PEDRO VITAL BRASIL RAMOS

GENETIC ANALYSES FOR ALTERNATIVE REPRODUCTIVE TRAITS IN NELLORE CATTLE UNDER A BAYESIAN FRAMEWORK

Dissertation presented to the Animal Science Graduate Program of the Universidade Federal de Viçosa, in partial fulfillment of the requirements for the degree of *Magister Scientiae*.

VIÇOSA
MINAS GERAIS – BRAZIL
2019

Ficha catalográfica preparada pela Biblioteca Central da Universidade Federal de Viçosa - Câmpus Viçosa

T

Ramos, Pedro Vital Brasil, 1994-

R175g Genetic analyses for alternative reproductive traits in
2019 Nellore cattle under a Bayesian framework / Pedro Vital Brasil
Ramos. – Viçosa, MG, 2019.
vii, 50 f. : il. ; 29 cm.

Orientador: Fabyano Fonseca e Silva.
Dissertação (mestrado) - Universidade Federal de Viçosa.
Inclui bibliografia.

1. Bovinos de corte. 2. Vacas - Genética. 3. Fecundidade.
I. Universidade Federal de Viçosa. Departamento de Zootecnia.
Programa de Pós-Graduação em Zootecnia. II. Título.

CDD 22. ed. 636.2082

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APPROVED: July 19th, 2019.

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ACKNOWLEDGEMENTS

Firstly, I would like to thank the Universidade Federal de Viçosa and the Graduate Program in Animal Science for providing me the opportunity to complete my master's degree and the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) for the financial support.

I am grateful to my advisor Dr. Fabyano Fonseca e Silva for giving me the opportunity to take part in his research group. His guidance and teachings during my master's degree effectively contributed to my professional and academic career. It was rewarding for me to work with someone who has so much knowledge and humility as you.

I am extremely grateful to Dr. Luiz Otavio Campos da Silva for the great friendship, the unparalleled support and for all the knowledge that was transmitted to me. Thank you for believing in me since my undergraduate degree.

I thank my co-advisers Dr. Gilberto Romeiro de Oliveira Menezes for the valuable suggestions and for giving me the opportunity to have his participation in this work, and Dr. Rodolpho de Almeida Torres Filho for the valuable teachings during my undergraduate degree. I would like to extend my sincere thanks to Dr. Paulo Sávio Lópes, Dra. Renata Veroneze and Dra. Camila Ferreira Azevedo for the great teachings during the master's degree.

I am very thankful to my mother Adriana Vital Brasil and my father Roberto do Carmo Ramos for always being by my side at all times, contributing all their efforts to my success. They are the ones that make me strong enough to chase my dreams. I am also very grateful to my brother Matheus Vital Brasil Ramos for his friendship and all advices that undoubtedly contributed to my personal and professional development.

Special thanks to my girlfriend Luisa Crivelli Alvarenga for the companionship. Your friendship, encouragement and love give me support and make me stronger to follow my goals.

I would like to thank my great friends Marcus Vinicius Costa and Hans Reuter for their friendships. I would also like to thank my friend Bruno da Costa Perez who, since my undergraduate degree, has contributed a lot to my academic development.

I would like to thank all the friends that I had the opportunity to meet and who taught me a lot, especially Túlio Vilar, José Teodoro Paiva, Delvan Alves, Hugo Teixeira Silva, Matheus Vieira, Cristian Silva Teixeira and Alessandra Alves.

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ABSTRACT

RAMOS, Pedro Vital Brasil, M.Sc., Universidade Federal de Viçosa, July, 2019. **Genetic analyses for alternative reproductive traits in Nellore cattle under a Bayesian framework.** Adviser: Fabyano Fonseca e Silva. Co-advisers: Luiz Otavio Campos da Silva, Gilberto Romeiro de Oliveira Menezes and Rodolpho de Almeida Torres Filho.

Reproductive traits are determinant for the profitability of beef cattle. Therefore, several reproductive traits are used by Brazilian breeding programs to evaluate fertility, sexual precocity and cows' longevity. Although it has been less studied, days to calving (DC) is a relevant alternative trait related to female's fertility. However, it tends to present asymmetric distribution (such as Exponential) because it represents time to an event occurrence, i.e., calving. In addition, some females may not present records for DC due to late calving, thus characterizing censored data. Among other important reproductive traits, currently the stayability stands out given its economic importance, since it is closely related to fertility and cow's longevity. However, stayability is belatedly measured (conventionally at 76 months) and enables reproductive failures in the considered evaluation period. Facing these features, the genetic improvement of females' reproductive traits is a wide challenge to be overcome in animal breeding. In this context, the inclusion of genomic information under a single-step (ssGBLUP) approach is a promising method to increase the prediction accuracy for these traits. Therefore, the following aims were exploited here: 1) to propose and evaluate the Exponential censored Bayesian model for genetic evaluation of DC in Nellore cattle taking into account the predictive ability and goodness-of-fit; 2) to perform comparison analysis (prediction accuracy) between traditional BLUP and ssGBLUP methods. 3) to propose and investigate new traits related to the cow's longevity and fertility (stayability42, stayability53, stayability64 and consecutive rebreeding ability - CRA), as well as to evaluate their genetic associations with the conventional stayability definition (stayability63) and other productive traits. The proposed Exponential model was not indicated for genetic evaluations of DC; on the other hand, other investigated censored models can be recommended instead the conventional Gaussian model. The ssGBLUP seems to be an advantageous alternative to improve the prediction accuracy of stayability. In summary, stayability42 can be a feasible selection criterion for reproductive efficiency in young females; whereas the staybility53 can be additionally indicated for female's longevity, since it is closely related to cow's fertility and can be measured earlier than the conventional stayability63. Finally, the proposed CRA has shown to be a promising alternative for fertility selection in Nellore females.

RESUMO

RAMOS, Pedro Vital Brasil, M.Sc., Universidade Federal de Viçosa, julho de 2019. **Análises genéticas para caracteristicas reprodutivas alternativas em bovinos Nelore sob enfoque Bayesiano.** Orientador: Fabyano Fonseca e Silva. Coorientadores: Luiz Otavio Campos da Silva, Gilberto Romeiro de Oliveira Menezes e Rodolpho de Almeida Torres Filho.

Características reprodutivas são determinantes para a lucratividade da pecuária de corte. Portanto, diversas características reprodutivas são utilizadas pelos programas brasileiros de melhoramento genético para avaliar fertilidade, precocidade sexual e longevidade da vaca. Embora tenha sido menos estudado, dias para o parto (DPP) é uma característica alternativa relevante relacionado à fertilidade da fêmea. No entanto, tende a apresentar distribuição assimétrica (como a exponencial), uma vez que representa o tempo para a ocorrência de um evento, que neste caso, trata-se do parto. Além disso, algumas fêmeas podem não apresentar registros fenotípicos confiáveis devido ao parto tardio e então, estes dados podem ser considerados como censurados. Dentre outras características reprodutivas importantes, destaca-se atualmente a stayability devido sua grande importância econômica, pois está intimamente relacionada com a fertilidade e a longevidade da vaca. No entanto, a stayability é medida tardiamente (tradicionalmente aos 76 mese) e assume sucesso a vacas que apresentam falhas reprodutivas durante o periodo de avaliação considerado. Diante desses aspectos, o melhoramento genético das características reprodutivas das fêmeas é um grande desafio a ser superado no melhoramento animal. Neste contexto, a inclusão de informações genômicas por meio do BLUP genômico em um único passo (ssGBLUP) é um método promissor para aumentar a acurácia de predição destas características. Portanto, objetivou-se: 1) propor e avaliar o modelo bayesiano censurado exponencial para avaliação genética de DPP em bovinos Nelore, considerando a habilidade preditiva e a qualidade de ajuste. 2) realizar análise comparativa (acurácia de predição) entre os métodos BLUP e ssGBLUP. 3) propor e investigar novas características relacionadas a fertilidade e longevidade da vaca (stayability42, stayability53, stayability64 e habilidade de reconcepções consecutivas- HRC), bem como avaliar suas correlações genéticas com a stayability tradicional (stayability63) e com outras características produtivas. O modelo exponencial proposto não foi indicado para avaliações genéticas da DPP; por outro lado, outros modelos censurados investigados podem ser recomendados em vez do modelo gaussiano convencional. O ssGBLUP pode ser considerado uma alternativa vantajosa para melhorar a acurácia de predição da stayability. Em resumo, a stayability42 pode ser uma alternativa para seleção de eficiência reprodutiva em fêmeas jovens;

enquanto a stayabilitu53 pode ser adicionalmente indicada para seleção de longevidade da fêmea, uma vez que está intimamente relacionada à fertilidade da vaca e pode ser medida antes da stayability tradicional (stayability63). Por fim, a HRC mostrou-se uma alternativa promissora para seleção de fertilidade em fêmeas Nelore.

CHAPTER 1

1.1 General Introduction

Currently, Brazil has a beef cattle population estimated at 214,686 million animals, which is mostly composed of Nellore cattle raised under extensive system. In addition, Brazil has a beef production of approximately 10,959 million tons of carcass weigh equivalent (CWE) and exports of 2,205 million tons of CWE. In the year of 2018, the beef cattle production represented 8.7% of the gross national product (ABIEC, 2019). This information highlights the importance of beef cattle in the national economic scenario.

Among the factors that contribute effectively to the evolution of Brazilian livestock productivity, animal breeding has great importance. Through the genetic evaluations of productive traits, it is possible to select genetically superior animals that will be the parents of future generations. The genetic gain of the herd allows reducing the production cycle, maximizing productive and reproductive potential of the herd.

In the current beef cattle production system, reproductive traits have great relevance in the overall profitability and long-term sustainability. (CHUD et. al 2014). Therefore, improving the reproductive efficiency of beef cows is of extreme importance, since the late onset of reproduction and reproductive failures increase the total production costs (COSTA et. al. 2015). According to Brumatti et al. (2011), reproductive traits are up to 13 times more important economically than growth traits.

However, the genetic improvement of reproductive traits in females is generally challenging due to difficulties in measuring the traits as well as to the low genetic variability, which results in a small annual genetic gain (ELER et.al. 2014). Therefore, different reproductive traits are tested as selection criterion by Brazilian breeding programs.

Among them, days to calving (DC) has been recommended for evaluation of bovine reproductive efficiency (GARCIA et. al. 2016). DC is defined as the interval (in days) between the first day of the breeding season, when the female is exposed to the sire, and its subsequent calving date. Thus, it is an efficient alternative to evaluate female reproductive performance in extensive production systems. However, some females may not present phenotype due to non-occurrence or late occurrence of calvings. This partially unknown information can be considered as censored data (Famula, 1981). Additionally, DC represents the time to an event occurrence and then, tends to present an asymmetric distribution. Thus, mixed models approaching both censored data and asymmetric distribution can be investigated as an alternative to the conventional Gaussian model.

Stayability is another important reproductive trait, which has received great emphasis on genetic breeding programs as selection criteria of cow's reproductive efficiency and longevity. Stayability used to be defined as a binary trait, assuming success for females that obtain three or more calvings in 76 months (stayability63), and failure otherwise (Silva et al. 2017; Schmidt et al. 2018). Thus, it is associated with the ability of the cow to provide economic return in terms of its maintenance cost (Mwansa et.al. 2002). According to Evans et. al. (2003) cows are the animal category responsible for consuming most of the farm's food resources, accounting for 70% of feed costs. Besides that, the maintenance requirement cost of a cow that does not produce one calf per year is similar to the cost of the cow that does. (Bittencourt et al. 2006). Thus, cow's reproductive efficiency is determinant to the herd's profitability.

However, stayability is belatedly measured in cow's life, implying in a lower amount of phenotyped females, which contribute to the lower prediction accuracy (Beef Improvement Federation, 2016). Additionally, Brazilian reproductive management system generally consists in an annual breeding season, where heifers start to be exposed to bulls around 14 months (technified systems) or 26 months of age (conventional systems). Thus, the traditional stayability (STAY63) can attributes success phenotype to females that have obtained two or one reproductive failure, during 76 months, according to the farm reproductive management. Therefore, the investigation of new stayability definitions, which are measured earlier and consider fewer reproductive failures, can optimize genetic selection for reproductive efficiency and longevity.

In addition, the definition of a multi-categorical trait that considers female's ability to present consecutive rebreedings may be an alternative to stayability, for genetic evaluation of fertility. According to Neves et al. (2012), rebreeding is considered a major challenge to improve the productive efficiency of Nellore cows. Zebu females have difficulty in rebreeding due to the environmental influence of low throughput extensive systems that does not meet the nutritional requirement imposed by the growth and lactation of younger cows (Recoules et. al 2013). In this context, consecutive rebreeding ability (CRA) is defined as the ability of the female to have consecutive parturitions with calving intervals of less than 14 months, and thus, it is highly related to female fertility.

Due to the low heritability of reproductive traits, methodologies using genomic information may be advantageous, since allows the inclusion of SNPs (single nucleotide polymorphisms) in genetic analyses, providing greater prediction accuracy, especially for traits such as stayabillity that are late expressed and manifested in only one sex (Sollero et. al. 2019). However, due to the large quantity of animals in Brazilian breeding programs and the high cost of genotyping, the number of genotyped animals is limited. Thus, it is necessary to combine genomic results with those of traditional genetic evaluations, using the single-step genomic BLUP (ssGBLUP) methodology (Legarra et al., 2009; Aguilar et al., 2010). The ssGBLUP method combines pedigree and genomic information into a single matrix (H) to predict the genomic breeding value, allowing simultaneous genetic evaluation of genotyped and non-genotyped animals.

Therefore, the main objectives of this study were: 1) to propose and evaluate the Exponential censored Bayesian model for genetic evaluation of days to calving in Nellore cattle and perform comparison analysis (predictive ability and goodness-of-fit) with conventional Gaussian models. 2) to perform comparison analysis (prediction accuracy) beetween traditional BLUP and ssGBLUP methods. 3) to propose and investigate new traits related to the cow's longevity and fertility (stayability42, stayability53, stayability64 e consecutive rebreeding ability- CRA), as well as, evaluate their genetic associations with the conventional stayability definition (stayability63) and other productive traits.

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CHAPTER 2

Genetic evaluation for days to calving in Nellore heifers using Exponential and Gaussian censored Bayesian models[1]

2.1 Abstract

Days to calving (DC) plays a key role in the overall profitability and long-term sustainability of tropically-adapted beef cattle breeds (e.g. Nellore), especially those raised under extensive production systems. However, some females usually do not have reliable phenotypic records because of late calving and even failures in its recording, which can be considered as censored data. Furthermore, DC tends to present an asymmetric distribution (such as Exponential) as it represents the time to an event occurrence, i.e., calving. Thus, we aimed to propose and evaluate the Exponential censored Bayesian models for genetic evaluation of DC in Nellore cattle as well as to perform comparison analysis (predictive ability and goodness-of-fit) with the conventional Gaussian models. Additionally, different scenarios were based on censoring definition according to cut-off values: 321, 351 and 381 days to calving. The predictive ability was evaluated under a cross-validation approach, and the goodness-of-fit were performed using the Deviance Information Criterion (DIC). Gaussian presented higher predictive ability and lower DIC (better goodness-of-fit) compared to Exponential models. The highest predictive performance was observed for Gaussian models, which also reported more realistic heritability estimates (ranging from 0.03 to 0.23). Additionally, Spearman correlations and coincidence rates were higher between different censored scenarios in Gaussian models. Although the inclusion of censored data into genetic evaluations could be recommended for Gaussian, the proposed Exponential model was not suitable for genetic evaluations of DC.

Key words: Calving ability, Censored records, Reproductive traits, Tropically-adapted cattle.

[1] Paper submitted for publication in Livestock Science as Short Communication.

2.2 Introduction

The profitability and long-term sustainability of tropically-adapted cattle breeds is largely dependent on reproductive performance. Several female reproductive traits have been proposed as selection criteria (Boligon et al., 2012; Berry et al., 2014), but a less studied and very promising trait in beef cattle is the days to calving (DC). DC is defined as the interval (in days) between the first day of the breeding season, when the female is exposed to the sire, and its subsequent calving date. Thus, it is a practical and efficient alternative to evaluate female fertility in extensive production systems with natural mating during the breeding season (Boligon et al., 2012).

As some females usually do not present reliable records because of late calving and even failures in its recording, this partially unknown information can be considered as censored data (Famula, 1981). Thus, appropriate models have been proposed and tested in terms of accommodating censored records in genetic evaluations (Brito et al., 2018).

To the best of our knowledge, all previous studies on DC have used only Gaussian-based mixed models. However, DC tends to present an asymmetric distribution (such as Exponential) as it represents the time to an event occurrence, i.e., calving. Thus, mixed models approaching both censored data and asymmetric distribution can be investigated as an alternative to the conventional Gaussian model. In this context, Bayesian inference is recommended because its versatility in dealing with complex models through Markov chain Monte Carlo (MCMC) algorithms. Following this orientation, we aimed to propose and evaluate the Exponential censored Bayesian model for genetic evaluation of DC in Nellore cattle, as well as to perform comparison analysis (predictive ability and goodness-of-fit) with conventional and censored Gaussian models.

2.3 Material and methods

2.3.1 Data description

The pedigree and phenotypic datasets were provided by the Mundo Novo Farm, located at Uberaba, Minas Gerais State, Brazil. This farm is dedicated to Nellore cattle breeding under extensive conditions. The reproductive management is based on a breeding season, when the females are exposed to the sires (natural mating) during one period around 3 months in spring and summer.

After data cleaning, the final database consisted of 940 phenotyped heifers, so that a portion of these heifers presented high number of days to calving. These large intervals may be related to management practices and failures associated with reproductive pathologies (Brito et al., 2018). In this context, the records could be biased, which would mask the real variability of the trait. In this way, the data was right-censored (Famula, 1981, Kachman 1999) based on DC excess.

These censoring scenarios were defined based on the cut-off values: 321 (Censoring 1), 351 (Censoring 2) and 381 (Censoring 3) days to calving. Values above these thresholds were considered censored in the Censored models and missing in the traditional models. The total number of uncensored (censored) records were 437 (503), 684 (256) and 810 (130), respectively for the scenarios 1, 2 and 3. In addition, the observed DC mean (standard deviation) were 307.10 (8.69), 321.10 (16.9) and 330.00 (22.73), respectively for the scenarios 1, 2 and 3. Values greater than 381 DC represent females that became pregnant after 3 months of the breeding season, considering a mean gestation length of 291 days for Nellore heifers (Boligon et al., 2007). This is a very long DC period, with possible inconsistencies and incompatible with what is recommended in a short-cycle breeding system. Values greater than 351 days to calving represent females that became pregnant after 2 months of the breeding season, and also had late calving. Finally, values greater than 321 DC represent females that became pregnant after the first month of the breeding season. Thus, the uncensored records refer to females with greater reproductive efficiency.

2.3.2 Statistical analyses

Different censoring scenarios and distributions (Gaussian and Exponential) were evaluated: Censored Gaussian model 1 (CGM1) and Censored Exponential model 1 (CEM1), considering censoring scenario 1; Gaussian model 1 (GM1) and Exponential model 1 (EM1), considering exclusion of DC records above 321 days; Censored Gaussian model 2 (CGM2) and Censored Exponential model 2 (CEM2), considering censoring scenario 2; Gaussian model 2 (GM2) and Exponential model 2 (EM2), considering exclusion of DC records above 351 days; Censored Gaussian model 3 (CGM3) and Censored Exponential model 3 (CEM3), considering censoring scenario 3; Gaussian model 3 (GM3) and Exponential model 3 (EM3), considering exclusion of DC records above 381 days.

The conventional Gaussian model was given by:

$$\mathbf{y}=\mathbf{X}\boldsymbol{\beta}+\mathbf{Z}\mathbf{a}+\mathbf{e},$$

where: **y** is the vector of observations (realized and censored values for DC); **β** is the vector of systematic effects (management group at de breeding season, year and season of heifer birth, and heifer age and weight at the beginning of the breeding season as linear covariates); **a** is the vector of random additive genetic effects; **e** is the vector of residuals; **X** and **Z** are the incidence matrices of systematic and random effects, respectively. For the Gaussian model, the data distribution is: $\mathbf{y}|\boldsymbol{\beta},\mathbf{a},\sigma_a^2,\sigma_e^2 \sim \mathrm{N}(\mathbf{X}\boldsymbol{\beta}+\mathbf{Z}\mathbf{a},\ \mathbf{I}\sigma_e^2)$, where **I** is an identity matrix.

For the Exponential distribution, the generalized Bayesian mixed model theory proposed by Hadfield and Nakagawa (2010) was used. In this context, the general model is given by:

$$\boldsymbol{\lambda}=\mathbf{X}\boldsymbol{\beta}+\mathbf{Z}\mathbf{a}+\mathbf{e},$$

where: **λ** is the vector of the latent variable (Exponential rate parameter) according to canonical parameters described by Hadfield and Nakagawa (2010): $\boldsymbol{\lambda}|\boldsymbol{\beta}, \mathbf{a}, \sigma_a^2,\ \sigma_e^2 \sim \mathrm{N}(\mathbf{X}\boldsymbol{\beta}+\mathbf{Z}\mathbf{a}, \mathbf{I}\sigma_e^2)$. Under this framework, the probability distribution of y_i given the rate parameter is: $P(y_i|\lambda_i)=\lambda_i\, e^{-\lambda_i y_i}$. Thus, the general likelihood function can be specified as: $P(\mathbf{y}|\boldsymbol{\lambda},\boldsymbol{\beta},\mathbf{a},\sigma_a^2,\sigma_e^2)=\prod_{i=1}^{N} P(y_i|\boldsymbol{\lambda})\ (\boldsymbol{\lambda}|\boldsymbol{\beta}, \mathbf{a}, \sigma_a^2, \sigma_e^2)$. The vector $\mathbf{y}'= [\mathbf{y}_{un}\ \mathbf{y}_{cen}]'$ contains a subvector of uncensored ($\mathbf{y}_{un}$) and censored ($\mathbf{y}_{cen}$) records of DC. The values of $\mathbf{y}_{cen}$ were simulated values from their posterior predictive distributions assumed as the truncated Gaussian and truncated Exponential according to the assumed distribution.

In terms of prior distributions for the location parameters from both models, it was assumed that $\boldsymbol{\beta}|\sigma_\beta^2 \sim \mathrm{N}(\mathbf{0}, \mathbf{I}\ \sigma_\beta^2)$, in which σ_β^2 is equal to 1 x 10^9, corresponding to a non-informative prior; and $\mathbf{u}|\sigma_a^2 \sim \mathrm{N}(\mathbf{0}, \mathbf{A}\ \sigma_a^2)$, where **A** is the numerator relationship matrix. Regarding the prior distributions for variance components (σ_a^2 and σ_e^2), inverse chi-squared distributions were assumed, in which $\sigma_a^2|v_a,S_a^2 \sim \chi^{-2}(v_a,S_a^2)$ and $\sigma_e^2|v_e,S_e^2 \sim \chi^{-2}(v_e,S_e^2)$.

The posterior means of the Gaussian and Exponential models, censored and uncensored, were obtained by Monte Carlo simulation methods via Markov chains, using the MCMCglmm package (Hadfiel, 2010) of R software. For the censored Gaussian and Gaussian models, 400,000 iterations, burn-in of 100,000 and thin of 10 were considered. For the censored

Exponential and Exponential models, we considered 700,000 iterations, burn-in of 200,000, and thin of 20.

2.3.3 Models comparison

The predictive ability of each model was verified using the cross-validation approach, in which the phenotypic information from the last 3 generations of heifers was removed and their breeding values predicted from the analysis without phenotypes were correlated (predict ability) with those from the analysis with phenotypic information. Bias was also obtained as the difference between the regression coefficients and "1".

The goodness-of-fit was performed by Deviance Information Criterion (DIC; Spiegelhalter et al., 2002) using the full dataset. However, only models fitted to the same data were compared under this framework. The influence of the models on the animals' ranking was evaluated by Spearman correlation coefficient and the percentage of individuals in common (top 10% and 30% of females).

2.4 Results

The predict ability and bias obtained from cross-validation analysis are presented in Table 1. The highest predict ability was 0.84, obtained with CGM2 and CGM3 models, which also presented the lowest bias (-0.09 and -0, 01, respectively). Lower predict ability were obtained for the Exponential models EM1 (0.26), EM2 (0.43) and EM3 (0.36), which showed high bias values, -0.94, -0.49 and -0.60, respectively. In general, Gaussian outperformed Exponential models. The DIC values for Gaussian models GM1, CGM1, GM2, CGM2, GM3, CGM3 were 2,132, 3,335, 4,853, 5,800, 6,289 and 7,011, respectively. For Exponential models EM1, CEM1, EM2, CEM2, EM3 and CEM3 DIC values were 4,100, 4,671, 7,932, 8,393, 10,016 and 10,298, respectively.

Table 1. Predict ability (r) and Bias obtained from cross-validation analysis.

Gaussian	r***	Bias	Exponential	r***	Bias
GM1	0.44	-0.12	EM1	0.26	-0.94
CGM1	0.77	0.38	CEM1	0.81	0.18
GM2	0.64	0.71	EM2	0.43	-0.49
CGM2	0.84	-0.09	CEM2	0.81	-0.15
GM3	0.78	0.35	EM3	0.36	-0.60
CGM3	0.84	-0.01	CEM3	0.75	-0.27

*** $P < 0.001$

GM1= Gaussian model 1; CGM1= Censored Gaussian model 1; GM2= Gaussian model 2; CGM2= Censored Gaussian model 2; GM3= Gaussian model 3; CGM3= Censored Gaussian model 3; EM1= Exponential model 1; CEM1= Censored Exponential model 1; EM2= Exponential model 2; CEM2= Censored Exponential model 2; EM3= Exponential model 3; CEM3= Censored Exponential model 3.

The posterior means of heritability and their respective 95% highest probability density intervals (HPD95) are presented in Table 2. Exponential and Gaussian models presented heritability estimates ranging from 0.50 to 0.57 and from 0.03 to 0.23, respectively.

Table 2. Posterior means (h^2), standard deviations (SD) and 95% highest probability density intervals (HPD95) of the heritability for days to calving.

Gaussian	h^2	SD	HPD95		Exponential	h^2	SD	HPD95	
GM1	0.06	0.08	0.0001	0.2706	EM1	0.51	0.25	0.0760	0.9357
CGM1	0.23	0.15	0.0004	0.5327	CEM1	0.57	0.28	0.0592	0.9678
GM2	0.05	0.07	0.0002	0.2462	EM2	0.51	0.24	0.0923	0.9245
CGM2	0.16	0.08	0.0300	0.3668	CEM2	0.51	0.26	0.0843	0.9353
GM3	0.03	0.05	0.0001	0.1918	EM3	0.50	0.23	0.0933	0.8948
CGM3	0.20	0.09	0.0601	0.4119	CEM3	0.50	0.24	0.0864	0.9038

GM1= Gaussian model 1; CGM1= Censored Gaussian model 1; GM2= Gaussian model 2; CGM2= Censored Gaussian model 2; GM3= Gaussian model 3; CGM3= Censored Gaussian model 3; EM1= Exponential model 1; CEM1= Censored Exponential model 1; EM2= Exponential model 2; CEM2= Censored Exponential model 2; EM3= Exponential model 3; CEM3= Censored Exponential model 3.

The Spearman correlation coefficients between the breeding values for DC and percentage of individuals in common (considering 10% and 30% percentiles) for different Gaussian models (previously identified as better) are described in Table 3.

Table 3. Spearman correlations between the breeding values for days to calving and percentage of individuals in common, considering 10% (above diagonal) and 30% (below diagonal) percentiles for Gaussian models.

Model	GM1	CGM1	GM2	CGM2	GM3	CGM3
Spearman correlations***						
GM1	-	0.08	0.30	0.25	0.49	0.20
CGM1	0.11	-	0.54	0.73	0.26	0.71
GM2	0.45	0.67	-	0.28	0.50	0.24
CGM2	0.37	0.75	0.50	-	0.30	0.85
GM3	0.58	0.47	0.72	0.56	-	0.35
CGM3	0.31	0.79	0.45	0.93	0.57	-
Percentage of individuals in common						
GM1	-	20.27	36.49	21.63	27.03	18.92
CGM1	38.74	-	54.05	59.46	58.10	60.81
GM2	46.40	66.67	-	36.49	56.76	39.20
CGM2	35.13	73.87	56.31	-	63.51	89.19
GM3	43.24	67.11	67.57	71.17	-	62.16
CGM3	37.39	79.28	60.81	90.09	69.72	-

*** $P < 0.001$

GM1= Gaussian model 1; CGM1= Censored Gaussian model 1; GM2= Gaussian model 2; CGM2= Censored Gaussian model 2; GM3= Gaussian model 3; CGM3= Censored Gaussian model 3.

2.5 Discussion

2.5.1 Models comparison

The censored presented higher predicted ability in relation to uncensored models, being similar to the results reported by Garcia et al. (2016) that tested different models for genetic prediction for age at first parity and DC in Nellore cattle. Additionally, among the censored Gaussian models, CGM1 presented worse predictive ability (0.77), maybe due to the excess of censored data, so that some relevant records were missing. Thus, it is recommended to consider the higher cut-off (351 and 381) values for censored data, since these are more related to data inconsistencies.

The Gaussian showed lower DIC in all comparisons with the Exponential models, indicating that this latter was not efficient to describe the used data. To the best of our knowledge, there are no studies in the literature comparing Gaussian and Exponential models for the genetic evaluation of DC.

2.5.2 Heritability estimates

Additionally to the low goodness-of-fit and predictive ability, Exponential models presented heritability estimates that are incompatible with previous results reported in the literature (Boligon et al., 2012, Garcia et al., 2016). This suggests that these models are not suitable to perform genetic evaluations of DC considering the used data. On the other hand, Gaussian models provided consistent heritability estimates.

2.5.3 Ranking classification of animals

The Spearman correlations between the breeding values for DC predicted by the censored and traditional models CGM1xGM1, CGM2xGM2 and CGM3xGM3 were ranged from 0.08 to 0.57. Therefore, the percentage of individuals in common between these models did not exceed 70% in any of the two percentiles. Thus, as reported by Garcia et al. (2016), these results show that the exclusion of the censored data may have a direct impact on the genetic gain of the population due to discrepancies in the ranking of animals and differences in the selected animals.

The censored models 2 and 3 presented the highest Spearman correlation and percentage of individuals in common in both 10% (0.85, 89.19%) and 30% percentiles (0.93, 90.09%), showing that besides presenting superiority in predictive ability, these models also presented greater similarity between the ranking of animals and higher percentage of individuals in common in the considered percentiles. Therefore, the use of any of these models would lead to the selection of almost the same individuals, which is the most important information for breeding decisions.

2.6 Conclusion

Censored provided higher predicted ability than uncensored models. Gaussian presented higher predictive ability and lower DIC (better goodness-of-fit) compared to Exponential models. The highest predictive performance was observed for Gaussian models, which also reported more realistic heritability estimates (ranging from 0.03 to 0.23). Additionally, Spearman correlations and coincidence rates were higher between different censored scenarios in Gaussian models. The inclusion of censored data into genetic evaluations could be recommended for Gaussian, and the proposed Exponential model was not suitable for genetic evaluations of DC.

2.7 Acknowledgements

The authors greatly acknowledge the Mundo Novo Farm for providing the datasets, FAPEMIG (PPM-00563-16), CNPq and CAPES.

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CHAPTER 3

Genomic analysis for different stayability definitions in Nellore cattle

3.1 Abstract

Stayability is closely related to the reproductive efficiency and cow's longevity, which are factors of great economic impact on beef cattle. This impact is due to their influence on the female's ability to provide an economic return in terms of its maintenance costs. However, the usual definition of stayability (stayability63) results in selection of females having reproductive failures during 76 months of age. Additionally, stayability is measured belatedly in cow's life and presents low heritability, resulting in slow response to selection. Thus, the inclusion of genomic information through single-step (ssGBLUP) method has been successfully applied to increase prediction accuracy for this trait. We aimed to perform comparison analysis (prediction accuracy and individuals breeding values accuracies) between BLUP and ssGBLUP methods, and investigate the genetic association between stayability63 and alternative measures of stayability (stayability42, stayability53, and stayability64, which are measured at 52, 64 and 76 months of cow's age, respectively). The ssGBLUP provided higher prediction accuracy for all stayability definition and positive changes in individual breeding values accuracies. Thus, ssGBLUP seems to be a promising alternative to optimize genetic selection for stayability. Heritability estimates obtained for Stayability42, Stayability53, Stayability63 and Stayability64, were 0.09 (0,008), 0.15 (0,013), 0.15 (0,015) and 0.14 (0,014), respectively. Estimates of genetic correlation between traits ranged from 0.89 to 0.98. Thus, Stayability42 may be a feasible alternative for selection of reproductive efficiency of young females. The high genetic correlation beetween stayability42 and stayability63 suggests that the latter one is related to cow longevity besides to reproductive efficiency of young cows. Finally, stayability53 may be indicated as selection criterion for reproductive efficiency in reason of higher heritability, positive genetic correlation with other measured stayability traits, and shorter time to provide phenotypic records when compared to conventional stayability63 and stayability64.

3.2 Introduction

Reproductive efficiency is extremely related to the productivity and profitability of beef cattle production systems (Costa et al., 2018). In addition, reproductive traits have a great influence on the generation interval and the intensity of selection, which provides greater genetic gain in less time (Kluska et al., 2018). Different reproductive traits associated with female reproductive performance have been proposed as selection criterion in several beef cattle Brazilian breeding programs.

Among them, stayability has great relevance because it expresses the female's ability to remain in the herd up to a given age with regular reproductive performance (Schmidt et al, 2018). Therefore, it has a great economic impact in production system since it is jointly related to reproductive efficiency and female's longevity, which are important factors that contributes to economic return taking into account its maintenance costs (Mwansa et.al. 2002)

However, the usual stayability63 (STAY63) is a binary traits whose definition assumes as success a cow providing three calvings at 76 months of age (Silva et al. 2017; Schmidt et al. 2018). This late measurement limits the number of phenotyped cows because young animals will not have yet records until 76 months of age and also many of them may be culled before this threshold age. The lower amount of phenotypic information, in turn, results in low breeding values accuracies (Beef Improvement Federation, 2016), and consequently in significant reduction of the annual genetic gain.

Besides that, depending on the moment of onset of female exposure to the bull, STAY63 allows the cow having up to two reproductive failures and, even so, still obtain the success phenotype. Thus, it may lead to the selection of females with reproductive failures concentrated at the beginning of their reproductive life, which is not economically interesting, since these cows would take longer to give economic returns. Therefore, different definitions of stayability, which attribute success to the phenotype that presents a lower number of reproductive failures, may better represent the cow reproductive efficiency. Furthermore, the possibility to early evaluate stayability records could speed up the genetic selection process for reproductive efficiency and longevity.

In this context, other definitions of stayability can be investigated. Stayability42 (STAY42) is defined as the ability of the female to remain in the herd for 52 months and presents 2 calvings. Thus, this definition is more related to the sexual precocity of the heifer and the ability of primiparous to rebreed in a short period. Stayability53 (STAY53) and stayability64 (STAY64) are defined as the ability of the cow to remain 64 and 76 months in the herd and present 3 and 4 calvings, respectively. In this way, the success is attributed to females with better reproductive efficiency, considering only one reproductive failure for heifers that were challenged in reproduction season at around 14 months old.

In addition, the use of Single-Step GBLUP (ssGBLUP) methodology (Legarra et al., 2009; Aguilar et al., 2010) allows the inclusion of SNPS (single nucleotide polymorphisms) in genetic evaluation, providing greater prediction accuracy, especially for traits such as stayabillity that are late expressed and manifested in only one sex. The ssGBLUP has the advantage of combining the information of pedigree, phenotype and SNP markers simultaneously in the analysis. This method is particularly relevant for Brazilian breeding programs that have large numbers of phenotyped animals but limited number of genotyped animals.

Thus, we aimed to perform comparison analysis (prediction accuracy and individuals breeding values accuracies) between BLUP and ssGBLUP methods, and investigate the genetic association between stayability63 and alternative measures of stayability (stayability42, stayability53, and stayability64).

3.3 Material and methods

The data was provided by the Geneplus-Embrapa Program, which is a Brazilian breeding program of beef cattle breeds, situated at the Embrapa Gado de Corte that is located in the municipality of Campo Grande - MS. The data refers to *Bos indicus* Nellore breed animals, most of them raised under extensive system, in several farms located in different regions from Brazil.

3.3.1 Phenotypic data

Four different measures of stayability were evaluated: the ability of the female to remain in the herd 76 months with 4 calving (STAY64), 76 months with 3 calving (STAY63), 64 months with 3 calving (STAY53) and 52 months with 2 calving (STAY42). For the four traits, phenotype “2” (success) was established for females that reached the respective number of calvings and “1” (failure) for females who had the opportunity, however, did not reach the number of calvings. Missing values were set to zero.

The data consistency analysis was performed through the software R (R Core Team, 2019). The contemporary groups considered in the analysis were determined by the herd, year and the season (1 = January to March, 2 = April to June, 3 = July to September, 4 = October to December) of cows birth as well as its management groups. Females belonging to groups of contemporaries with less than three information or groups that had only cows with the same phenotype were excluded from the analysis. It was also discarded, records of females that obtained age at first calving above or below the established threshold of three standard deviations, from the population mean. The complete pedigree used in the analysis to calculate the numerator relationship matrix contained 2,042,151 animals. The descriptive statistics of the data after the consistency analysis is presented in Table 4.

Table 4. Number of records (N*º*), records assigned as 1 (*n*1), records assigned as 2 (*n*2), sucess percentage (%Sucess) and number of contemporary groups (GC) represented for each stayability trait in Nellore cattle.

Trait	Nº	Categories		%Sucess	GC
		*n*1	*n*2		
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

STAY42 = stayability42; STAY53 = stayability53; STAY63 = stayability63; STAY64 = stayability64;

3.3.2 Genotypic data

The genotype file contained information for 11,177 animals that were genotyped through different densities: 3,333 animals were genotyped in 777k, 2,910 animals in 35k, 3,923 animals in 30k, 1,618 animals in 27k and 1,942 animals in 26k, with the Illumina High-Density BeadChip Array (San Diego, CA,USA).

The quality control of the each data set was performed through the snpStats v1.16.0 package (Clayton, 2014) of the R program (R Core Team, 2017) and the preGSf90 software (Misztal et al., 2002). It was considered for exclusion of SNPS, the following criteria: minor allele frequency (MAF) <0.05, samples and SNPs with call rate less than 95%, P value of the chi-square test for Hardy-Weinberg equilibrium <0.000001 and genotypes with calling score lower than 15%, as recommended by Illumina, Inc. company.

Pedigree verification was performed using seekparentf90 software. (Misztal et al., 2002). Kinship relationships between progenitor and progeny that presented mendelian inconsistencies above 1%, were excluded from the pedigree file. Then, the imputation of genotypes was performed using Fimpute v.2.2 software (Sargolzaei et al., 2014), aiming to combine the information present in all data sets. After the imputation, markers that presented MAF less than 5%, were excluded. After the quality control, the database was composed of 10,909 genotyped animals and 397,423 SNPs.

3.3.3 Statistical analyses

Variance components and genetic parameters were estimated through thresholds models using the THRGIBBS1f90 (Tsuruta and Misztal, 2006) software under both BLUP and ssGBLUP methods. The genetic correlations between four traits were estimated by means of bivariate analysis.

The bivariate threshold model can be written in matrix notation as follows:

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

where, **l** is the observation vector of threshold trait on the liability scale with continuous normal distribution, i.e. $\mathbf{y}|\mathbf{l},\boldsymbol{\beta},\mathbf{a},\Sigma_a\Sigma_e,\tau \sim N(\mathbf{X}\boldsymbol{\beta} + \mathbf{Z}\mathbf{a}, \mathbf{I} \otimes \boldsymbol{\Sigma}_e)$; **β** is the vector of systematic effects (contemporary groups and age at first calving as linear covariate) assuming an uniform prior distribution; **a** is the vector of additive genetic effect, $\mathbf{a}|\boldsymbol{\Sigma}_a \sim N(0, \mathbf{A} \otimes \boldsymbol{\Sigma}_a)$, where **A** is the relationship matrix and $\boldsymbol{\Sigma}_a$ is the additive genetic covariance matrix ; **e** is the vector of residual effects, $\mathbf{e}|\boldsymbol{\Sigma}_e \sim N(0, \mathbf{I} \otimes \boldsymbol{\Sigma}_e)$ where $\mathbf{I}$ and $\boldsymbol{\Sigma}_e$ are the identity and the residual covariance matrices, respectively.

A total of 300,000 MCMC iterations were used for inference of all evaluated traits. The burn-in and thin were given by 100,000 and 4 iterations, respectively. The POSTGIBBSF90 (Misztal et. al. 2002) was used for posterior inference, being the convergence evaluated through the Geweke test (1992).

Under a genomic single-step approach it was assumed that $\mathbf{a}|\boldsymbol{\Sigma}_a \sim N(0, \mathbf{H} \otimes \boldsymbol{\Sigma}_a)$. According to Aguilar et. al. (2010), the inverse H matrix is given by:

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

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

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

where:

$$\mathbf{Z} = \mathbf{M} - \mathbf{P},$$

M is the genotype matrix of *n* genotyped animals (rows) by *m* markers (columns); **P** is a matrix containing 2 times the observed frequency of the second allele (p_j).

Spearman's rank correlation between breeding values from different stayability definitions were computed to access possible rerankings. In addition, the percentage of sires and females selected in common among the traits at different percentiles (1%, 3% and 5%) were also calculated.

3.3.4 Methods comparisons

The predictive ability of each model was investigated based on cross-validation analysis. The reference population was composed by genotyped females and non-genotyped daughters of genotyped bulls. This criterion was assigned aiming to select individuals that had the greatest influence on the genomic information in the single-step analysis. Thus, it was possible to compare the prediction ability obtained from traditional BLUP and ssGBLUP focusing in the increment provided by the inclusion of genomic information. In summary, the phenotypic information from the reference population was removed and their breeding values predicted through both methods (BLUP and ssGBLUP). After, the predicted EBVs were correlated (prediction accuracy) with those from the analyses considering phenotypic information (complete dataset). Bias was also obtained as the difference between the regression coefficients and the unity to measure the degree of inflation/deflation of EBVs predictions.

Additionally to prediction accuracy, it was also investigated the individual breeding values accuracies (IBVAs). The IBVA was estimated by a Bayesian approach of BIF accuracy (Beef Improvement Federation, 2016). In this context, the IBVA was calculated assuming the squared posterior deviation as PEV (predictor error of variance). Studies reporting IBVAs are scarce in the literature. However, it has great relevance in breeding programs, being used as an uncertainty measure for the breeding values prediction.

3.4 Results and discussion

3.4.1 Methods comparisons

Prediction accuracy and bias estimates obtained through the cross-validation analysis for the different stayability evaluated traits under BLUP and ssGBLUP methods, are presented in Table 5.

Table 5. Prediction accuracy (r) of the EBVs, GEBVs and bias obtained through the BLUP and ssGBLUP method for stayability evaluated traits, and the percentage 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%

* $P < 0.001$

STAY42 = stayability42; STAY53 = stayability53; STAY63 = stayability63; STAY64 = stayability64;

The genomic prediction accuracy can be influenced by different factors, including the number of individuals in the training population, the number of genotyped individuals, marker density and the linkage disequilibrium between the SNPs. (de los Campos et al. 2013, Daetwyler et. al. 2010, Goddard, 2009). In the present study, the ssGBLUP method presented greater accuracy for all stayability analyses, presenting an increase of prediction accuracy ranging from 10% to 14% when compared with BLUP. The low magnitude of increase in accuracy may be related to the proportion of population genotyped animals. The pedrigree was composed of 2,042,151 animals, from which 10,909 were genotyped. Thus, even considering only genotyped females and non-genotyped daughters of genotyped sires in cross-validation analyses, the large size of the database and the extension of the traditional pedigree limited the positive impacts of genomic information. Therefore, it is expected that the increasing in the number of genotyped older animals (with higher EBV accuracy) and in the number of young animals will result in greater impact on the prediction accuracy provided by the genomic information (Lourenço, 2015). Thus, the results presented in this study suggests that the inclusion of molecular marker information in the analysis provides more accurate predictions of genomic breedings values.

The bias ranged from 0.23 to 0.29 and 0.16 to 0.27 in BLUP and ssGBLUP, respectively. Thus, it indicates that in BLUP method there was a higher overestimation of genetic predictions, which is not desired because the changes in the magnitude of the predictions may result in misinterpretation of breeding values. These results corroborate with Gao et al. (2012) and Su et al. (2012), who stated that single-step can improve accuracy and reduce the bias of genomic predictions. Therefore, this study provide a solid support for genetic evaluation programs, to focus on the ssGBLUP method for genomic evaluation of stayability.

Additionally to the cross-validation analysis, scatter plots (Figure 1) of the individual breeding values accuracies, obtained through the GBLUP and ssGBLUP methods was performed for the four different stayability measures.

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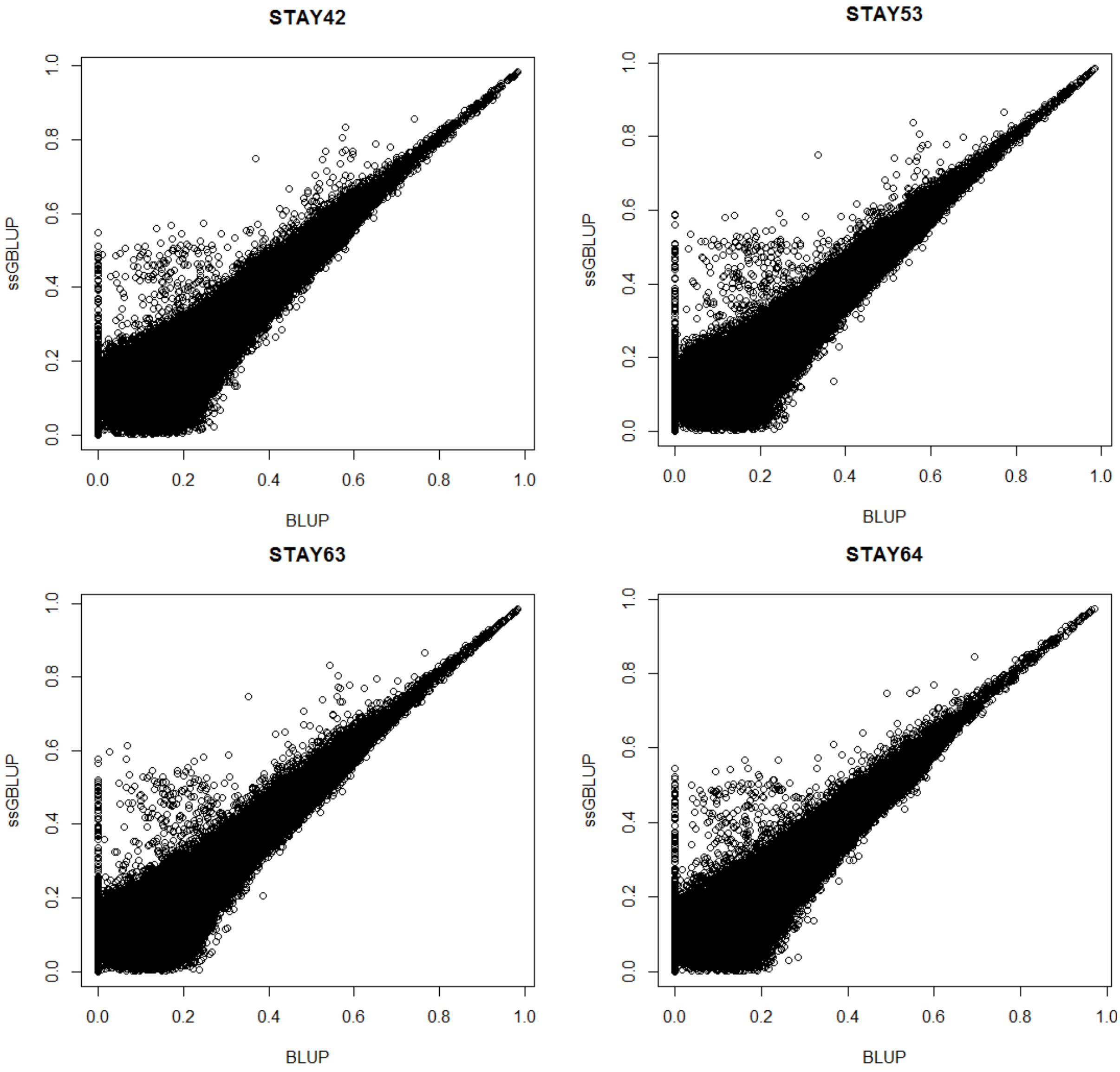

Figure 1. Scatter plots of individual breeding values accuracies estimates for different stayability measures, through the BLUP and ssGBLUP methods.

The figure 1 shows the similarity in the IBVAs behaviour, among the methods, for each stayability trait. However, it can also be seen through the plots (Figure 1), a great increase in

IBVAs of some animals. These differences in accuracy estimates are related to the genomic relationship matrix (G matrix), that considers the kinship coefficients calculated by the real proportion of marker alleles shared by identity by state (IBS). Thus, it captures more information than the traditional coefficient based on the pedigree (Meuwissen et al., 2001, Habier et al., 2011).

In this way, according to VanRaden (2008), G matrix makes possible to differentiate the relationship between full siblings, identify previously unknown kinship relationships and correct possible genealogy errors. Thus, a reorganization of kinship coefficients occurs, where descendants of individuals that are related in G will be related in H, even if they do not present kinship relationship in the traditional relationship matrix (Legarra et. al. 2014). Therefore, the greater kinship information obtained by the H matrix results in an increase in the IBVA, especially of genotyped animals.

3.4.2 Genetic parameters

The estimates of variance component, heritability, standard deviations (SD) highest probability density intervals (HPD95) of the stayability measures, obtained through the BLUP and ssGBLUP methods, are shown in Table 6. The Geweke test (1992) was not-significant (P> 0.05) for all parameters, indicating that MCMC convergence was obtained.

Table 6. Posterior means, standard deviations (in parentheses) and the 95% highest probability density intervals (HPD95) for direct additive genetic (σ^2_a), residual (σ^2_r) variances and heritability (h^2), obtained through BLUP and ssGBLUP methods, for the evaluated traits, in Nellore cattle.

BLUP						
Trait	σ^2_a	HPD95	σ^2_r	HPD95	h^2	HPD95
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						
Trait	σ_a^2	HPD95	σ^2_r	HPD95	h^2	HPD95
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

STAY42 = stayability42; STAY53 = stayability53; STAY63 = stayability63; STAY64 = stayability64.

There was no significant difference in the estimates of genetic parameters when genomic information was included in the analyses through matrix H. The four stayability measures presented low heritability, suggesting that the small proportion of phenotypic variances is determined by genes of additive action. In this way, the direct selection for these traits will result in small annual genetic gain. However, due to the fact of the economic importance, the use of them through a selection indexes composed with other productive traits could be interesting since the long-term selection of stayability can result in a positive economic impact on beef cattle production systems.

Among the evaluated traits, STAY42 had the lowest heritability (0.09). This result may be associated with the fact that STAY42 has a greater influence of the female rebreeding after the first calving, since for this trait, success phonotype is attributed to cows that reach two calvings in 52 months. The primiparous rebreeding is a major challenge in tropical extensive beef production due to nutritional limitation (Recoules et al., 2013) and the physiological demand imposed on young cows by growth and lactation (Mulliniks et al., 2012). Thus, it is subject to great environmental influence and may be responsible for the low genetic variance of STAY42.

Although it has lower heritability, STAY42 has a higher relation to reproductive efficiency of the female at the beginning of its reproductive life, approaching the ability of the heifer to become pregnant early and the primiparous rebreeding ability. Therefore, the long-term selection of STAY42 may be important to increase the reproductive performance of young cows. Genetic parameters for STAY42 were not found in the literature. Similarly, Queiroz et al. (2007), evaluated stayability measured at 48 months and reported a higher heritability of 0.27, in Caracu breed.

STAY64 presented heritability estimate of 0.14, statistically similar to STAY53 and STAY63, according to the HPD95. Genetic parameters for STAY64 were also not found in the literature. Van Melis et.al. (2007), in turn, obtained a superior heritability of 0.22 in a similar study of stayability measurement considering 6 years of cow age and four calvings.

STAY53 and STAY63 presented heritability equal to 0.15. These results were superior to that was reported by Silva et al (2017) who presented heritability estimates of STAY63, ranging from 0.03 to 0.07 in Nellore cattle. 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, through single-step genomic analysis, in Nellore breed. Valente et. al. (2017) evaluating Nelore cows ability to calve at least three times before reaching 65 months of age, obtained a similar result to the STAY53, reporting heritability of 0.13.

The Posterior means, standard deviations (SD) and their respective highest probability density intervals (HPD95) of genetic correlations between the four evaluated traits, are presented in Table 7.

Table 7. Posterior means, standard deviations (SD) and their respective HPD95 (the 95% highest probability density intervals) of genetic correlations (r_g) between stayability traits, in Nellore cattle.

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

STAY42 = stayability42; STAY53 = stayability53; STAY63 = stayability63; STAY64 = stayability64.

The high genetic correlations (Table 7) characterize the action of synergism between genes in the four measures of stayability. Therefore, the direct selection for one of them will provide positive and favorable response to the others.

The genetic correlation between STAY42 and STAY53, STAY63 and STAY64 was 0,899, 0,929 and 0,916, respectively. These results suggest that late stayability measures have a high correlation with sexual precocity and reproductive efficiency of young cows. Thus, it can be stated that although STAY63 allows the female to be successful with up to two reproductive failures, it is not associated to cows that present reproductive failures concentrated at the beginning of its reproductive life, even though this is the most challenging moment of the female's reproduction. This fact may be associated with traditional Brazilian beef cattle production system, where cows that do not rebreeds and heifers that do not become pregnant during the breeding season, are culled. Therefore, even in stayability63, females that obtain a successful phenotype are, in large majority, those that present consecutive rebreedings, since those that fail are culled and do not manifest the phenotype.

In addition, even though STAY42 presents a greater number of phenotypic records and high genetic correlation with the other measures of stayability, it is not suitable as indirect selection criterion for the others, since presented a considerably lower heritability estimate, which result in a reduction of the annual genetic gain.

On the other hand, the high genetic correlation of STAY53 with STAY42 and others measures of stayability suggests that it can be chosen as an indirect selection criterion of the others, since it has similar heritability to STAY63 and STAY64, and higher heritability than STAY42. STAY53 is measured earlier than STAY63 and STAY64 and thus, may result in early decision making of animals selection, what would provide a greater annual genetic gain. In other words, the selection based on STAY53, indirectly, select females that present reproductive efficiency at the beginning of reproductive life and also females that present four calvings in 76 months. Moreover, when compared to STAY63, STAY53 allows selecting females with three calvings in one year less, which provides a greater economic impact.

STAY63 also presented a high genetic correlation with STAY64, which suggests that STAY 64 may be prioritized in relation to STAY63, since it is related to the highest number of calving in the same period. Therefore, STAY64 allows the selection of cows with shorter intervals between calvings and, consequently, greater reproductive efficiency.

3.4.3 Genetic ranking of animals

The Spearman correlation coefficients between the breeding values and the percentage of individuals in common of different stayability measures, using the ssGBLUP method (considering 1%, 2% and 3% percentiles of sires and females) are described in Table 8.

Table 8. Spearman correlations between the breeding values and the percentage of individuals in common of stayability traits, considering 1%, 3% and 5% percentiles of sires and females.

		Spearman Correlation*			Percentage of individuals in common		
Traits	Sex	1%	3%	5%	1%	3%	5%
STAY42xSTAY53	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
STAY42xSTAY63	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
STAY42xSTAY64	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
STAY53XSTAY63	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
STAY53xSTAY64	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
STAY63xSTAY64	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

* *P* <0.001

F = Females; S = Sires; STAY42 = stayability42; STAY53 = stayability53; STAY63 = stayability63; STAY64 = stayability64.

The spearman correlations were higher between STAY53, STAY63 and STAY64 (Table 8), presenting correlations greater than 0.9, in the three evaluated percentiles, considering females and sires. This result suggests a small difference in the ranking of animals among these traits. STAY42, in turn, presented a greater difference in the animal's ranking, with spearman correlations ranging from 0.66 and 0.82.

The percentage of individuals in common of 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 almost the same individuals. Therefore, the similarity of the EBVs rankings between these measures of stayability and other previously results, reaffirm the potential of STAY53 as indirect selection criterion for the other stayability traits.

In comparisons with STAY42, the percentage of individuals in common ranged from 71.43% to 83.19%. These results indicate that among the evaluated traits, STAY42 presented the higher difference in the ranking of animals and in the percentage of animals in common, up to the 5% percentile. Thus, its choice as a selection criterion will result in a greater difference of selected animals when compared to the direct selection performed through the other stayability traits.

3.5 Conclusion

The ssGBLUP seems to be a promising alternative to improve the prediction accuracy of stayability.

Stayability42 may be a feasible alternative for selection of reproductive efficiency of young females. The conventional stayability measurement (STAY63) presented a high genetic correlation with STAY42, which suggests that besides related to cow longevity, STAY63 is also related to the reproductive efficiency of the female at the beginning of its reproductive life.

Stayability53 may be indicated as selection criterion for reproductive efficiency in reason of higher heritability, positive genetic correlation with other stayability traits, and shorter time to provide phenotypic records when compared to conventional stayability63 and stayability64.

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CHAPTER 4

Genetic analysis for consecutive rebreeding ability in Nellore cattle

4.1 Abstract

Female reproductive efficiency plays a key role in profitability of beef cattle production systems. Thus, stayability has a great emphasis in breeding programs as selection criterion for cow's fertility and longevity. However, stayability definition considers only two phenotypic categories (failure and success), leading to a limited variation to be exploited under genetic evaluation framework. Additionally, it is not an exact indicator for fertility, since it is also related with sexual precocity. In this context, consecutive rebreeding ability (CRA) is an alternative trait that is highly related to female fertility, which is measured as a multi-categorical trait approaching the ability to have consecutive parturitions with calving intervals less than 14 months. In order to evaluate the CRA potential as selection criterion for female fertility, we aimed to estimate genetic parameters as well as to investigate its genetic associations with stayability42 (STAY42), stayability53 (STAY53), rib eye area (REA), subcutaneous back-fat thickness (BF), age at first calving (AFC), post-yearling scrotal circumference (PSC) and post-yearling weight (PW), in Nellore cattle. The covariances components and genetic parameters were estimated through multi-trait Bayesian inference using THRGIBBS1F90 software. Heritability estimates for CRA, STAY42, STAY63, REA, BF, PW, AFC and PSC were 0.113 (0.036), 0.092 (0.009), 0.150 (0.013), 0.352 (0.015), 0.136 (0.013), 0.340 (0.012), 0.171 (0.005) and 0.416 (0.021), respectively. CRA presented genetic correlations with STAY42, STAY63, REA, BF, PW, AFC and PSC of 0.995 (0.002), 0.984 (0.009), 0.122 (0.033), 0.188 (0.086), 0.105 (0.052), -0.341 (0.049) and 0.152 (0.053), respectively. Therefore, CRA seems to be a feasible new indicator of Nellore cow fertility, and can be recommended to compose selection indexes for long-term selection given its positive economic impact. CRA presented higher genetic correlation with Stayability, indicating a satisfactory indirect selection response to be exploited in breeding programs. Futhermore, selection for consecutive rebreedings may imply positive genetic impact for PW, PSC, AFC and BF.

4.2 Introduction

Reproductive traits have great relevance for beef cattle breeding because significantly affects the profitability and productivity of the herds (Berry et.al. 2014). Thus, several reproductive traits have been used in Brazil as selection criteria for fertility and sexual precocity (Boligon et.al. 2012; Kluska et. al. 2018). Among them, stayability has a great emphasis on selection indexes, as it expresses the ability of cows to remain in the herd up to a certain age with regular reproduction (Guarini et. al. 2015). Widely, stayability is defined as a binary trait, assuming success for females that obtain 3 or more calvings in 76 months, and failure otherwise (Silva et. al. 2017; Schmidt et.al. 2018).

Stayability definition, as well as other traits assuming different numbers of calvings at a given age, limits genetic variance when considering only two phenotypic categories (failure and success), thus do not differentiating cows that had different number of calvings up to the threshold age. Additionally, stayability is not an exact indicator for fertility, since its definition is also related with sexual precocity, because females having the first parturition earlier, have more time to reach the number of calvings defined as threshold and hence to obtain the success phenotype.

Another problem of stayability evaluation is that it does not discriminate the success in female rebreeding, resulting in cows with reproductive failures at different stages of life with the same phenotype. Furthermore, in Brazilian beef cattle production systems that have a breeding season, it is common to cull females that do not rebreed during the period destined for reproduction, thus avoiding these females from manifesting the stayability phenotype.

According to Neves et al. (2012), rebreeding is considered a major challenge to improve the productive efficiency of Nellore cows, being the rebreeding ability a major concern for primiparous cows in the tropical extensive beef production. It is common for zebu females, raised under extensive systems, to have difficulty in rebreeding due to the environmental influence of low throughput systems (Recoules et. al. 2013) and the physiological demands imposed by the continued growth and lactation of younger cows (Mulliniks et. al. 2012). In this context, the consecutive rebreeding ability (CRA) is an alternative trait to evaluate the cow reproductive efficiency and longevity. This trait is defined as the ability of the female to have consecutive parturitions with calving intervals of less than 14 months, thus being highly related to female fertility.

To evaluate the potential of CRA as a selection criterion to improve cow fertility, we aimed to estimate genetic parameters and investigate genetic associations with stayability and other reproductive, growth and carcass traits commonly evaluated in Nellore breeding programs.

4.3 Material and methods

4.3.1 Data description

The data was provided by the Geneplus-Embrapa Program, which offers a specialized genetic breeding service to Brazilian breeders. The database refers to *Bos indicus* Nellore breed animals and is composed of farm records, where most of them have an extensive production system, located in several regions of Brazil.

Consecutive rebreeding ability (CRA) was defined and analyzed considering four categories of females based on consecutive rebreeding occurrences until their first reproductive failure. Category 1 was assigned to females with rebreeding failure after first calving; category 2 was assigned to females with rebreeding success after 1st calving followed by a rebreeding failure after 2nd calving; category 3 was assigned to females with rebreeding success after 1st and 2nd calving followed by a rebreeding failure after 3rd calving; category 4 was assigned to females that had rebreeding success after the first three calvings. The rebreeding was considered as success when the female presented a new calving within less than 14 months of the parture in question.

Additionally, genetic analyses for the following traits were also performed: rib eye area (REA), subcutaneous backfat thickness (BF), age at first calving (AFC), post-yearling scrotal circumference (PSC), post-yearling weight (PW), stayability63 (STAY63) and stayability42 (STAY42). STAY63 represents the traditional measure of stayability and considers 76 months (6.33 years) old of the cow and three calvings, while STAY42 is an alternative measure that considers 52 months (4.33 years) old of the cow and two calvings. For these two stayability traits, the value “1” was designated for females that failed and did not obtain the respective numbers of calvings and the value “2” for females that were successful and reached the respective numbers of calvings.

The contemporary groups considered in the analyses were defined by the association of the year and the season (1 = January to March, 2 = April to June, 3 = July to September, 4 = October to December) of the animal birth, as well as it management group. Animals belonging to contemporary groups with less than three records, or groups that had only cows with the same phenotype, in the case of the categorical traits, were discarded from the analysis. For linear traits, outliers were eliminated, adopting as a threshold three standard deviations above or below the mean.

PW and PSC were adjusted according to the age of the animals in the contemporary group. For animals with known weaning weight, PW was calculated based on post-weaning gain (GPD) adjusted for the contemporary group. While for animals with unknown weaning weight, the PW was calculated considering the average difference between pre-weaning and post-weaning gain rates of animals that presented these phenotypes.

The complete pedigree used in the analysis to calculate the numerator relationship matrix contained 2,042,151 animals. The descriptive statistics of the data after the consistency analysis is presented in Table 9.

Table 9. Number of records (Nº), categorical records assigned as 1 (*n*1), 2 (*n*2), 3 (*n*3) and 4 (*n*4), followed by means, maximum and minimum values and standard deviation (SD), represented for each trait.

Trait	Nº	Categories				Mean	Maximum	Mínimum	SD
		*n*1	*n*2	*n*3	*n*4				
CRA	171,641	108,767	33,839	13,589	15,446	-	-	-	-
STAY42	167,858	106,622	61,236	-	-	-	-	-	-
STAY63	121,475	90,939	30,536	-	-	-	-	-	-
REA (cm²)	40,934	-	-	-	-	55.83	89.34	23.36	11.18
BF (dm)	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 capacity; STAY42 = stayability42; STAY63 = stayability63; REA = rib eye area; BF = subcutaneous back fat thickness; PW = post-yearling weight; AFC = age at first calving; PSC = post-yearling scrotal circumference.

4.3.2 Statistical analyses

The (co)variances components and breeding values were obtained using the software THRGIBBS1F90 (Tsuruta and Misztal, 2006). Single-trait analyses were performed for all traits, whereas bivariate analyses between CRA and other traits were performed to estimate linear genetic associations between them.

Threshold models were proposed for CRA and Stayability bivariate analysis. For the analyses between CRA and other traits, the threshold-linear model has been used.

Threshold-linear model can be represented in matrix form as follows:

$$\begin{bmatrix}\mathbf{y}\\ \mathbf{l}\end{bmatrix}=\begin{bmatrix}\mathbf{X}_y & \mathbf{0}\\ \mathbf{0} & \mathbf{X}_l\end{bmatrix}\begin{bmatrix}\boldsymbol{\beta}_y\\ \boldsymbol{\beta}_l\end{bmatrix}+\begin{bmatrix}\mathbf{Z}_y & \mathbf{0}\\ \mathbf{0} & \mathbf{Z}_l\end{bmatrix}\begin{bmatrix}\mathbf{a}_y\\ \mathbf{a}_l\end{bmatrix}+\begin{bmatrix}\mathbf{e}_y\\ \mathbf{e}_l\end{bmatrix},$$

where **y** is the vector of observations of the linear trait (REA, BF, PSC, AFC or PW); **l** is the observation vector of the threshold trait (CRA, STAY63 or STAY42) on the liability scale with continuous normal distribution; **β** is the vector of fixed effects; **a** is the vector of direct additive genetic random effect; **X** is the incidence matrix of fixed effects; **Z** is the incidence matrix of the direct additive genetic random effect and **e** is the vector of random effect of the residuals, for each independent variable.

It was assumed, a priori, that **β** assumes an uniform distribution; $\mathbf{a}|\boldsymbol{\Sigma}_a \sim N(\mathbf{0}, \mathbf{A}\otimes\boldsymbol{\Sigma}_a)$ where **A** is the numerator relationship matrix of animals and $\boldsymbol{\Sigma}_a$ is the additive genetic covariance matrix; *e* assume $\mathbf{e}|\boldsymbol{\Sigma}_e \sim N(\mathbf{0}, \mathbf{I}\otimes\boldsymbol{\Sigma}_e)$ where **I** and $\boldsymbol{\Sigma}_e$ are the identity and the residual covariance matrices, respectively. The Inverse Wishart distribution was adopted as prior distribution for $\boldsymbol{\Sigma}_a$ and $\boldsymbol{\Sigma}_e$.

The stayability records were distributed as follows:

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

where τ_i is the threshold value that defines the two response categories (1 and 2). On the other hand, CRA record were similar distributed according to:

$$f(\mathbf{y}|\mathbf{l},\boldsymbol{\beta},\mathbf{u},\sigma_a^2,\sigma_e^2,\tau)=\prod_{i=1}^{n} f(y_i|l_i)=\prod_{i=1}^{n} I(l_i<\tau_1)I(y_i=1)+(\tau_1<l_i<\tau_2)I(y_i=2)+$$
$$+I(\tau_2<l_i<\tau_3)I(y_i=3)+(l_i>\tau_3)I(y_i=4),$$

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

For all evaluated traits, the contemporary group was considered as systematic effects. For REA, BF and PW, these effects were given by sex and contemporary groups. Additionally, some covariates were also assumed: individual's age at the moment of data collect (linear effect) for PSC, PW, PSC, REA and BF; post-yearling weight (linear effect) for PSC and AFC; age at first calving (linear effect) for CRA, STAY42 and STAY63; and mother's age at calving (linear and quadratic effect) for PW, PSC, REA and BF.

As mentioned before, the single-trait threshold analyses for STAY42, STAY63 and CRA were performed to obtained heritability estimates; whereas convectional linear analyses were carried out for REA, BF, PW, PSC and AFC traits.

A total of 400,000 MCMC iterations were used for inference of all evaluated models. The burn-in and thin sizes varied according to the traits; ranging from 100,000 to 150,000, and from 4 to 10, respectively. The POSTGIBBSF90 program (Misztal et. al. 2002) was used for posterior inference, being the convergence evaluated through the Geweke test (1992).

4.4 Results and discussion

Variance components, heritability, posterior standard deviations (SD) and the 95% highest probability density intervals (HPD95) are shown in Table 10. The Geweke test (1992) was not-significant (P> 0.05) for all parameters, indicating that MCMC algorithm convergence was achieved.

Table 10. Posterior means, standard deviations (SD) and the 95% highest probability density intervals (HPD95) for direct additive genetic (σ_a^2), residual (σ_e^2) variances and heritability (h^2) for the evaluated traits.

Trait	Parameter	Mean ± SD	HPD95
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
STAY42	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
STAY63	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 capacity; STAY42 = stayability42; STAY63 = stayability63; REA = rib eye area; BF = subcutaneous back fat thickness; PW = post-yearling weight; AFC = age at first calving; PSC = post-yearling scrotal circumference.

CRA showed low heritability (0.113), statistically similar to STAY42 and STAY63, which presented heritability values equal to 0.092 and 0.150, respectively. Thus, direct selection for these traits would result in a small annual genetic gain. However, the CRA characterizes a new proposal to evaluate the cow fertility, since the ability of the female not showing important reproductive failures after her first to 4th calving is desired and extremely important in beef cattle. Thus, its use in selection indices may be interesting due to its economic importance, since its long-term selection could result in a positive impact on the reproductive efficiency of the herd by selecting cows with the high capacity to rebreed every breeding season.

Boligon et al. (2012) reported heritability of 0.18 to subsequent primiparous rebreeding (SR) in Nellore cows. This result seems in accordance to the heritability value of 0.149 estimated by Guarini et al. (2015) also in a study of SR in Nellore breed. Moreover, Cavani et al. (2015) reported heritability value equal to 0.22 for SR in primiparous Brahman cows. The low heritability of CRA may be associated with the fact that it is a trait measured later in the life of the cow, which considers three rebreeding opportunities and, consequently, presents greater environmental influence than SR.

Heritability value for STAY63 was higher than those reported by Silva et al. (2017), which presented estimates of STAY63 ranging from 0.03 to 0.07 in Nellore breed. In contrast, the result is lower than that presented by Schmidt et al. (2018) and Guarini et al. (2015) who reported heritability values for STAY63 of 0.19 and 0.186, respectively, in Nellore breed. Genetic parameters for STAY42 were not found in the literature. Queiroz et al. (2007), similarly, evaluating stayability measured at 48 months considering two calvings, reported a higher value of heritability equal to 0.27, in Caracu breed.

The carcass traits BF and REA, obtained low and moderate to high heritability, respectively (Table 10). These results corroborate with those reported by Buzanskas et al. (2017) who presented heritability values of 0.16 for BF and 0.32 for REA in the Nellore breed.

AFC and PSC obtained low and high heritability estimates, respectively (Table 10). Buzanskas et al. (2017) reported high (although lower than observed in the present study) heritability for scrotal circumference at 420 days of age (0.38) and superior heritability for AFC (0.24). In contrast, Paterno et al. (2017a) observed a weaker additive genetic component permeating the phenotypic expression of AFC ($h^2 = 0.13$).

PW had moderate to high heritability (Table 10). Paterno et al. (2017b) and Kluska et al. (2018) reported higher heritability (0.5 and 0.43, respectively) for weight at 450 days of age

(W450). In contrast, Garnero et al. (2010) reported a similar heritability result for W450, (h^2 = 0.36).

The Posterior means, standard deviations and their respective HPD95 of genetic correlations between consecutives CRA and the other traits are presented in Table 11.

Table 11. Posterior means, standard deviations (SD) and their respective HPD95 (the 95% highest probability density intervals) of genetic correlations between consecutives rebreeding capacity (CRA) and the other traits of Nellore cattle.

Trait	Genetic correlations with CRA	
	Mean ± SD	HPD95
STAY42	0.995 ± 0.002	0.991 ; 0.999
STAY63	0.984 ± 0.009	0.968 ; 0.999
REA	0.122 ± 0.033	-0.003 ; 0.247
BF	0.188 ± 0.086	0.020 ; 0.356
PW	0.105± 0.052	0.003 ; 0.207
AFC	-0.341 ± 0.049	-0.438 ; -0.244
PSC	0.152 ± 0.053	0.048 ; 0.256

CRA= consecutives rebreeding capacity; STAY42 = stayability42; STAY63 = stayability63; REA = rib eye area; BF = subcutaneous back fat thickness; PW = post-yearling weight; AFC = age at first calving; PSC = post-yearling scrotal circumference.

In this study, CRA had a high magnitude of genetic correlations with STAY63 (0.984) and STAY42 (0.995). These results are similar to those reported by Guarini et al. (2015), who presented a genetic correlation of 0.97 between heifer rebreeding and STAY63.

The high genetic correlations suggests that most of the genes responsible for the phenotypic expression of CRA may also be involved in stayability traits. Thus, the direct selection of one of those three traits will result in a positive and favourable response to the others. In other words, selection based on stayability, in an indirect way, selects animals that have higher probability to present successful consecutive rebreedings until the 4th calving. This genetic correlation between CRA and stayability may be related to the fact that, in Brazil, producers usually cull females that do not rebreed in the breeding season. It means that a large number of females that obtain success for stayability are those that have consecutive rebreedings.

The genetic correlation between CRA and AFC (-0.341), although being low to moderate, suggest that the selection of younger females in the first calving may lead to the selection of adult females that have reproductive efficiency and a greater probability of having consecutives rebreedings. This result is not usually expected, since females who have a very early calf present high-energy demand due to growth and lactation occurring concomitantly. This physiological demand associated with an extensive system environment, which is often composed 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 severe enough to significantly impair the reproduction of this female, it tends to have a marked ability to rebreed in future calvings.

The genetic correlation between CRA and BF (0.188) indicates that in Nellore breed, fat deposition is a requirement for reproductive performance. According to Cunningham et al. (1999), activity of the reproductive axis is susceptible to adjustment by nutrition and metabolic reserves. The authors further report that 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. Thus, females with greater capacity to deposit fat, consequently, have more energy reserve and tend to exhibit a better ability to rebreed. In addition, the subcutaneous backfat thickness is an indicator of carcass finishing efficiency, which in turn is important because it acts as thermal insulation during the cooling process of the carcass inside the frigorific, avoiding losses in meat quality (Rotta et. al, 2009). Selection for CRA will, therefore, result in a low indirect genetic gain for BF.

Scrotal circumference is associated with fertility and sexual precocity in male (Fortes et.al. 2012; Latif et. al. 2009). The positive genetic correlation observed between PSC and CRA (0.152) shows a positive and favourable association suggesting that the selection for PSC tends to result in sires with fertile daughters with high capacity of exhibiting consecutive rebreedings. However, due to the low magnitude of this genetic correlation, the selection for PSC will result only in a small indirect genetic gain for CRA.

The genetic correlation between REA and CRA (0.122) assumes 0 in its HPD interval (-0.003; 0.247), thus, we considered that there is no evidence of linear genetic association between such traits in the present study. The genetic correlation between CRA and PW (0.105) suggests that selection for PW will result in little changes for CRA.

4.5 Conclusion

CRA seems to be a feasible new indicator of Nellore cow fertility, and can be recommended for long-term selection given its positive economic impact

CRA has a high genetic association with stayability measures, indicating satisfactory indirect selection response to be exploited in breeding programs

Selection for consecutives rebreedings would cause a positive genetic impact for rib eye area, subcutaneous back-fat thickness, age at first calving, post-yearling scrotal circumference and post-yearling weight.

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CHAPTER 5

5.1 General conclusions

The present study allowed extending the knowledge about reproductive traits of economic relevance, providing important information that could be considered in the genetic evaluations of breeding programs.

Firstly, though DC presents asymmetric distribution, the proposed Exponential model was not indicated for genetic evaluations. On the other hand, the inclusion of censored data in genetic analysis of DC can be recommended, since censored models presented higher predictive ability than non-censored models.

According to de Chapter 3, the ssGBLUP method seems to be an advantageous alternative to improve the prediction accuracy of stayability. However, the impact on accuracy is expected to be even higher with a greater number of genotyped animals. In summary, stayability42 may be a feasible alternative for selection of reproductive efficiency of young females. The conventional stayability measurement (stayability63) presented a high genetic correlation with stayability42, which suggests that besides related to cow longevity, stayability63 is also related to the reproductive efficiency of the female at the beginning of its reproductive life. Stayability53 may be indicated as selection criteria for sexual precocity, fertility and longevity, in reason of higher heritability, positive genetic correlation with the other stayability measures and shorter time to provide phenotypic records, when compared to stayability63 and stayability64.

Finally, the Consecutive rebreeding ability is a new alternative proposal for selection of cow fertility. Although CRA has low heritability, its long-term selection may result in a positive economic impact. Additionally, Selection for consecutive rebreedings would cause a positive genetic impact for rib eye area, subcutaneous back-fat thickness, age at first calving, post-yearling scrotal circumference and post-yearling weight.