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Genomic evaluation for novel stayability traits in Nellore cattle

Pedro Vital Brasil Ramos[1] | **Fabyano Fonseca e Silva[1]** | **Luiz Otávio Campos da Silva[2]** | **Gustavo Garcia Santiago[3]** | **Gilberto Romeiro de Oliveira Menezes[2]** | **José Marcelo Soriano Viana[4]** | **Roberto A. A. Torres Júnior[2]** | **Andrea Gondo[2]** | **Luiz F. Brito[5]** 🆔

[1]Department of Animal Science, Federal University of Viçosa, Viçosa, Brazil

[2]Embrapa Gado de Corte, Campo Grande, Brazil

[3]Faculty of Veterinary Medicine and Animal Science, Federal University of Mato Grosso do Sul, Campo Grande, Brazil

[4]Department of Biology, Federal University of Vicosa, Vicosa, Brazil

[5]Department of Animal Sciences, Purdue University, West Lafayette, IN, USA

Correspondence
Luiz F. Brito, Department of Animal Sciences, Purdue University, 270 Russell Street, West Lafayette, 47907, IN, USA.
Email: britol@purdue.edu

Abstract

Cow stayability plays a major role on the overall profitability of the beef cattle industry, as it is directly related to reproductive efficiency and cow's longevity. Stayability (STAY63) is usually defined as the ability of the cow to calve at least three times until 76 months of age. This is a late-measured and lowly heritable trait, which consequently constrains genetic progress per time unit. Thus, the use of genomic information associated with novel stayability traits measured earlier in life will likely result in higher prediction accuracy and faster genetic progress for cow longevity. In this study, we aimed to compare pedigree-based and single-step GBLUP (ssGBLUP) methods as well as to estimate genetic correlations between the proposed stayability traits: STAY42, STAY53 and STAY64, which are measured at 52, 64 and 76 months of cow's age, considering at least 2, 3 and 4 calving, respectively. ssGBLUP yielded the highest prediction accuracy for all traits. The heritability estimates for STAY42, STAY53, STAY63 and STAY64 were 0.090, 0.151, 0.152 and 0.143, respectively. The genetic correlations between traits ranged from 0.899 (STAY42 and STAY53) to 0.985 (STAY53 and STAY63). The high genetic correlation between STAY42 and STAY53 suggests that besides being related to cow longevity, STAY53 is also associated with the early-stage reproductive efficiency. Thus, STAY53 is recommended as a suitable selection criterion for reproductive efficiency due to its higher heritability, favourable genetic correlation with other traits, and measured earlier in life, compared with the conventional stayability trait, that is STAY63.

KEYWORDS
cow fertility, genomic selection, longevity, reproductive trait, threshold model

1 | INTRODUCTION

Reproductive efficiency plays a major role on the productivity and profitability of beef cattle production systems (Costa et al., 2018; Summers, Shelby, & Scholljegerdes, 2018). In addition, reproductive traits have great influence on generation interval and selection intensity (Kluska et al., 2018) and consequently, on the rates of genetic progress per time unit. Thus, various indicator traits of female reproductive performance have been evaluated as selection criterion in beef cattle breeding programs around the world. In this context, stayability is a key trait as it indicates the female's ability to remain in the herd up to a given age with regular reproductive performance (Schmidt et al., 2018). Therefore, stayability has a great economic impact on the production systems, since it combines reproductive efficiency and cow's longevity (Mwansa, Crews, Wilton, & Kemp, 2002).

The most common stayability measurement (STAY63) is usually defined as a binary trait assuming as success the cow that had three (or more) calving up to 76 months of age (Schmidt et al., 2018; Silva et al., 2017). This definition limits the number of cows with measurements, as young animals will not have records until they reach 76 months of age. Furthermore, many of them may be culled (due to other reasons) before reaching this age. Consequently, the reduced amount of phenotypic information results in lowly accurate breeding values and thus in significant reduction of the annual genetic gain for cow longevity. Additionally, STAY63 allows cows having up to two reproductive failures and, even so, still obtain the success phenotype (i.e., calving at least three times until 76 months of age). This may lead to the selection of females with reproductive failures concentrated at the beginning of their reproductive life, which is not economically desirable, since these cows will delay their economic return to producers.

Novel stayability traits that lead to lower number of reproductive failures may better represent the cow's reproductive efficiency. Furthermore, obtaining phenotypic records at an earlier stage will fastener genetic progress for both reproductive efficiency and cow longevity. In this context, STAY42 can be defined as the ability of the female to remain in the herd for 52 months with at least two calving, thus being more related to sexual precocity and ability of first-parity cows to re-breed in a short period. In addition, STAY53 and STAY64 are defined as the ability of the cow to have three and four calving up to 64 and 76 months of age, respectively. In this way, the success phenotype is attributed to females with better reproductive efficiency, considering only one reproductive failure for heifers that were bred (or artificially inseminated) at around 14 months of age.

Independently of the trait definition, genomic information is essentially required to ensure feasible accuracies for stayability at an early age, since it is characterized as a late-measured and sex-restricted trait (van Eenennaam, Weigel, Young, Cleveland, & Dekkers, 2014). In this context, the single-step GBLUP methodology (ssGBLUP; Aguilar et al., 2010; Christensen & Lund, 2010; Misztal, Legarra, & Aguilar, 2009) has the advantage of simultaneously combining genomic, pedigree and phenotypic information in a single model. This method is particularly relevant for breeding programs in developing countries that have large number of animals with phenotypes, but a limited number of genotyped individuals. Thus, we aimed to compare the use of BLUP and ssGBLUP for genetically evaluating different stayability traits and investigate the genetic association between the commonly used STAY63 trait and the alternative traits (STAY42, STAY53, and STAY64) proposed in this study.

2 | MATERIALS AND METHODS

2.1 | Ethics statement

Animal care and approval of an ethics committee were not necessary as all the data used here were obtained from pre-existing databases provided by national breeding programs.

TABLE 1 Number of records (N), records assigned as failure (*n1*) or success (*n2*), success percentage (%Success) and number of contemporary groups (CG) represented for each stayability trait in Nellore cattle

| Trait | N | Categories | | %Success | CG |
		n1	*n2*		
STAY42	167,858	106,622	61,236	36.48%	15,509
STAY53	121,766	91,170	30,596	25.12%	9,828
STAY63	121,475	90,939	30,536	25.14%	9,802
STAY64	87,780	70,756	17,024	19.39%	6,287

Note: STAY42, STAY53, STAY63 and STAY64 = female's ability to remain in the herd up to 52, 64, 76 and 76 months of age calving at least 2, 3, 3 and 4 times, respectively.

The datasets were provided by the Geneplus EMBRAPA Program, which is a Brazilian beef cattle breeding program located at Campo Grande, Mato Grosso do Sul (Brazil). The data are from Nellore animals raised under extensive system in several farms from different Brazilian regions.

2.2 | Phenotypic data

Four stayability definitions were evaluated: the ability of the female to remain in the herd for 76 months with four (or more) calving (STAY64), 76 months with three (or more) calving (STAY63), 64 months with three (or more) calving (STAY53) and 52 months with two calving (STAY42). All traits are binary, in which the value '2' (success) is used for females that reached the respective number of calving, and '1' (failure) otherwise. Missing values were set as zero.

Data editing was performed using the R software (R Core Team, 2019). The contemporary groups (CG) were determined based on herd, year and season (1 = January to March, 2 = April to June, 3 = July to September and 4 = October to December) of cows' birth. Animals belonging to CG with less than three records, or CG that had only cows with the same phenotype were excluded. Records of females with age at first calving above or below three standard deviations from the mean within CG were also removed. The complete pedigree contained 2,042,151 animals. The descriptive statistics after data editing are presented in Table 1.

2.3 | Genotypic data

The genotype files contained a total of 13,726 animals (8,921 males and 4,805 females) as follow: 3,333, 2,910, 3,923, 1,618 and 1,942 animals genotyped using the 777K, 35K, 30K, 27K and 26K SNP panel, respectively. All SNP panels were from the Illumina BeadChip Arrays. Some animals were genotyped more than once, so duplicate genomic data were excluded. The genomic quality control was performed using the *snpStats v1.16.0* package (Clayton, 2014) and

the preGSf90 software (Misztal et al., 2002). The following criteria for SNP exclusion were considered: minor allele frequency (MAF) lower than 0.05, samples and SNP call rate <95%, p-value of the chi-squared test for Hardy–Weinberg equilibrium lower than .000001 and genotypes with calling score lower than 15% (as recommended by Illumina Inc).

Pedigree consistency analysis was evaluated through the seekparentf90 software (Aguilar, 2014). After pedigree corrections, kinship relationships between parent and progeny that had Mendelian inconsistencies above 1% were excluded. The imputation of all previously mentioned genotypes was performed using the Fimpute v.2.2 software (Sargolzaei, Chesnais, & Schenkel, 2014). Imputation accuracy was estimated via cross-validation analysis based on random exclusion of genotyped animals. Genotype imputation accuracy was higher than 97% as previously reported by Carvalheiro et al. (2014). After the imputation process, markers with MAF <5% were excluded, resulting in a final dataset with 10,909 genotyped animals (7,309 males and 3,600 females) and 397,423 SNPs.

2.4 | Statistical analyses

Variance components and genetic parameters were estimated by fitting thresholds models using the THRGIBBS1f90 software (Tsuruta & Misztal, 2006) under both BLUP and ssGBLUP approaches. The genetic correlations between the four traits were estimated by means of bivariate analysis. The bivariate threshold model can be written in matrix notation as follows:

$$\mathbf{l} = \mathbf{X}\boldsymbol{\beta} + \mathbf{Za} + \mathbf{e},$$

where $\mathbf{l}$ is the observation vector of threshold trait on the liability scale with continuous normal distribution, that is $\mathbf{y}|\mathbf{l}, \boldsymbol{\beta}, \mathbf{a}, \boldsymbol{\Sigma}_\mathbf{a} \boldsymbol{\Sigma}_\mathbf{e}, \tau \sim N(\mathbf{X}\boldsymbol{\beta} + \mathbf{Za}, \mathbf{l} \otimes \boldsymbol{\Sigma}_\mathbf{e})$; $\boldsymbol{\beta}$ is the vector of systematic effects (CG and age at first calving as linear covariate) assuming an uniform prior distribution; $\mathbf{a}$ is the vector of additive genetic effects, $\mathbf{a}|\boldsymbol{\Sigma}_\mathbf{a} \sim N(0, \mathbf{A} \otimes \boldsymbol{\Sigma}_\mathbf{a})$, where $\mathbf{A}$ is the relationship matrix and $\boldsymbol{\Sigma}_\mathbf{a}$ is the additive genetic covariance matrix; $\mathbf{e}$ is the vector of residual effects, $\mathbf{e}|\boldsymbol{\Sigma}_\mathbf{e} \sim N(0, \mathbf{l} \otimes \boldsymbol{\Sigma}_\mathbf{e})$, where $\mathbf{l}$ and $\boldsymbol{\Sigma}_\mathbf{e}$ are the identity and the residual (co)variance matrices, respectively. A total of 300,000 MCMC iterations were used for inference of all evaluated traits. The burn-in and thinning were given by 100,000 and four iterations, respectively, according to the Raftery and Lewis test implemented in the *boa* package (Smith, 2007). The POSTGIBBSF90 software (Misztal et al., 2002) was used for posterior inference, being the convergence evaluated through the Geweke test (Geweke, 1992). Under a ssGBLUP approach, it was assumed that $\mathbf{a}|\boldsymbol{\Sigma}_\mathbf{a} \sim N(0, \mathbf{H} \otimes \boldsymbol{\Sigma}_\mathbf{a})$. According to Aguilar et al. (2010), the inverse of the $\mathbf{H}$ matrix is given by,

$$\mathbf{H}^{-1} = \mathbf{A}^{-1} + \begin{bmatrix} 0 & 0 \\ 0 & \mathbf{G}^{-1} - \mathbf{A}_{22}^{-1} \end{bmatrix}$$

where $\mathbf{H}$ is the matrix of relationship coefficients that combines pedigree and SNP data information; $\mathbf{A}_{22}^{-1}$ is the inverse of the additive relationship matrix for genotyped animals; and $\mathbf{G}^{-1}$ is the inverse of the genomic relationship matrix ($\mathbf{G}$). The $\mathbf{G}$ matrix was obtained as follow (VanRaden, 2008):

$$\mathbf{G} = \frac{\mathbf{ZZ'}}{2\sum_{j=1}^{m} p_j (1 - p_j)'}$$

where $\mathbf{Z} = \mathbf{M} - \mathbf{P}$, in which $\mathbf{M}$ is the genotype matrix of n genotyped animals (rows) by m markers (columns), and $\mathbf{P}$ is a matrix containing 2 times the observed frequency of the second allele (p_j).

Spearman's rank correlation between breeding values for different stayability traits was computed to assess potential re-rankings based on breeding values. In addition, the percentage of sires and females selected in common among the traits at different percentiles (1%, 3% and 5%) were also calculated.

2.5 | Methods comparisons

The predictive ability of each model was investigated based on forward validation analysis. The validation population (n = 35,057) was defined by genotyped females and non-genotyped daughters of genotyped bulls. Thus, it was possible to compare the prediction ability obtained from traditional BLUP and ssGBLUP focusing on the increment provided by the inclusion of genomic information. In brief, the phenotypic information of females from the validation population was removed. Thus, their breeding values were predicted and posteriorly correlated with those obtained from the analysis using full phenotypic information (full dataset). This correlation is termed as predictive ability and was calculated for both methods (BLUP and ssGBLUP). Bias was also obtained as the difference between the regression coefficients and the unity to measure the degree of inflation/deflation of EBV predictions. In addition to the overall predictive ability, the individual breeding value accuracies (IBVAs) were also investigated. The IBVAs were calculated under a Bayesian framework by assuming the squared posterior deviation as the predictor error variance (PEV).

3 | RESULTS AND DISCUSSION

3.1 | Method comparisons

The prediction accuracy and bias estimates obtained through the validation analysis for the four stayability traits are presented in Table 2. The genomic prediction accuracy can be influenced by different factors, such as the number of individuals in the training population, the number of genotyped individuals, marker density and the linkage disequilibrium between SNPs (de los Campos, Hickey, Pong-Wong, Daetwyler, & Calus, 2012; Goddard, Hayes, & Meuwissen, 2011). The ssGBLUP method yielded the highest

TABLE 2 Prediction accuracy (r) of estimated breeding values (EBVs), genomic EBVs (GEBVs) and bias obtained through the BLUP and ssGBLUP methods for four stayability traits, and the percentage of increase in prediction accuracy (>Acc) obtained by the ssGBLUP method, in Nellore cattle

	BLUP		ssGBLUP		
Trait	r*	Bias	r*	Bias	>Acc
STAY42	0.53	0.26	0.58	0.16	10%
STAY53	0.51	0.27	0.58	0.23	14%
STAY63	0.51	0.29	0.57	0.27	13%
STAY64	0.55	0.23	0.62	0.18	12%

Note: STAY42, STAY53, STAY63 and STAY64 = female's ability to remain in the herd up to 52, 64, 76 and 76 months of age calving at least 2, 3, 3 and 4 times, respectively.

*p < .001.

accuracy for all stayability traits, resulting in an increase ranging from 10% to 14% when compared to traditional BLUP. This increase in accuracy was expected due to the low proportion of genotyped animals (n = 10,909) compared with the total number of animals in the pedigree file (n = 2,042,151). By increasing both the number of genotyped older animals (with higher EBV accuracy) and young animals will result in greater impact on the prediction accuracy provided by the incorporation of genomic information (Lourenço et al., 2015).

The bias estimates ranged from 0.23 to 0.29 and 0.16 to 0.27 for BLUP and ssGBLUP, respectively. Thus, traditional BLUP yielded higher overestimation of EBV than the ssGBLUP method, which is not desirable as changes in the magnitude of the predictions may result in misinterpretation of the breeding values. These results are similar to those reported by Silva et al. (2016), who concluded that ssGBLUP improves the accuracy and reduces the prediction bias of genomic breeding values in comparison with pedigree-based traditional BLUP. Therefore, our results imply in a solid methodological support for genomic evaluation of stayability in beef cattle. In addition to the validation analysis, scatter plots (Figure 1) of IBVAs were performed for the four different stayability traits under both BLUP and ssGBLUP approaches.

Figure 1 shows the similarity of IBVAs among the methods for each stayability trait. However, a great increase in IBVAs for some animals was observed when genomic information was incorporated. These differences in accuracy estimates are related to the inclusion of genomic information (through the **G** matrix), by considering kinship coefficients calculated by realized proportion of marker alleles shared by identity-by-state (IBS) markers, thus capturing more information than the traditional coefficients based on pedigree (Habier, Fernando, Kizilkaya, & Garrick, 2011; Meuwissen, Hayes, & Goddard, 2001). According to VanRaden (2008), the **G** matrix enables to assess Mendelian sampling and to identify previously unknown relationships or correct genealogy errors. Thus, a reorganization of kinship coefficients resulted in IBVA increase, especially for genotyped animals.

3.2 | Genetic parameter estimates

The variance component estimates, heritability, standard deviations (*SD*) and highest probability density intervals (HPD95) of the four stayability traits, obtained through both BLUP and ssGBLUP methods, are shown in Table 3. The Geweke test was not significant (*p* > .05) for all parameters, which indicates that MCMC convergence was achieved.

No differences were observed in the genetic parameters when genomic information was included through the **H** matrix in comparison with the use of **A** for the analysis. The four stayability traits presented low to moderate heritability, suggesting a significant environmental influence in these traits. Direct selection for these traits is feasible, but the annual genetic gains might be limited in comparison with traits with higher heritability estimates. Considering the economic importance of stayability for the beef cattle industry, it is recommended to include this trait in selection indexes approaching long-term selection in beef cattle breeding programs.

Among the four stayability traits, STAY42 had the lowest heritability estimate (0.09). This may be associated with a greater influence of non-genetic effects of female re-breeding after the first calving, as the success (score = 2) phenotype is attributed to cows that calved twice in 52 months. First-parity cows' re-breeding is a major challenge in tropical extensive beef production due to nutritional limitations (Recoules, De La Torre, Agabriel, Egal, & Blanc, 2013) and physiological demand simultaneously imposed by growth and lactation processes (Mulliniks et al., 2012). Thus, the greater environmental influence might be the cause of the lower genetic variance observed for STAY42.

Although presenting low heritability, STAY42 is linked to reproductive efficiency at the beginning of the beef cow reproductive life. Thus, STAY42 might indicate the heifer ability to become pregnant at an earlier age in addition to first-parity re-breeding. Therefore, the long-term selection of STAY42 may be important to increase the reproductive performance of young cows. To our best knowledge, this is the first report of genetic parameters for STAY42 and STAY64.

The heritability estimate for STAY64 was 0.14, which is similar to the estimates obtained for STAY53 and STAY63 based on HPD95. STAY53 and STAY63 presented heritability estimates equal to 0.15. These estimates are greater than those reported by Silva et al. (2017), who presented heritability estimates of STAY63 in Nellore cattle ranging from 0.03 to 0.07. In contrast, the results of the present study corroborate with Teixeira et al. (2017) and Bonamy et al. (2018) who reported heritability for STAY63 of 0.14 and 0.16, respectively. Valente et al. (2017) evaluating Nellore cows' ability to calve at least three times before reaching 65 months of age, obtained similar results for STAY53, including a heritability estimate equal to 0.13. The posterior means, *SD* and respective HPD95 for genetic correlations between the four evaluated traits are presented in Table 4.

The high genetic correlations (Table 4) characterize the synergism between the four stayability traits. Therefore, direct selection for one of them will provide positive and favourable response on the
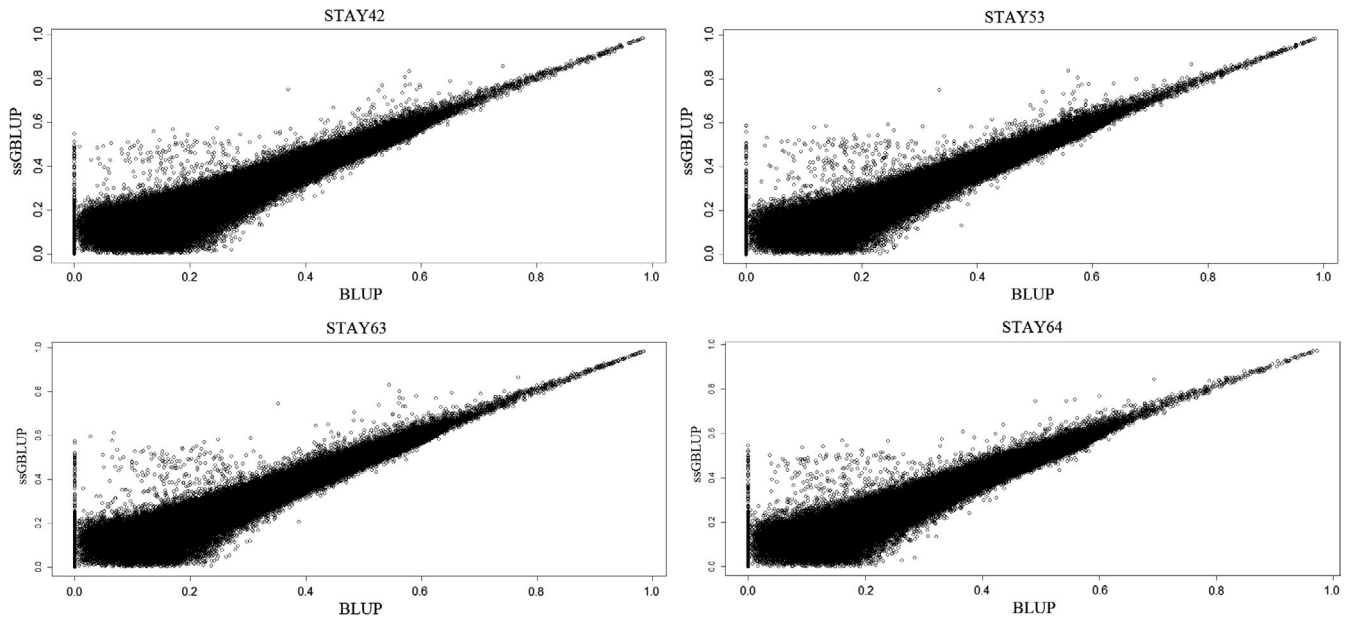
FIGURE 1 Scatter plots of individual breeding value accuracies estimates for four stayability traits, through the BLUP and ssGBLUP methods. STAY42, STAY53, STAY63 and STAY64 = female's ability to remain in the herd up to 52, 64, 76 and 76 months of age calving at least 2, 3, 3 and 4 times, respectively

others. The genetic correlations of STAY42 with STAY53, STAY63 and STAY64 were 0.899, 0.929 and 0.916, respectively. These results suggest that late stayability definition have high correlation with sexual precocity and reproductive efficiency of young cows. Thus, one can conclude that, although STAY63 allows the female to be successful with up to two reproductive failures, it is not directly associated with cows that present reproductive failures concentrated at the beginning of its reproductive life. This may be associated with traditional Brazilian beef cattle production systems, where cows that do not re-breed and heifers that do not become pregnant during the breeding season, are culled. Therefore, even for STAY63, females obtaining the successful phenotype are, in large majority, those that present consecutive re-breeding, since those that fail to conceive are usually culled before this trait can be recorded.

Even though STAY42 has a greater number of phenotypic records and high genetic correlation with the other stayability traits, it is not suitable as an indirect selection criterion for the others. This is because STAY42 has a considerably lower heritability estimate, which may result in lower rate of genetic progress per year compared with the other traits. On the other hand, the high genetic correlations between STAY53 and the other traits suggest that it can be recommended as an indirect selection criterion for the other indicators of stayability, since it is similarly heritable compared with STAY63 and STAY64, and has higher heritability than STAY42. Furthermore, STAY53 is measured at an earlier stage in comparison with STAY63 and STAY64. Taken together, selection based on STAY53 will result in earlier decision on the selection candidates, which will result in greater annual rates of genetic gain. In other words, selection based on STAY53 results in females presenting improved reproductive efficiency at the beginning of reproductive life and also in females that will calve at least four times in 76 months. Moreover, when

compared to STAY63, STAY53 allows selecting females that calved at least three times in a shorter period, thus providing greater economic return to the beef cattle industry.

The STAY64 trait also presented a high genetic correlation with STAY53, which suggests that this trait may be prioritized in comparison with STAY63, since it is related to the highest number of calving in the same period. Therefore, STAY64 enables the selection of cows with shorter intervals between calving, and, consequently, greater reproductive efficiency and economic return to the beef industry.

3.3 | Genetic ranking of animals

Spearman correlations between breeding values and the percentage of individuals selected in common for different stayability traits under ssGBLUP method (with 1%, 3% and 5% percentiles of sires and females) are described in Table 5.

The Spearman correlations were higher between STAY53, STAY63 and STAY64 (Table 5), with values greater than 0.9 in the three evaluated percentiles (considering females and sires). This result suggests that small differences in the ranking of animals selected based on these traits would be expected. However, STAY42 resulted in a greater proportion of re-ranking, with Spearman correlations ranging from 0.66 to 0.82. The percentage of commonly selected individuals considering females and sires ranged from 89.42% to 95.85% between STAY53, STAY63 and STAY64. Thus, the use of any of these traits as selection criterion would lead to the selection of a very similar set of individuals. Therefore, the similarity of the EBV rankings between these stayability traits and other previous results reinforce the potential of STAY53 as the best indirect selection criterion for all other evaluated traits.

TABLE 3 Posterior means and standard deviations (in parentheses), and 95% highest probability density intervals (HPD95) for direct additive genetic (σ_a^2) and residual (σ_r^2) variances and heritability (h^2), obtained through BLUP and ssGBLUP methods, for four stayability traits in Nellore cattle

Trait	σ_a^2	HPD95	σ_r^2	HPD95	h^2	HPD95
BLUP						
STAY42	0.108 (0.012)	0.083; 0.132	1.056 (0.005)	1.046; 1.066	0.093 (0.010)	0.074; 0.112
STAY53	0.186 (0.016)	0.155; 0.217	1.044 (0.006)	1.033; 1.056	0.151 (0.011)	0.129; 0.178
STAY63	0.185 (0.018)	0.149; 0.220	1.044 (0.006)	1.033; 1.056	0.150 (0.012)	0.125; 0.175
STAY64	0.170 (0.019)	0.134; 0.208	1.037 (0.007)	1.024; 1.051	0.141 (0.014)	0.116; 0.165
ssGBLUP						
STAY42	0.104 (0.001)	0.085; 0.124	1.056 (0.005)	1.046; 1.066	0.090 (0.008)	0.074; 0.105
STAY53	0.186 (0.018)	0.150; 0.222	1.044 (0.006)	1.033; 1.056	0.151 (0.013)	0.126; 0.176
STAY63	0.188 (0.022)	0.145; 0.231	1.044 (0.006)	1.033; 1.056	0.152 (0.015)	0.123; 0.182
STAY64	0.174 (0.020)	0.136; 0.212	1.045 (0.007)	1.032; 1.056	0.143 (0.014)	0.116; 0.167

Note: STAY42, STAY53, STAY63 and STAY64 = female's ability to remain in the herd up to 52, 64, 76 and 76 months of age calving at least 2, 3, 3 and 4 times, respectively.

TABLE 4 Posterior means and standard deviations (*SD*) and their respective HPD95 (95% highest probability density intervals) of genetic correlations (r_g) between stayability traits in Nellore cattle

Traits	r_g	HPD95
STAY42 and STAY53	0.899 (0.023)	0.854; 0.945
STAY42 and STAY63	0.929 (0.016)	0.899; 0.961
STAY42 and STAY64	0.916 (0.020)	0.876; 0.955
STAY53 and STAY63	0.985 (0.020)	0.972; 0.997
STAY53 and STAY64	0.981 (0.006)	0.968; 0.993
STAY63 and STAY64	0.973 (0.005)	0.963; 0.984

Note: STAY42, STAY53, STAY63 and STAY64 = female's ability to remain in the herd up to 52, 64, 76 and 76 months of age calving at least 2, 3, 3 and 4 times, respectively.

In comparison with STAY42, the percentage of individuals selected in common ranged from 71.43% to 83.19%, indicating that among the evaluated traits, STAY42 presented the highest difference in the re-ranking of animals. Thus, its choice as a selection criterion would result in a greater difference of selected animals when compared to the direct selection performed through the other stayability traits.

4 | CONCLUSIONS

The ssGBLUP method is recommended to improve the predictive performance (accuracy and bias) of stayability traits in Nellore

TABLE 5 Spearman correlations between the breeding values (obtained via ssGBLUP) and the percentage of commonly selected individuals based on the four stayability traits, considering 1%, 3% and 5% percentiles of sires and females

Traits	Sex	Spearman Correlation*			Percentage of individuals selected in common		
		1%	3%	5%	1%	3%	5%
STAY42 and STAY53	S	0.66	0.74	0.73	80.24	77.78	78.07
	F	0.75	0.73	0.74	74.76	77.69	79.43
STAY42 and STAY63	S	0.82	0.8	0.82	81.55	82.14	83.19
	F	0.80	0.79	0.80	79.59	81.48	83.13
STAY42 and STAY64	S	0.75	0.72	0.77	71.43	78.37	81.64
	F	0.74	0.72	0.75	74.66	79.11	80.53
STAY53 and STAY63	S	0.93	0.95	0.95	92.40	93.29	95.85
	F	0.94	0.95	0.96	91.46	94.26	95.25
STAY53 and STAY64	S	0.92	0.95	0.95	92.31	91.37	93.99
	F	0.92	0.94	0.95	90.57	92.79	93.51
STAY63 and STAY64	S	0.93	0.94	0.93	89.51	90.44	94.27
	F	0.91	0.93	0.94	89.42	91.53	92.61

Note: STAY42, STAY53, STAY63 and STAY64 = female's ability to remain in the herd up to 52, 64, 76 and 76 months of age calving at least 2, 3, 3 and 4 times, respectively.

Abbreviations: F, Females; S, Sires.

*$p < .001$.

cattle. STAY42 may be a feasible alternative for selection of reproductive efficiency of young females. The conventional stayability trait (STAY63) presented high genetic correlation with STAY42. This suggests that besides being related to cow longevity, STAY63 is also associated with reproductive efficiency at the beginning of the cow's reproductive life. However, STAY53 is recommended as the selection criterion for reproductive efficiency due to the higher heritability, positive and favourable genetic correlation with all other stayability traits, and is measured at an earlier age when compared to the conventional STAY63.

CONFLICT OF INTEREST

None of the authors have any conflict of interest to declare.

AUTHOR CONTRIBUTIONS

FFS, LOCS, GGS and GROM designed the study; PVBR and FFS analysed the data and wrote the first version of the manuscript. All the other co-authors contributed to the discussions and to draft the final version of the manuscript.

DATA AVAILABILITY

The data that support the findings of this study are presented in the paper. The raw data cannot be made available, as it is property of the Nellore cattle producers in Brazil and this information is commercially sensitive.

ORCID

Luiz F. Brito (iD) https://orcid.org/0000-0002-5819-0922

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