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Stayability and consecutive rebreeding ability associated to carcass and growth traits in Brazilian Nellore cattle: A Bayesian framework

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HIGHLIGHTS

- Rebreeding is one of the major challenges to improve the productive efficiency of Brazilian Nellore cows.
- Consecutive rebreeding ability is as a new multi-categorical trait associated to the female fertility.
- Consecutive rebreeding ability is a feasible indicator of Nellore fertility for long-term selection.
- Consecutive rebreeding ability has high genetic association with stayability.

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ABSTRACT

Stayability(STAY) plays a substantial role in Nellore breeding programs in Brazil, but it does not differentiate cows with different rebreeding successes. Thus, we propose consecutive rebreeding ability (CRA) as a new multi-categorical trait related to the capacity of consecutive parturitions at calving intervals of less than 14 months. The heritability for CRA and its genetic correlations with stayability at 52 (STAY52) and 76 (STAY76) months, rib eye area (REA), subcutaneous backfat thickness (BF), age at first calving (AFC), post-yearling scrotal circumference (PSC), and post-yearling weight (PW) were estimated. The pedigree information provided a genealogical relationship matrix that contained 2,042,151 animals. The genetic parameters were estimated by multiple-trait Bayesian inference using the THRGIBBS1F90 software. The heritability estimates (posterior means and posterior standard deviations) for CRA, STAY52, STAY76, REA, BF, PW, AFC and PSC were, respectively, 0.11 (0.036), 0.092 (0.009), 0.15 (0.013), 0.35 (0.015), 0.13 (0.013), 0.34 (0.012), 0.17 (0.005) and 0.41 (0.021). In general, for a proposed trait (such as CRA) be considered as a replacement for existing ones, then it must be able to significantly increase the rate of genetic progress, that is a function of genetic variation, selection intensity and generation interval. Thus, the current STAY76 remains the most appropriate criterion for Nellore breeding programs. In this context, STAY76 still being recommended as a simple and practical trait for long-term Nellore cow selection. Additionally, the genetic association for CRA would not have a negative genetic impact on subcutaneous backfat thickness (BF), age at first calving (AFC) and post-yearling scrotal circumference (PSC).

1. Introduction

Stayability (STAY) plays a substantial role in Nellore breeding programs in Brazil as a selection criterion for longevity and fertility. STAY is generally defined as a binary trait. Value 2 (success) is assigned to cows with three or more calvings by 76 months of age, and value 1

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(failure) otherwise (Costa et al., 2019). Therefore, this trait does not distinguish females that reconceived within a short period after calving during lactation (females with rebreeding success) since cows with different numbers of calvings may have the same phenotype. Furthermore, STAY is not a suitable specific indicator of fertility because it is also associated with sexual precocity, with females that have their first calve earlier being more likely to achieve success.

In general, the ability to reconceive is a major challenge for improving the reproductive efficiency of Brazilian Nellore herds. The low rebreeding rates are mainly related, among other factors, to the influence of the environment on extensive systems under tropical conditions (Recoules et al., 2013) and the physiological demands imposed by the continued growth and lactation of younger cows (Mulliniks et al., 2012). Within this context, the profitability of tropically-adapted cattle breeds is largely dependent on reproductive efficiency (Brumatti et al., 2011). Therefore, we propose consecutive rebreeding ability (CRA) as a new multi-categorical trait associated with the female's capacity to provide consecutive parturitions at calving intervals of less than 14 months. Unlike stayability, which is a binary trait, CRA is defined by classes of cows established according to their rebreeding success until the fourth calving. Using different categories, CRA thus allows to differentiate females that had reproductive failures at different ages. This approach permits to identify females with more or less regular parturitions. Four calvings were assumed for the definition of CRA because the Brazilian reproductive management system generally consists of an annual breeding season in which heifers begin to be exposed to bulls at about 26 months of age. Thus, four calvings are the maximum number of parturitions of the cow within a period similar to traditional stayability.

Given the relevance of ultrasound carcass, growth and other reproductive traits for Nellore breeding programs, it is important to determine the genetic associations between these traits and the proposed CRA trait. Genetic parameters estimates are essential to implement reliable selection indexes (Ochsner et al., 2017), which may allow the use of consecutive rebreeding ability (CRA) as a selection criterion for fertility by simultaneous selection for different traits. Within this context, we aimed to estimate the genetic parameters and genetic correlations of with stayability at 52 (STAY52) and 76 (STAY76) months of age, rib eye area (REA), subcutaneous backfat thickness (BF), age at first calving (AFC), post-yearling scrotal circumference (PSC), and post-yearling weight (PW). For this purpose, we used a substantial pedigree file that contained 2,042,151 Nellore animals.

2. Material and methods

2.1. Data description

The data were provided by the Geneplus-Embrapa Breeding Program, which offers a specialised genetic breeding service to Brazilian breeders. The database refers to *Bosindicus*Nellore breeding animals and is composed of farm records. Most of the farms have a tropical extensive production system and are located in different regions of Brazil. However, this should not be the desired pattern for a reliable genetic improvement of national Brazilian beef cattle.

The full pedigree contained a total of 2,042,151 animals. Consecutive rebreeding ability was divided into four categories of cows based on rebreeding occurrences until their first reproductive failure. According to the database used in the study, females spent an average of 4.36 months in the breeding season. Thus, considering an average gestation period of Nellore females of 294 days (9.62 months) plus the breeding season period (4.36 months), the average interval of consecutive calvings over the years was 14 months in these cows. Therefore, rebreeding was classified as successful when the female reconceived during lactation and calved again within less than 14 months in relation to the parturition in question. The categories were defined as follows: Category 1: assigned to females with rebreeding failure after first calving; Category 2: assigned to females with rebreeding success after first calving followed by rebreeding failure after second calving; Category 3: assigned to females with rebreeding success after first and second calving followed by rebreeding failure after third calving; and Category 4: assigned to females with rebreeding success after the first three calvings.

Situations in which the cow aborted or calved a stillborn calf were not considered a valid calving and were interpreted as failure.

Genetic analyses were also performed for the following traits: consecutive rebreeding ability (CRA), stayability at 52 (STAY52) and 76 (STAY76) months, rib eye area (REA), subcutaneous backfat thickness (BF), age at first calving (AFC), post-yearling scrotal circumference (PSC), and post-yearling weight (PW). STAY76 represents the conventional measure of stayability in Brazil, which considers cows with at least three calvings at 76 months of age. Differently, STAY52 considers only cows with at least two calvings at 52 months of age. For both STAY definitions, value 2 was assigned for success and 1 for failure. Value zero was assumed for missing data. In addition, for STAY and CRA, value 1 was assigned to females who had their first calving after 40 months because of their low reproductive efficiency when they did not conceive in their first breeding season at about 26 months of age. Reproductive data were collected by trans-rectal ultrasound scanning performed by specialised veterinarians. The REA and BF were obtained from cross-sectional images of the longissimus muscle between the 12th and 13th rib. The post-yearling traits (PSC and PW) were measured in animals at 375 to 600 days of age. The ages were adjusted according to contemporary group.

The contemporary groups were defined by combining the birth year and season (1 = January to March, 2 = April to June, 3 = July to September, 4 = October to December) and management group. However, the prediction error variance can increase when the contemporary groups exhibit no variance or contain only few animals, which might affect the genetic parameters results and the prediction accuracy of the expected progeny differences (Van Vleck, 1987). Therefore, animals belonging to contemporary groups with fewer than three records or contemporary groups containing cows with the same phenotypic observation for categorical traits were eliminated from the analysis. For the continuous traits, the outliers were identified and removed if the observation was outside of the three standard deviations for the trait. Descriptive statistics of the data (collected from 1991 to 2017) are presented in Table 1.

2.2. Statistical analysis

The (co)variances components and breeding values were estimated under a Bayesian framework using the THRGIBBS1F90 software (Misztal et al., 2002). Single-trait analyses were performed for all traits to estimate heritabilities, whereas bivariate analyses ("two by two") between CRA and the other traits were performed to estimate all genetic correlations.

A bivariate threshold model was used for the analysis involving consecutive rebreeding ability (CRA) and stayability traits, whereas the following bivariate linear-threshold model was used for the analysis of CRA and continuous traits:

$$\begin{bmatrix} y \\ l \end{bmatrix} = \begin{bmatrix} X_y & 0 \\ 0 & X_l \end{bmatrix} \begin{bmatrix} \beta_y \\ \beta_l \end{bmatrix} + \begin{bmatrix} Z_y & 0 \\ 0 & Z_l \end{bmatrix} \begin{bmatrix} a_y \\ a_l \end{bmatrix} + \begin{bmatrix} e_y \\ e_l \end{bmatrix},$$

where $\mathbf{y}$ is the vector of observations for the continuous traits: rib eye area (REA), subcutaneous backfat thickness (BF), age at first calving (AFC), post-yearling scrotal circumference (PSC), and post-yearling weight (PW); $\mathbf{l}$ is the vector of observations for the underlying threshold trait measured on the liability scale for the categorical traits (CRA, STAY76, or STAY52); $\boldsymbol{\beta}$ is the vector of systematic effects (described in detail later);$\mathbf{a}$ is the vector of additive genetic random effects, and $\mathbf{X}$ and $\mathbf{Z}$ are the incidence matrices for vectors$\boldsymbol{\beta}$ and $\mathbf{a}$,

Table 1
Number of records (N), response categories classified as 1 (n1), 2 (n2), 3 (n3) and 4 (n4), means, maximum and minimum values, and standard deviations (SD) obtained for each trait.

Trait	N	Category n1	n2	n3	n4	Mean	Maximum	Minimum	SD
CRA	171,641	108,767	33,839	13,589	15,446	1.62	4	1	0.816
STAY52	167,858	106,622	61,236	-	-	1.36	2	1	0.491
STAY76	121,475	90,939	30,536	-	-	1,25	2	1	0.441
REA (cm^2)	40,934	-	-	-	-	55.83	89.34	23.36	11.18
BF (mm)	30,667	-	-	-	-	2.21	3.86	1.02	0.55
PSC (cm)	126,075	-	-	-	-	24.91	36.59	13.33	3.88
AFC(day)	245,859	-	-	-	-	1177	1620	780	176.98
PW(kg)	322,191	-	-	-	-	300.50	433.00	144.10	52.67

CRA = consecutive rebreeding ability; STAY52 = stayability at 52 months; STAY76 = stayability at 76 months; REA = rib eye area; BF = subcutaneous backfat thickness; PW = post-yearling weight; AFC = age at first calving; PSC = post-yearling scrotal circumference.

respectively.

The prior distributions required for Bayesian analysis were given by $\boldsymbol{\beta}$ assuming a uniform distribution (noninformative prior); $a|\Sigma_a \sim N(0, A \otimes \Sigma_a)$, where **A** is the relationship matrix and $\boldsymbol{\Sigma}_a$is theadditive genetic covariance matrix; $e|\Sigma_e \sim N(0, I \otimes \Sigma_e)$,whereIand$\Sigma_e$are the identity and the residual covariance matrices, respectively. An inverse Wishart distribution was adopted as prior distribution for both covariance matrices, $\Sigma_a$and Σ_e.

The data distribution for the stayability traits (with only two possible classes, 1 and 2) was assumed to be:

$$f(yl, \beta, u, \sigma_a^2, \sigma_e^2, \tau) = \prod_{i=1}^{n} f(y_i|l_i) = \prod_{i=1}^{n} I(l_i < \tau)I(y_i = 1) + (l_i > \tau)I(y_i = 2),$$

where τ is the threshold value that defines the two response categories (1 and 2). On the other hand, for CRA (with four different classes), the following data distribution was assumed:

$$\begin{aligned} f(yl, \beta, u, \sigma_a^2, \sigma_e^2, \tau) = \prod_{i=1}^{n} f(y_i|l_i) = \prod_{i=1}^{n} & I(l_i < \tau_1)I\ (y_i = 1) \\ & + (\tau_1 < l_i < \tau_2)I(y_i = 2) \\ & + I(\tau_2 < l_i < \tau_3)I(y_i = 3) \\ & + (l_i > \tau_3)I(y_i = 4), \end{aligned}$$

where τ_1, τ_2, and τ_3 are thresholds that define the four response categories (1, 2, 3 and 4).

For all traits evaluated, the contemporary group was included as a systematic effect. For rib eye area (REA), subcutaneous backfat thickness (BF), and post-yearling weight (PW), the model included sex and contemporary group as systematic effects. The following covariates were also included: individual's age at the time of data recording (linear effect) for rib eye area (REA), subcutaneous backfat thickness (BF), age at first calving (AFC), post-yearling scrotal circumference (PSC), and post-yearling weight (PW); post-yearling weight (linear effect) for PSC and AFC; age at first calving (linear effect) for CRA, STAY52 and STAY76, and dam age at calving (linear and quadratic effect) for PW, PSC, REA, and BF.

A total of 400,000 Markov chain Monte Carlo (MCMC) iterations were used for the Bayesian inference of all fitted models. The burn-in and thinning intervals varied according to trait. The burn-in period ranged from 100,000 to 150,000 iterations and the thinning interval from 4 to 10 iterations. The convergence of the Gibbs sampler was checked by the Geweke test.

3. Results and discussion

Variance components, heritabilities, posterior standard deviations, and 95% highest probability density intervals (HPD95) are shown in Table 2. The Geweke test was not significant (P>0.05), indicating that convergence of the MCMC algorithm was achieved.

Table 2
Posterior means, posterior standard deviations (PSD) and 95% highest probability density intervals (HPD95) for additive genetic variance (σ_a^2), residual variance (σ_e^2), and heritability (h^2) obtained for the traits evaluated in Nellore cattle.

Traits	Parameter	Mean ± PSD	HPD95Lower; Upper
CRA	σ_a^2	1.197 ± 0.130	0.950; 1.444
	σ_e^2	10.490 ± 4.071	2.634; 18.346
	h^2	0.113 ± 0.036	0.043; 0.183
STAY52	σ_a^2	0.107 ± 0.012	0.084;0.130
	σ_e^2	1.044 ± 0.005	1.034;1.054
	h^2	0.092 ± 0.009	0.075; 0.011
STAY76	σ_a^2	0.185 ± 0.018	0.149; 0.220
	σ_e^2	1.044 ± 0.006	1,033;1.056
	h^2	0.150 ± 0.013	0.125; 0.175
REA	σ_a^2	14.021 ± 0.678	12.692;15.349
	σ_e^2	25.755 ± 0.508	24.760; 26.750
	h^2	0.352 ± 0.015	0.339; 0.365
BF	σ_a^2	0.020 ± 0.002	0.016; 0.024
	σ_e^2	0.127 ± 0.002	0.123; 0.130
	h^2	0.136 ± 0.013	0.111; 0.161
PW	σ_a^2	309.12 ± 11.960	285.68; 332.56
	σ_e^2	601.15 ± 8.768	584.04; 618.25
	h^2	0.340 ± 0.012	0.317; 0.362
AFC	σ_a^2	3.950 ± 0.130	3.695; 4.205
	σ_e^2	19.181 ± 0.113	18.960; 19.402
	h^2	0.171 ± 0.005	0.160; 0.181
PSC	σ_a^2	2.613 ± 0.148	2.323; 2.903
	σ_e^2	3.672 ± 0.109	3.458; 3.886
	h^2	0.416 ± 0.021	0.375; 0.456

CRA = consecutives rebreeding ability; STAY52 = stayability at 52 months; STAY76 = stayability at 76 months; REA = rib eye area; BF = subcutaneous backfat thickness; PW = post-yearling weight; AFC = age at first calving; PSC = post-yearling scrotal circumference.

Consecutive rebreeding ability showed low heritability (0.11), which was similar to STAY52 (0.09) and STAY76 (0.15). However, consecutive rebreeding ability (CRA) is a new trait to evaluate cow fertility since it allows differentiating females according to their reproductive failures until the fourth calving. This trait enables to identify and select long-lived cows with the ability to rebreed every breeding season. Therefore, long-term selection for CRA based on selection indexes are relevant due to its economic importance, as fertility and longevity are very important for beef cattle breeding because they significantly affect the profitability and productivity of herds (Brumatti et al., 2011).

The heritability estimate for STAY76 was higher than those reported by Silva et al. (2017), ranging from 0.03 to 0.07 in Nellore cattle.

Genetic parameters for STAY52 were not found in the literature. Although STAY52 is measured earlier, it is not a suitable alternative to STAY76 since, according to the HPD95, STAY52 has a lower heritability than STAY76, which will reduce the genetic progress per year.

The carcass traits (subcutaneous backfat thickness-BF and rib eye area-REA) exhibited low and high heritability, respectively, in agreement with Buzanskas et al. (2017) who reported estimates of 0.16 for BF and 0.32 for REA in Nellore cattle. The heritability estimates for AFC and PSCwere low and high, respectively. Buzanskas et al. (2017) reported a high heritability (although lower than that observed in the present study) for scrotal circumference at 420 days of age (0.38) and a higher heritability for age at first calving-AFC (0.24). In general, differences in the heritability estimates for AFC are related to the period of the breeding season of the evaluated populations. Restricted breeding seasons may reduce heritability. In situations in which females are reproducing for longer periods, the genetic variance for AFC may be higher because the time restriction for phenotype expression is lower. Another reason that may explain the difference in heritability is the environmental influence. A better controlled environment for heifer development has a positive impact on the heritability for AFC (Buzanskas et al., 2017).

Post-yearling weight showed moderate to high heritability. Paterno et al. (2016) reported a higher heritability (0.50) for weight at 450 days of age in Nellore cattle.

The posterior means, standard deviations and HPD95 intervals for the genetic correlations between CRA and the other traits evaluated are presented in Table 3.

CRA showed high genetic correlations with STAY76 (0.98) and STAY52 (0.99), indicating that selection for stayability (STAY) will result in animals with a higher probability of successful consecutive rebreedings until the fourth calving. This high correlation may be related to the fact that Brazilian producers usually cull females that did not rebreed in the breeding season. In summary, females that consecutively rebreed will achieve successful STAY. However.

The negative genetic correlation between CRA and AFC (-0.34) suggests that selection of younger females in the first calving may lead to the selection of reproductively efficient adult females. This result is usually not expected since females that calve very early have a high-energy demand due to the concomitant occurrence of growth and lactation (Berry et al., 2014). This physiological demand associated with the environment of an extensive system, which is often characterised by nutritional limitations, results in a low body condition score and, consequently, in reproductive failures. However, the genetic correlation observed suggests that, if the environmental influence is not strong enough to significantly impair the reproduction of this female, the animal tends to have a suitable ability to rebreed in future calvings.

The genetic correlation between CRA and BF (0.18) indicates that fat deposition is a requirement for reproductive performance in Nellore cattle. According to Cunningham et al. (1999), the activity of the reproductive axis is sensitive to the adequacy of nutrition and metabolic reserves. The authors further report that the adipose tissue reserves of a female can influence reproductive capacity at the onset of puberty (at the time of first ovulation) and the ability to maintain good reproductive efficiency during adult life. Consequently, females with a greater fat deposition capacity have more energy reserves and tend to exhibit a better ability to rebreed. In addition, BF is an indicator of carcass finishing efficiency by acting as a thermal insulation during the cooling process of the carcass in the slaughterhouse, preventing declines in meat quality (Rotta et al., 2009). In summary, selection for CRA may result in a low indirect genetic gain in BF. The genetic correlation between rib eye are-REA and CRA (0.12) was not significant because the HPD95 interval (-0.003; 0.247) was assumed to be zero. In general, the correlations between BF and REA are relatively low (0.23±0.02) in Nellore cattle (Zuin et al., 2012). However, Riley et al. (2002) emphasized that heritability and genetic correlations indicate that the genetic variation in Zebu cattle (in this case, the Brahman breed) is sufficient to design and implement effective selection programs for important carcass quality and yield traits. Reports combining the traditional importance of carcass traits and the current relevance of fertility traits (such as CRA) are scarce in the literature, a fact that highlights the importance of the present study for the field of beef cattle breeding under tropical conditions.

Table 3
Posterior means, posterior standard deviations (PSD) and 95% highest probability density intervals (HPD95) for the genetic correlations between consecutive rebreeding ability (CRA) and the other traits evaluated in Nellore cattle.

Trait	Genetic correlation with CRA Mean ± PSD	HPD95 Lower; Upper
STAY52	0.99 ± 0.002	0.991; 0.999
STAY76	0.98 ± 0.009	0.968; 0.999
REA	0.12 ± 0.033	-0.003; 0.247
BF	0.18 ± 0.086	0.020; 0.356
PW	0.10± 0.052	0.003; 0.207
AFC	-0.34 ± 0.049	-0.438; -0.244
PSC	0.15 ± 0.053	0.048; 0.256

STAY52 = stayability at 52 months; STAY76 = stayability at 76 months; REA = rib eye area; BF = subcutaneous backfat thickness; PW = post-yearling weight; AFC = age at first calving; PSC = post-yearling scrotal circumference.

The genetic correlation between CRA and PW- post-yearling weight (0.10) was significant (Table 3), but there are no evidences in previous reports that PW is highly genetically correlated to extended live weight production in both male and female cattle, then that assumption should not avoided (Holroyd et al., 2000).

In summary, according to Brumatti et al (2011), it was evaluated that the reproductive traits, such as stayability and PP14, were around four and thirteen times more economically important than the growth traits (post-weaning weight, weaning weight and steer weight at 18 months). In front of these results, it is clear the advantages on investments on breeding programs focusing on female reproductive traits as highlighted in the present study.

Additionally, as previously mentioned, for a given existing trait replaces a traditional one, this proposed trait must be able to significantly increase the rate of genetic progress. In the present study, although consecutive rebreeding ability presented as a reliable alternatively trait for the current status of the modern beef cattle breeding, the binary stayabiliy trait still being as easier, quicker and cheaper to measure.

4. Conclusion

After several comparisons, stayability (STAY) still being recommended as a simple and practical trait for long-term Nellore cow selection. Additionally, the genetic association for STAY would not have a negative genetic impact on subcutaneous backfat thickness (BF), age at first calving (AFC) and post-yearling scrotal circumference (PSC).

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