for the yearling weight (Moreira et al., 2015; Souza et al 2018; Santos et al., 2019; Barbosa et al., 2017), from 0.17 to 0.44 for post-yearling weight (Moreira et al., 2015; Souza et al., 2018; Santos et al., 2019; Barbosa et al., 2017), and from 0.20 to 0.26 for post-weaning weight gain (Duitama et al., 2015; Santana et al., 2017).

Adverse results were obtained by Ferreira et al. (2014), Santos et al. (2019), and Bresolin et al. (2015), who verified the effect of heterogeneity of variances for body weight at 205 days of age in Nellore cattle, with heritability estimates ranging from 0.11 to 0.34, values for genetic correlations from 0.52 to 0.84 showing a GEI. Similarly, Espasandin et al. (2013), in the Angus breed, verified the presence of the GEI for weaning weight, with estimates ranging from 0.31 to 0.54 and correlations ranging from 0.20 to 0.44, proving that there is interaction between the environment and genotype.

Regarding the posterior means of variance components between the SD classes for PC, the posterior mean of heritability observed in the high SD class was greater than both in low SD class and in general analyses, indicating the presence of the GEI in the form of heterogeneity of variances. However, the posterior mean of additive genetic correlation equal to 0.83 implied that the genetic variance of the trait in the two classes of SD, despite presenting divergent posterior means between the classes, oscillated in a similar way, thus implying a small change in the classification of the same sires in the two classes of SD.

For W210, the posterior heritability means in the low and high SD classes and in general analyses (0.22±0.02, 0.27±0.02, and 0.23±0.02, respectively) were presented all within the same range of credibility interval, therefore being similar to each other. This fact, associated with the high value of the posterior mean of additive genetic correlation (0.85), reveals that for this body weight, the models of genetic evaluation should not consider the effect of heterogeneity of variances.

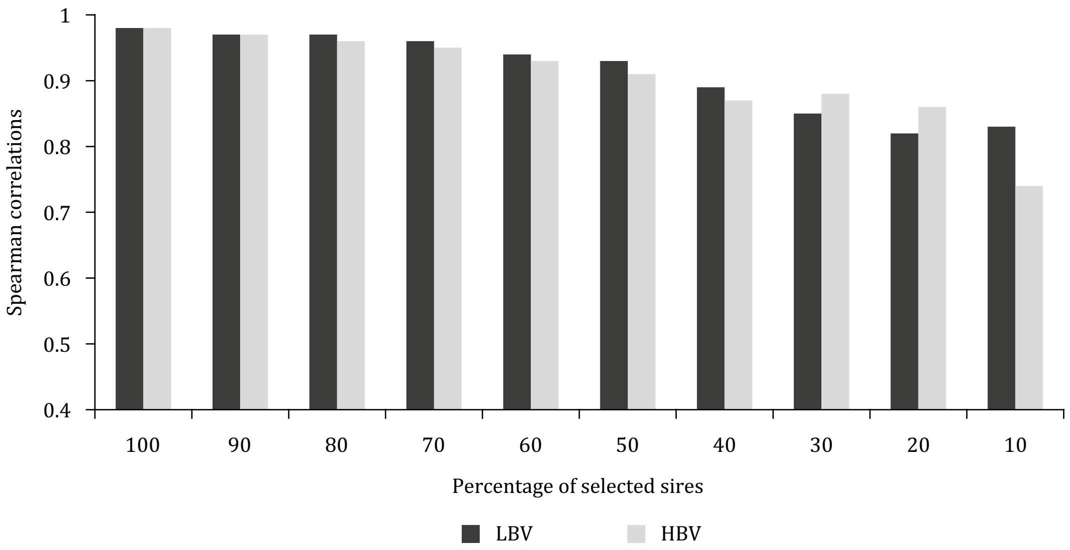
The posterior means of heritability for the ADG in the two classes of SD and in the analyses that disregarded the heterogeneity of variances presented themselves in the same credibility interval and, therefore, are similar. However, the posterior mean of additive genetic correlation equal to 0.71 obtained for this weight in the high and low phenotypic SD classes, indicates the presence of GEI. Therefore, changes in the breeding order were expected, considering the presence of the effect of heterogeneity of variances for this trait.

Considering the analyses of Spearman correlation between the low and high SD, the result obtained by the genetic correlations for P210 (Figure 1) indicated that there are no changes in the ordering of the breeding values of the sires, considering or not the heterogeneity of variances, with both all sires with progenies in production and the different samples of the best sires classified in general analyses.

Similarly, for the variable PC (Figure 2), there were no changes in the ranking of sires with the increase in their selection intensity. Although the correlations were high in all situations, with the increase in selection intensity, the predictions obtained in general analyses were more correlated with those obtained in the high SD class.

On the other hand, for ADG (Figure 3), considering the data containing all sires with offspring with records of body weight, Spearman correlation values between the predictions of changes in the sires ranking in general analyses and those predicted in each class of SD were high, therefore, without changes in the sires ranking regardless of the range of heterogeneity in the environment.

However, as the selection intensity increased, the correlations between predictions of breeding values for general analyses and those predicted in high SD class remained high, while correlations with the



W210 - weight at 210 days of age.

Figure 1 - Spearman correlations of the breeding values analyzed between general analyses with high (HBV) and low (LBV) SD classes for W210 of Nellore sires.

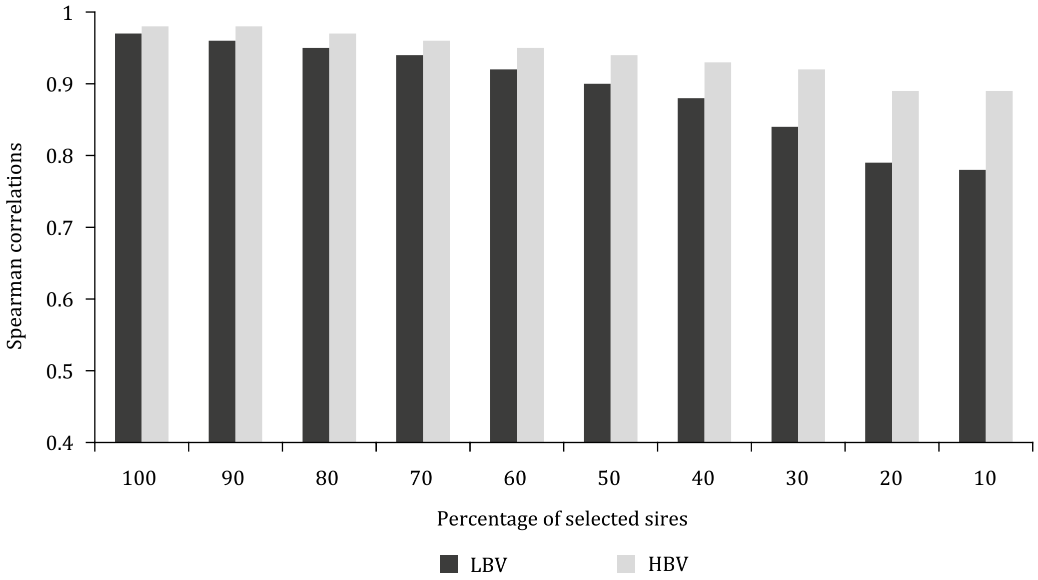


Figure 2 - Spearman correlations of the breeding values analyzed between general analyses with high (HBV) and low (LBV) SD classes for principal component of Nellore sires.

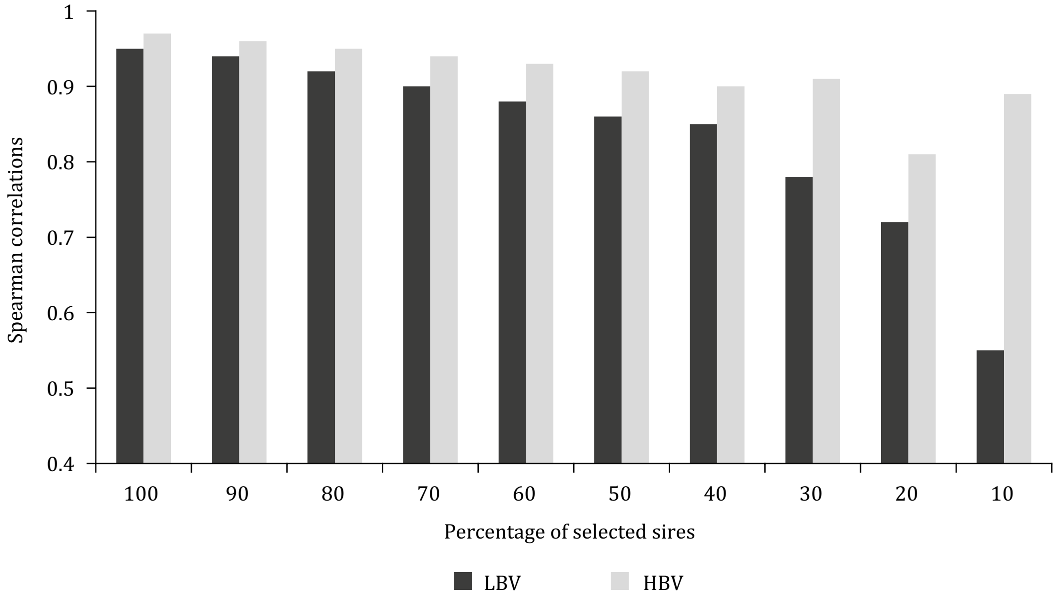


Figure 3 - Spearman correlations of the breeding values analyzed between general analyses with high (HBV) and low (LBV) SD classes for average daily gain of Nellore sires.

low SD class decreased. Therefore, when there is a selection pressure on the sires for the ADG trait, the predictions of breeding values obtained by the genetic evaluation model in which the heterogeneity of variances are disregarded are more weighted by the class of greater heterogeneity.

5. Conclusions

There is no presence of the genotype by environment interaction in the form of heterogeneity of variances for weight at 210 days and, thus, no change in the classification of genetic merit of sires. For the variable principal components, despite the differences between posterior means of heritability in the SD classes, there is no changes in the ranking of sires, even with the increasing intensity of selection. However, for average daily gain, although the posterior means of heritability are the same the SD classes, there is a greater selection pressure on the sires, based on their breeding values. Thus, for average daily gain, the predictions of breeding values obtained by the genetic evaluation model in which the heterogeneity of variances are not considered are more weighted by the class of greater heterogeneity.

Conflict of Interest

The authors declare no conflict of interest.

Author Contributions

Conceptualization: F.L. Menezes, C.V. Araújo, L.C. Novo, M.M.M. Laureano, S.I. Araújo, R.B. Lôbo, L.M. Castro, L.R.M. Nakabashi and F. Baldi. Data curation: F.L. Menezes, C.V. Araújo, S.I. Araújo, R.B. Lôbo, L.M. Castro, L.R.M. Nakabashi and F. Baldi. Formal analysis: C.V. Araújo, S.I. Araújo, L.M. Castro, L.R.M. Nakabashi and F. Baldi. Funding acquisition: C.V. Araújo, R.B. Lôbo, L.M. Castro and F. Baldi. Investigation: F.L. Menezes, C.V. Araújo, L.C. Novo, M.M.M. Laureano, S.I. Araújo, L.M. Castro and F. Baldi. Methodology: F.L. Menezes, C.V. Araújo, M.M.M. Laureano and F. Baldi. Project administration: C.V. Araújo. Resources: F.L. Menezes, C.V. Araújo and M.M.M. Laureano. Software: F.L. Menezes, C.V. Araújo, L.C. Novo and S.I. Araújo. Supervision: F.L. Menezes and C.V. Araújo. Validation: F.L. Menezes, C.V. Araújo and L.C. Novo. Visualization: F.L. Menezes and C.V. Araújo. Writing – original draft: F.L.

Menezes, C.V. Araújo, L.C. Novo and M.M.M. Laureano. Writing – review & editing: F.L. Menezes, C.V. Araújo, L.C. Novo and M.M.M. Laureano.

Acknowledgments

This study was financed in part by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES) - Finance Code 001, and Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq). The authors would like to thank the Associação Nacional de Criadores e Pesquisadores (ANCP), for providing the data used in this study, and the Instituto de Ciências Agrárias e Ambientais - Universidade Federal de Mato Grosso.

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