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**GENETIC RELATIONSHIP BETWEEN REPRODUCTIVE
TRAITS IN NELLORE CATTLE**

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Aline Rocha Guarini

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*“O correr da vida embrulha tudo.
A vida é assim: esquentada e esfria,
aperta e daí afrouxa,
sossega e depois desinquieta.
O que ela quer da gente é coragem.”*

Grande Sertão: Veredas - Guimarães Rosa

"I've learned over the years that when it comes to success, consistency is key. Consistent hard work that we may not like doing today, but for a payoff we'll love tomorrow. Earn it. Enjoy it."

Dwayne Johnson

"Don't lose faith. I'm convinced that the only thing that kept me going was that I loved what I did. You've got to find what you love. And that is as true for your work as it is for your lovers. Your work is going to fill a large part of your life, and the only way to be truly satisfied is to do what you believe is great work. And the only way to do great work is to love what you do. If you haven't found it yet, keep looking. Don't settle. As with all matters of the heart, you'll know when you find it. And, like any great relationship, it just gets better and better as the years roll on. So keep looking until you find it. Don't settle."

Steve Jobs

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GENETIC RELATIONSHIP BETWEEN REPRODUCTIVE TRAITS IN NELLORE CATTLE

ABSTRACT - The aim of this study was to estimate genetic parameters between scrotal circumference obtained at 18 months of age (SC) and reproductive traits measured directly in Nellore females, such as number of calvings at 53 months (NC53), heifers rebreeding (HR) and stayability (STAY) in order to investigate the possibility of using traits measured directly in females as a selection criteria in cattle breeding programs, besides, studying and evaluating if number of calvings at 53 months could be used as an alternative way for measuring longevity in cattle herds. Two methods were applied for estimating variance components in order to predict breeding values: restricted maximum likelihood (REML) and Bayesian inference. The average estimates of heritability by bivariate model using REML were equal to 0.013 ± 0.003 , 0.057 ± 0.007 , 0.039 ± 0.007 and 0.530 ± 0.013 for NC53, STAY, HR and SC, respectively. Using the Bayesian method, the estimates were 0.22 ± 0.009 , 0.19 ± 0.025 , 0.15 ± 0.021 and 0.52 ± 0.019 for NC53, STAY, HR and SC, respectively. Based on the correlations between reproductive traits measured in females, the selection of animals for NC53 will cause anticipation on genetic evaluation of bulls for longevity, based on the performance of their daughters, from 76 to 53 months.

Keywords: beef cattle, heritability, reproductive efficiency, sexual precocity, stayability

CHAPTER 1 - GENERAL CONSIDERATIONS

The subject studied in this work relates to reproductive traits measured in Nellore females as well as their relations with scrotal circumference, an indicator of sexual precocity in males. Furthermore, it involves the study of different approaches of genetic parameters estimation for length of productive life of cows in the herd. The text is divided into three chapters, briefly described below.

This chapter includes an introduction to the topic, followed by a literature review and the objectives.

Chapter 2 summarizes the results obtained comparing the reproductive traits measured in females with scrotal circumference in Nellore cattle, using the Restricted Maximum Likelihood method.

In chapter 3, we studied the same traits described in Chapter 2 using Bayesian approach, comparing the results obtained in the different methods of analyses.

INTRODUCTION

Brazilian beef cattle industry has advanced in recent years and has an important role in the evolution of economy and country's development. Statistics published by the Brazilian Association of Meat Exporters (Abiec) show that in 2011, Brazil had 208 million cattle, 39.5 million head slaughtered, produced 9.1 million tonnes of carcase and exported 1.5 million tons of equivalent carcass weight (16.5% of production).

However, Brazilian cattle outcome rate is still considered low (approximately 22%), when compared to other countries. Animal production in countries located in Temperate Zone, for example, taking into consideration the land use, may be up to four times higher when compared to tropical countries (PEREIRA, 2001).

This disparity in productivity is mainly due to extensive management adopted in Brazil and problems of sanity, reproductive management and genetic potential of animals for meat production (HENDRICKSEN et al., 1994), which leads Brazilian herd to need more time to reach an ideal weight at slaughter compared to developed countries.

The increase in production and productivity of livestock, due of rising demand, is the technical and political challenge of our time. To meet the needs of a market that demands high quality meat and aggregate value, is of fundamental importance to implement a strategy that seeks to offer standardized raw material, especially in weight, age and degree of finish (BARROZO, 2009).

One of the ways to obtain higher outcome rates is through sexually precocious herds with high fertility rates. This can be achieved through breeding programs that prioritize the selection of economically important traits such as reproductive traits. Thus, it is essential that accurate estimates of genetic parameters are available, as these constitute the basic elements in the establishment of guidelines for selection.

To make possible an increase in productivity and continue to meet the demand for beef and conquer new markets, it is necessary to be competitive, in other words, it is necessary that the sector presents good performance and, especially, be efficient, providing quality products at competitive prices. Combine appropriate environmental and management conditions in order to improve the genetic potential

of the animals are still important points to achieve greater efficiency of production systems.

Make use of tools to somehow contribute to these improvements in a sustainable livestock system is the best way to get good results and overcome the difficulties of the production system. For this, a production under short cycle with the use of genetically superior animals for sexual precocity, growth and carcass finish is required.

LITERATURE REVIEW

The current market trend is the search for the earliest cows, which are more economically viable, as they remain longer in herd and have a greater progeny during the productive life. Working with resources of genetic improvement area in order to optimize productivity of this cows is an interesting alternative to adopt. Among these features, greater emphasis should be given to selection. It can be used to change the frequencies of the alleles that determine the expression of economically important traits, thus altering the genetic makeup of beef cattle population promoting productivity gains and economic benefits (PEREIRA, 2004).

The inclusion of new criteria of selection in genetic evaluation programs, as well as studies related to its relations with traits linked to production efficiency of animals is of utmost importance to achieve improvements across the production system.

Efficiency is a feminine noun that according to the dictionary refers to the *action, the ability to produce an effect; income* (WEISZFLOG, 1998). Analyzing the efficiency of Nellore females, it is possible to study it from two aspects: productive and reproductive. Thus, a female that is considered as being efficient, should perform well in both.

To Perotto (2008), the efficiency of beef production can be defined in biological terms as productivity (weight/food consumed) or, in economic terms, as profitability (income/expenses). Valle et al. (1998) also emphasize that the production efficiency of a female can be measured by the performance of their progeny expressed in pounds of calf weaned per hectare per year, this being one of the most important factors in determining the profit or loss in the system.

Given that a limiting factor to the efficiency of production in beef cattle is the reproduction, the inclusion of reproductive traits in selection objectives becomes extremely important for the profitability of national beef cattle system (GEARY, 2003; FORMIGONI et al., 2005). However, the adoption of these traits in the composition of selection indexes for genetic improvement programs in Brazil, compared to those related with growth, is still negligible, mainly due to low heritability found for these

traits, low accuracy of genetic tests and the lack of information about the topic (NEVES et al., 2012).

Tanaka et al. (2012) addressed the importance of studying traits that evaluate sexual precocity, stayability and maternal productivity, since a herd and its productivity are maintained by the quality of all females that comprise it.

Stayability

The longevity of females in a herd is considered of great importance; their inclusion in breeding programs, besides allowing the selection of bulls that produce daughters more likely to stay productive in the herd for a longer period (VAN MELIS et al., 2007), brings a reduction in costs with the purchase of replacement females, since reproductive failure is one of the leading causes of cows being discarded from the herd (RENQUIST et al., 2006; CUSHMAN et al., 2009).

One way of evaluating the longevity of cows is through the stayability (STAY), which takes into account the reproduction management adopted. Is the measure of whether or not an animal remains and produces in the herd until a specified point in time. In other words, the stayability has two phenotypic classes of answers: whether they stay in the herd or not if applied "cutoff criteria" according to the age. Thus, it is assumed that females that have reached a certain age would have one product produced per crop (SILVA et al., 2003a).

Again, according to Silva et al. (2003a), one of the main causes of culling of beef cows under extensive system, is the reproductive failure. Assuming that the levels of culling due to mortality, unsatisfactory performance of progeny health and other reasons are considered low or not important, then the ability of cows to remain productive in the herd up to a certain age can be considered as a trait able to be selected.

Studies related to stayability in Nellore cattle, although they are currently getting more attention from researchers, are still rare in literature. However, due to recent advance in computational area, new software development and improvement of statistical techniques, further investigation may be made in order to clarify issues left unclear to this trait.

The stayability is traditionally defined as the probability of the animal to remain in the herd until six years of age since it had the opportunity to reach this age and has already given birth (BRIGHAM et al., 2007) In its usual form, is a binary trait with probability of success (1), if the cow remain productively in the herd until pre-determined age; or failure (0) indicating the non-permanence of the animal during the same period. Buzanskas et al. (2010) considered the cows with at least three calvings up to 76 months of age as success and cows with less than three calvings to the same age as failure.

Number of calvings at 53 months

The adoption of number of calvings at 53 months (NC53) as a selection criteria to productive longevity, when compared with stayability, usually used in genetic evaluation programs, would establish a maximum age (53 months) and evaluate females under different reproductive managements (1st service at 18 or 24 months) more efficiently than just by binary observations (where zero is failure and one is success) and, moreover, this trait (NC53) may be included as a selection criterion to increase reproductive efficiency of females.

The threshold was defined at 53 months to accommodate the critical period of rebreeding of primiparous, would also allow some emphasis on the sexual precocity of cows (TANAKA et al., 2012; CARVALHEIRO et al.; 2005, PIMENTEL et al., 2006) and, compared to STAY, could anticipate the genetic evaluation of sires based on progeny data. Besides enabling the distinction between cows with two calves of those that did not became pregnant until established age, another advantage of using NC53 is to consider in the analysis all heifers that did not became pregnant during this period.

Neves et al. (2012) estimated the heritability for NC53 under a threshold model and defined it as a moderately heritable trait (~ 0.17) and, thus, able to be selected. Furthermore, the high correlation found by these authors between NC53 and NC89 (~ 0.87) and low heritability found for NC89 (~ 0.12), suggests that NC53 would be a key indicator of productive longevity to later ages.

Heifers rebreeding

It is remarkable the importance of reproductive traits and how they affect the productivity and profitability of livestock herd, especially in a cow-calf production system (BURNS et al., 2010 and HULSEGGE et al., 2013). Among the main reproductive traits, the rebreeding of primiparous females is one of the critical points to be explored in beef cattle, since sudden drops in fertility rates are observed. Even though most production systems provide a favorable environment under better management and nutrition for primiparous, pregnancy rates between the first and second births are still much lower compared to the others (VIEIRA et al., 2005; MERCADANTE et al. 2003).

The cow that conceives in the next breeding season allows a quick return of the investment made to its creation. Thus, increments in rebreeding rates of primiparous may increase the economic efficiency of beef cattle. Studies such as Doyle et al. (2000) and Lobato and Magalhães (2001), also emphasize the importance of selecting heifers with higher genetic potential for fertility, in other words, it's necessary to conciliate high pregnancy rates with a reduction on age at first calving.

Mercadante et al. (2003) analyzed Nellore animals and reported a difference of 20% between the herd's conception total average and rebreeding of primiparous.

There are still disagreement in the literature regarding estimates of genetic parameters for rebreeding of primiparous when using different models, mainly because of lack of studies on the subject. Silva et al. (2002) analyzed 1,727 Nellore females using threshold model and Bayesian inference, and estimated an heritability of 0.25 for the rebreeding. However, Pereira (2008), analyzing Nellore primiparous using nonlinear model and Bayesian inference reported estimates of heritability of 0.15.

Scrotal circumference

Currently, among reproductive traits, scrotal circumference (SC) is the most used in the composition of selection indexes used in breeding programs, as well as being the most used trait in studies as an indicator of sexual precocity.

The selection for scrotal circumference, despite not bring direct economic benefit, is genetically correlated with several reproductive traits of both males and females (BERGMANN, 1993) and weight traits (BERGMANN et al., 1996).

It is one of the most used traits to improve reproductive efficiency in beef cattle, especially because of its favorable genetic association with age at puberty and fertility coupled with the ease of its measurement. In addition, studies show that SC has moderate to high heritability. Boligon et al. (2007) estimated heritability at 12 months of age of 0.25 to 0.26 and, 0.35 to 0.37 when measured at 18 months of age.

Another contributing factor to the adoption of scrotal circumference as a selection criterion is their association with favorable genetic traits linked to weight gain of animals (BOLIGON et al., 2011), besides presenting favorable and negative correlation with age at first calving (PEREIRA et al., 2000; BOLIGON et al., 2007; BORBA et al., 2011), indicating response to selection, changes in the weights of males and females and changes in sexual precocity of females.

Toelle and Robison (1985) found that selection for scrotal circumference is favorable to genetic breeding of females with regard to reproductive traits such as pregnancy rate, age at first service, age at first calving and calving interval.

There is also evidence that selection for scrotal circumference should not affect the length of stay (longevity) of females in the herd (GIANLORENÇO et al., 2003) nor increasing mature weight and reduces the rate of maturation of females (SILVA et al., 2000).

General Objective

Investigate the possibility of using traits measured directly in females as selection criteria for genetic improvement in Nelore cattle reproductive efficiency.

Specific Objectives

1. Estimate genetic parameters in single and bi-trait analyses for number of calvings at 53 months, stayability, heifers rebreeding and scrotal circumference.
2. Studying number of calvings at 53 months of age as an alternative criteria of evaluating the ability to stay in herd.

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CHAPTER 2 - ESTIMATION OF GENETIC PARAMETERS FOR REPRODUCTIVE TRAITS MEASURED IN FEMALES AND SCROTAL CIRCUMFERENCE IN NELLORE CATTLE USING RESTRICTED MAXIMUM LIKELIHOOD METHOD

ABSTRACT - The reproductive efficiency of the herd shows considerable improvements by identifying and multiplying the genotypes most appropriate to the production system and also the environmental conditions conducive to expression of these genes. Identify reproductive traits with easy measurement; economically importance with selective potential is essential. Herds with high fertility and sexual precocity have a greater availability of animals, whether for sale or for selection, allowing more intense selective and, consequently, higher genetic progress. This study aims to estimate heritability for the traits number of calvings at 53 months (NC53), heifers rebreeding (HR), stayability up to 76 (STAY) months and scrotal circumference (SC); determine genetic and phenotypic correlations between NC53 and the other traits, and consider the possibility of using the traits measured directly in females as selection criteria for genetic improvement in Nellore cattle. It was intended to estimate the (co)variance and genetic parameters for the traits mentioned by maximum likelihood estimation using the software ASREML. Number of calvings at 53 months, heifers rebreeding and stayability were analyzed assuming a threshold model, which relates the observed response (in discrete scale) to an underlying normal scale, while scrotal circumference was analyzed under a linear model. The average estimates of heritability by bivariate model were equal to 0.013 ± 0.003 , 0.057 ± 0.007 , 0.039 ± 0.007 and 0.530 ± 0.013 for NC53, STAY, HR and SC, respectively. Based on the correlations and results for indirect selection between measurements of SC and reproductive traits measured in females, the selection for increasing scrotal circumference should result, at long-term, in improvements in heifer subsequent rebreeding rate and number of calvings at 53 months.

Keywords: correlated response, maximum likelihood, Nellore cattle, selection criteria, underlying scale

1. INTRODUCTION

Due to the low reproductive rate, the bovine cows represents the animal category that consumes most of the food resources available for the herd. Moreover, also considering the cost of replacement of females due to reproductive failure, their maintenance becomes a major component of the cost of production of beef cattle (SILVA et al., 2003b).

A factor of great impact within a cattle production system, is the difficulty encountered in females rebreeding from the first to the second birth. So it is very important to have selection programs directed towards animals fertility, seeking females that start their reproductive life sooner and, the most important, show rebreeding in the following breeding seasons.

For higher profitability of the production system, cows should remain in production until their costs of growing and maintenance are paid (SNELLING et al., 1995; FORMIGONI et al., 2002; MWANSA et al., 2002). High costs on cows maintenance and heifers replacement justify the inclusion of longevity indicative traits in selection indexes (FORMIGONI et al., 2005 e PANETO et al., 2002), since animals that remain in the herd productively for longer are highly desirable and can achieve better economic results (RIBEIRO et al., 2005).

Formigone et al. (2005) showed that stayability had great economic importance, reaching up to 3.27 times higher than the probability of pregnancy at 14 months, a indicative trait of precocity.

In the major cattle production systems in Brazil, where Nellore is used, productive longevity is evaluated using the most common definition of stayability: whether or not an animal remains and produces in the herd until six years old. However, the estimated heritability for this trait is of small magnitude (SILVA et al., 2006; VAN MELIS et al., 2010). The main problem of evaluating the stayability using such definition is the fact of being measured later in life, being necessary to wait at least six years until the female shows phenotype for evaluation, what leads to a slow improvement. Also the sire of such female will be at least eight years old by this time,

resulting in low accuracy of genetic evaluations of young bulls (JAMROZIK et al., 2013).

In order to minimize the adversities encountered with the analysis of stayability by the usual method, this study proposed the evaluation of the number of calvings at 53 months as an alternative form of evaluating the ability to stay in herd, since it would soften the existing difficulties by using the usual method; and also verify the magnitude that yearling scrotal circumference measured in males is related to reproductive efficiency traits measured directly in females.

With the results were investigated the possibility of inclusion of reproductive traits measured directly in females in selection indexes used by breeding programs of Nellore cattle.

2. MATERIAL AND METHODS

1. Description of the dataset

This study used a file formed by the dataset of herds belonging to different cattle breeding programs, in the North, Northeast, Southeast, Midwest and southern Brazil and Paraguay.

The animals were from 37 different farms belonging to the dataset *Aliança Nelore* (GENSYS, 2010). The feeding adopted in these farms consisted basically of tropical pastures, mineral salt and water *ad libitum*. In general, supplementation was not performed for any category of females. On some farms where there was no uniformity of quality and availability of forage, the breeding females were allocated in the best pastures.

The breeding season traditionally lasts 90 days and its onset must be determined by weather and nutrition conditions of each region. In order to identify early females, part of the herds adopted two breeding seasons: one anticipated that, in general, occurs from March to April, and the traditional season, usually between the months of November and February. The remaining herds adopted only the traditional breeding season. Females were mostly inseminated and, if the pregnancy was not detected, they were exposed to a breeding system with more than one sire for a group of cows. The natural mating was controlled, that is, a group of 30 to 50 females were placed with a single-sire.

Most participating herds exposed the primiparous to controlled natural mating or breeding groups, thus increasing the pregnancy rate in this category. Heifers that became pregnant early in the season were favored, since they had more time to recover and conceive at the beginning of the traditional breeding season.

2. Evaluated Traits

The scrotal circumference was obtained approximately at 18 months of age, by measurements made transversely in the region of larger diameter of the scrotum, with the use of specific scrotal tape measure.

The stayability records (STAY) were analyzed categorically, applying scores "1" for females that remained in the herd up to 76 months and that conceived at least three products until this age. Cows receiving "0", representing the failure, were applied to females that did not remain in the herd, in other words, were discarded for not becoming pregnant in previous breeding seasons.

Similarly, number of calvings at 53 months (NC53) was used as an alternative way of measuring the ability to stay in herd. It was computed the number of calvings that the cow had up to 53 months, ranging from 0 to 3.

Heifers rebreeding (HR) was also calculated using scores. If the heifer calved, since it had given birth in the first breeding season, it received a score of 1, indicating success. Otherwise, if the heifer failed, it received a score of 0. For analyses considering this traits, a maximum interval of 15 months between first and second births was considered for females submitted to a normal breeding season and, for those submitted to an early breeding season, the maximum interval accepted was of 24 months.

3. Preliminary analyses

The editing and initial exploration of data were performed using the software SAS® (SAS Inst., Inc., Cary, NC).

For the analyses were carried out investigations concerning to the identifications of animal, sire, dam, sex, season of birth, age and number of calvings. Animals that did not have dates of birth and / or calving were discarded. To study the reproductive traits measured in females, we calculated age at first calving, calving interval, number of births and season of birth. The season of calving was defined by two classes: raining, between October and March and another dry, from April to September.

The assumptions taken by the animal model does not become true when working on a dataset with presence of animals with unknown ancestry, from populations of different genetic merit of the population base, in other words, the existing genetic differences are not taken into account in genetic evaluations (THOMPSON, 1979)

When this occurs, there is an underestimation of genetics trends and occurrence of genetic prediction bias during the evaluation (HENDERSON, 1975). To minimize these problems, were adopted the inclusion of genetic groups assigned to individuals whose relationship information was incomplete in the pedigree file. These groups were used so that the genetic merit of each group were predicted and used to correct the genetic value of each animal based on their relationship with their respective group (WESTEEL et al., 1988)

According to Phocas and Laloê (2004), the use of genetic groups must be considered, especially with a large number of animals per group, high genetic link between groups and, above all, significant genetic differences between sub-populations of base animals.

For this study, the groups were created based on the season of birth. It was not necessary to include parental sex, since all dams were known and only the sires had missing information. In this case, it was formed 22, 21, 17 and 26 genetic groups for NC53, HR, STAY and SC, respectively.

The description of the dataset used in the analyses are presented in Table 1.

Table 1. Description of dataset used in the analyses of number of calvings at 53 months (NC53), stayability (STAY), heifers rebreeding (HR) and scrotal circumference (SC) of Nelore cattle.

Information	NC53	STAY	HR	SC
No. of observations	104,559	48,403	63,130	59,576
Period of calving	1984 to 2008	1984 to 2005	1984 to 2008	1984 to 2010
Contemporary groups	932	668	796	3789
No of animals in relationship matrix	116,766	90,195	116,558	134,638

To evaluate STAY and NC53, the consistency of the data was performed similarly. There were eliminated from the dataset females whose ages at first calving were less than 20 months and only births to 76 and 53 months for STAY and NC53, respectively, were considered.

For both traits, the models included the fixed effects of contemporary groups, defined by season and year of birth, farm of weaning to long yearling and classification of precocity status. In addition, for STAY analyses, the effects of mating system to which the cow was submitted in its last calving, was included as a covariate in the model, and may be artificial insemination, single or multiple sires.

For analysis of STAY, it was considered only females that had the opportunity to express the trait and therefore only births up to 76 months were considered. This trait was coded with score 1 for cows with at least three calvings up to 76 months of age or score zero for those that had fewer than three calvings. According to Formigoni et al. (2005), achieved three calvings, pre and post-weaning costs of the cow would be paid. The 76 months were considered for the cows reach three calvings, establishing that, on average, the first calving occurred at 30 months of age.

The reproductive management adopted by farms that were part of this work does not allow cows that were not pregnant in the breeding season to remain on the herd. Thus, if a cow produces a calf at a certain age, it is because it came calving regularly in previous seasons.

Preliminary investigations were carried out on the significance of the variables used for the formation of contemporary groups (CG) and covariates included in the model by GLM procedure of SAS[®] software (SAS Inst., Inc., Cary, NC). Only variables that were statistically significant at 5% level were used in the analyses.

CGs without variability were eliminated, that is, those in which all animals showed the same response category and CGs with less than 5 observations. The number of observations and the frequency of different values for STAY and NC53 are described in Table 2.

Table 2. Frequency of observation of stayability and number of calvings at 53 months of Nellore females.

Stayability	No. of observations	Frequency (%)
0	32,901	67.97
1	15,502	32.03
Total	48,403	100%

No. of calvings at 53 months	No. of observations	Frequency (%)
0	58,730	56.17
1	31,500	30.13
2	14,111	13.50
3	218	0.20
Total	104,559	100%

The definition of contemporary groups for scrotal circumference included year and season of birth, farm and group of management at birth, weaning and long yearling beyond the dates when the animals were weaned and when measurements of scrotal circumference were taken. The scrotal circumference was previously adjusted for age and long yearling weight. As a covariate in the model, the linear and quadratic effects of age of cows at calving were included in the models.

Heifers rebreeding (HR) was defined as success (1) or failure (0) for heifers that calved or not, respectively, since they had previously given birth. The contemporary groups included the classification of being precocious heifers or not, season and year of birth and farm from weaning to long yearling. It was included in the model, as a covariate, age at first calving, obtained from the difference between the date of the first calving and the date of birth of the female, the type of service that the female was submitted when it entered the breeding season and the sex of the first offspring.

A descriptive summary of the data of heifers rebreeding is shown in Table 3.

Table 3. Frequency of observation of heifers rebreeding of Nellore females.

Heifers rebreeding	No of observations	Frequency (%)
0	30,193	47.83
1	32,937	52.17
Total	63,130	100%

The percentage shown in Table 3 refers to the total of females that conceived or not, regardless the age they were exposed in the breeding season. The percentages of females that conceived were 75.14% and 50.11% for precocious and not precocious females, respectively.

4. Estimation of genetic parameters

Considering the frequentist method, the components of (co)variance and genetic parameters were estimated by single and bi-trait analyses (for all possible trait combinations) considering a generalized linear animal model using the computer program ASREML (GILMOUR et al., 1999). The software ASREML provides estimates of maximum likelihood (*quasi*-likelihood) for the random effect in the case of generalized linear mixed model.

The model used in the analyses considered the CG as fixed effect and additive genetic effect of the animal as random. It can be represented by:

$$Y = Xb + Za + ZQ_1g + e$$

where:

Y = vector of observations;

X = incidence matrix that relate observations to fixed effect of CG;

Z = incidence matrix that relate observations to direct genetic effect of animal;

Q₁ = incidence matrix that relate animals to fixed effect of genetic groups;

b = vector of fixed effects;

a = random additive direct genetic effect of the animal;

\mathbf{g} = vector of fixed effects of genetic groups;
 \mathbf{e} = vector with random residual effects.

The model considered the following assumptions:

$$\begin{bmatrix} \mathbf{a} \\ \mathbf{e} \end{bmatrix} \sim N \left\{ \begin{bmatrix} \mathbf{0} \\ \mathbf{0} \end{bmatrix}, \begin{bmatrix} \mathbf{G} & \mathbf{0} \\ \mathbf{0} & \mathbf{R} \end{bmatrix} \right\}$$

\mathbf{G} is the matrix of (co)variances of the random effect of the vector \mathbf{a} , and \mathbf{R} is the matrix of residuals (co)variances. The matrices \mathbf{G} and \mathbf{R} are described as $\mathbf{G} = \mathbf{A} \times \mathbf{G}_0$ where \mathbf{A} is the relationship matrix, \mathbf{G}_0 is the additive direct genetic (co)variance matrix between traits and \mathbf{x} is the direct product between the matrices; and $\mathbf{R} = \mathbf{I} \times \mathbf{R}_0$, where \mathbf{I} represents an identity matrix and \mathbf{R}_0 is the matrix of residual (co)variances between the traits, and $\mathbf{0}$ represents a null matrix.

It was considered that the convergence was achieved when the log-likelihood function changed less than 0.002 between two consecutive iterations and the estimated individual variance changed less than 1%.

According to Marcondes (2003), the adoption of linear models for analysis of stayability shall not affect the classification of animals regarding the predicted values. Furthermore, by having a reduced processing time, it becomes more advantageous as compared to the threshold model.

In the case of a threshold model, estimates heritabilities are obtained in underlying scale, unlike linear models, in which estimates heritabilities are obtained on the observed scale.

Thus, to make possible the comparison between this study, which used a linear model for analyses of interest traits with other studies, which used threshold models, were used the formula suggested by Robertson in Dempster and Lerner (1950) for transformation of the estimates obtained in underlying scale to observed scale:

$$h_o^2 = [(h_u^2 \times w^2) \div (\alpha \times (1 - \alpha))]$$

Being:

$$w = [(e^{-0,5 \times z^2}) \div (\sqrt{2\pi})]$$

Where:

h_o^2 is the heritability in observed scale;

h_u^2 is the heritability in underlying scale;

α is the proportion of individuals with the phenotype in the population of interest;

e is the exponential constant;

z is the height of the normal curve.

Saying that two traits are genetically correlated, implies that the selection applied to one of them will cause a change in another. Thus, when the goal is to improve a trait based on the selection of another, there is indirect selection. According to Falconer and Mackay (1996), the magnitude of change in a trait when indirect selection applied to other traits, is used, can be obtained by knowing the heritability of the two traits and the correlation between them. The answer of the trait under selection, for example X, is equivalent to the average of the breeding values of the selected individuals. Thus, the response in the correlated trait, Y, is given by the regression of the genetic value of the trait Y in the genetic value of X:

$$b_{(a)yx} = \frac{COV_a}{\sigma_{ax}^2} = r_a \frac{\sigma_{ay}}{\sigma_{ax}}$$

The response of X, the trait that is under selection, can be described by:

$$R_x = ih_x \sigma_{ax}$$

Therefore, the correlated response of Y is:

$$R_y = (b_{(a)YX})(R_x) = ih_x \sigma_{ax} (r_a (\sigma_{ay} / \sigma_{ax})) = ih_x r_a \sigma_{ay}$$

Replacing σ_{ay} for $ih_y \sigma_{py}$, the response of Y is:

$$R_y = ih_x h_y r_a \sigma_{py}$$

In order to verify if the indirect selection would be advantageous over direct selection, we adopted the criteria described Falconer and Mackay (1996) that calculates the merit of indirect selection relative to direct selection (CR_x/R_x) using the following formula:

$$\frac{CR_x}{R_x} = \frac{i_y h_y r_A \sigma_{A_x}}{i_x h_x \sigma_{A_x}} = \frac{i_y h_y r_A}{i_x h_x}$$

Where:

R_x is the response of the primary trait;

CR_x is the response of trait X when selection is practiced on a secondary trait Y ;

$i_{x,y}$ is the intensity of selection applied to the traits;

$h_{x,y}$ is the heritability of the traits;

r_A is the correlation between traits;

σ_{A_x} is the standard deviation;

Therefore, it can be said that, the higher the ratio CR_x/R_x , greater the efficiency of selection, in other words, the indirect selection proves advantageous over direct selection.

In order to know the effect of the selection of SC on other traits, it was assumed intensity of selection equal to 2.67 (selection of 1% of the animals) and direct selection for SC. For evaluation of longevity in females by analyzing the number of calvings at 53 months it was adopted selection intensities of 1.16 (selection of 30% of the animals).

2. RESULTS

1. Estimates of parameters in single-trait analyses

Heritabilities estimates and their respective standard deviations, obtained from single-trait analyses were 0.021 ± 0.004 , 0.035 ± 0.007 , 0.060 ± 0.009 and 0.53 ± 0.012 for NC53, HR, STAY and SC, respectively. In Table 4 are described, in addition to estimates of heritability, genetic, residual and phenotypic variances of studied traits by single-trait analyses.

Table 4. Heritability estimates and estimated variance for the number of calvings at 53 months (NC53), heifers rebreeding (HR), stayability (STAY) and scrotal circumference (SC), in single-trait analyses.

Parameters	NC53	HR	STAY	SC
σ_a^2	0.003	0.006	0.011	3.230
σ_e^2	0.152	0.174	0.160	2.857
σ_p^2	0.155	0.180	0.170	6.086
h^2	0.021 ± 0.004	0.035 ± 0.007	0.060 ± 0.009	0.530 ± 0.012

σ_a^2 : direct additive genetic variance, σ_e^2 : residual variance, σ_p^2 : phenotypic variance, h^2 : heritability.

2. Estimates of parameters in bi-trait analyses

Estimates of genetic, residual and phenotypic variances and average heritabilities for the studied traits, obtained in bi-trait analyses are presented in Table 5.

Table 5. Estimates of variances and heritabilities for number of calvings at 53 months (NC53), heifers rebreeding (HR), stayability (STAY) and scrotal circumference (SC), in bi-trait analyses.

Parameters	NC53	HR	STAY	SC
σ_a^2	0.0015	0.007	0.007	3.243
σ_e^2	0.1153	0.179	0.116	2.934
σ_p^2	0.1167	0.187	0.123	6.177
h^2	0.013 ± 0.003	0.039 ± 0.007	0.057 ± 0.007	0.525 ± 0.013

σ_a^2 : direct additive genetic variance, σ_e^2 : residual variance, σ_p^2 : phenotypic variance, h^2 : heritability.

Estimates of genetic and residual correlations between traits were positive, ranging from low to high magnitudes (Table 6). Genetic correlations between NC53, HR and STAY were equivalent and superior in relation to those estimated between SC and the other traits.

Table 6. Estimates of genetic correlations above the diagonal and residual correlations below the diagonal between traits obtained in bi-trait analyses.

Parameters	NC53	HR	STAY	SC
NC53		0.836±0.196	0.994±0.002	0.203±0.0745
HR	0.996±0.000		0.991±0.017	0.152±0.065
STAY	0.887±0.001	0.513±0.005		0.112±0.055
SC	0.048±0.004	0.057±0.001	0.056±0.001	

NC53: number of calvings at 53 months; HR: heifers rebreeding; STAY: stayability; SC: scrotal circumference.

3. Direct and correlated genetic responses to selection

Due to low heritabilities estimated in this study for reproductive traits and high genetic correlations among them, it is important that conclusions about the association between them are made based not only on the estimated correlations, but in the possible genetic changes obtained in indirect selection using correlated responses.

Initially, in order to know the effect of the selection of SC on other traits, it was assumed intensity of selection equal to 2.67 (selection of 1% of the animals) and direct selection for SC (Table 7).

Table 7. Effect of direct selection on scrotal circumference and the response on number of calvings at 53 months (NC53), heifers rebreeding (HR) and stayability (STAY).

Parameters	Correlated response	Direct response	Indirect selection efficiency
NC53	0.015	0.005	2.969
HR	0.025	0.019	1.284
STAY	0.018	0.023	0.782

For evaluation of longevity in females by analyzing the number of calvings at 53 months it was adopted selection intensity of 1.16 (selection of 30% of the animals) and direct selection for NC53 (Table 8).

Table 8. Effect of direct selection on number of calvings at 53 months and the response on heifers rebreeding (HR), stayability (STAY) and scrotal circumference (SC).

Parameters	Correlated response	Direct response	Indirect selection efficiency
HR	0.009	0.019	0.475
STAY	0.011	0.023	0.475
SC	0.048	3.484	0.014

3. DISCUSSION

The estimated heritability obtained for yearling scrotal circumference was high (0.53 ± 0.013) and similar to those reported by Dias et al. (2003) and Brito et al. (2003). Using part of the same dataset in bi-trait analyses, Terakado et al. (2011) reported lower value of 0.20 ± 0.06 for scrotal circumference measured at 18 mo. The low estimate found in that study can be explained by the fact that these authors had not adjusted the values found for scrotal circumference for age and weight. The results found in the literature and in the present study suggest the existence of enough genetic variability to obtain genetic progress with the selection of this trait in young bulls. According to Sesana (2005), the difference in heritability estimates for SC in different studies is due, in part, to methods of data analysis and the differences between breeds and groups.

Heritability estimates of traits related to female fertility in observed scale are, generally, of low magnitude. For traits that measure longevity of cows, as stayability and number of calvings at 53 months, the heritability values, obtained from bi-trait analyses, 0.057 ± 0.007 and 0.013 ± 0.003 , respectively, are considered of low magnitude.

Some authors reported similar heritability values to those obtained in this study for stayability. Westhuizen et al. (2001) studied STAY in crossbred animals using a sire model, the trait was defined as the probability of an animal surviving a specific age (36, 48, 60, 72 and 84 months), given the opportunity to reach that age, and obtained heritability estimates of 0.06, 0.10, 0.06, 0.03 and 0.11, respectively. Silva et al. (2003) and Marcondes et al. (2005) estimated values of heritability equal to 0,065 for STAY in Nellore cattle in analysis with a linear model. In the same breed, Balieiro et al. (2008) reported values of heritability for that trait equal to 0.04 and 0.05. Beckman et al. (2006), working with Red Angus animals, reported values between 0.08 and 0.19 for heritability of stayability at six years.

Hernández et al. (2011), working with cattle *Mambi de Cuba*, reported values similar to the estimated in this study (0.06 ± 0.02) for the heritability of the trait number of calvings.

Some studies found in literature have reported slightly higher rates for different definitions of stayability at five, six or seven years, often obtained with a threshold sire model. After transformation to observed scale, estimates varied from 0.09 to 0.14 (MARCONDES et al., 2009; QUEIROZ et al., 2007; SILVA et al., 2003b).

In agreement with published literature up to date, it can be inferred that for the studied herds, the indicator traits of ability to remain productive in the herd, since the heritability estimates were of small magnitude, will have a small selection response per year.

The high magnitude and positive genetic correlation between stayability and number of calvings at 53 months (0.994 ± 0.002) would allow anticipation at long-term from 76 to 53 months, of genetic evaluation of bulls based on the performance of their daughters. Moreover, according to Silva et al. (2003), this anticipation in the study of productive longevity of cows would enable greater accuracy in predictions of genetic merit, as a consequence of a larger number of observations available in the data file and decrease the generation interval.

This fact was confirmed by Van Melis et al. (2007) in study of stayability (STAY) in three different ages (five, six and seven years) in Nellore cows. These authors observed that STAY measured at different ages were related linearly, which indicates that selection based on traits evaluated earlier in productive life of the cow would be more efficient.

Tanaka et al. (2012) concluded in their study that the ability of cows to stay productive in the herd, measured by the number of calvings at 53 months, when considered in a selection index, was the component that resulted in greater variation of maternal return (estimated return in kilograms of live weight produced per cow per year, when discounted the estimated cost of maintenance), when there was an increase in one unit of the number of calving of the female.

The estimated values for the additive and residual genetic variance for heifers rebreeding were 0.007 and 0.179, respectively, resulting in a heritability estimate of 0.039 on the observed scale. These heritability estimates are consistent with those reported by Silva et al. (2008), who found values ranging from 0.04 to 0.07 for Nellore heifers rebreeding and Buddenberg et al. (1989), who reported values

ranging from 0.01 to 0.04 to rebreeding of Hereford and Angus heifers, also using linear models .

Other authors have reported values higher than described here: Smith et al. (2002) and Doyle et al. (2000) estimated heritability of 0.25 for Nellore heifers and 0.18 for Angus heifers, respectively, using non-linear model, thus in underlying scale. However, Doyle et al. (2000) discussed the inconsistency of the results obtained as half of the subsamples used in the analyses produced heritability estimates outside the parameter space.

The average estimate of heritability (0.039 ± 0.007) obtained in this work to rebreeding, shows that there is a low genetic variation for this trait. PEREIRA (2008) suggests that reproductive traits, in general, are affected by environmental effects such as climate and food, and that heifers rebreeding is affected mainly by physiological wastage due to lactation concomitant with her own growth, which would increase furthermore the effect of environmental factors on the performance of primiparous females .

The genetic correlations between scrotal circumference and reproductive traits obtained in this study were favorable, although of low magnitude. For SC and HR, the estimated correlation (0.152 ± 0.065) indicates that a work of selection for scrotal circumference could moderately increase the rate of reconception in primiparous females. It should also be taken into consideration that, when working with indirect selection of HR through SC, the values obtained for correlated response (0.025) were higher than those for direct response (0.019), showing greater efficiency of indirect selection of heifers rebreeding.

This fact can also be observed when indirect selection of NC53 through SC is applied: the correlated response (0.015) was higher than the direct response (0.005), showing that gains could be achieved through indirect selection.

4. CONCLUSIONS

The obtained results in this study allow us to conclude that:

The scrotal circumference is more heritable than traits measured in females, denoting the existence of sufficient additive genetic variability for obtaining genetic progress with the selection of young sires for this trait.

The positive genetic correlations, although of low magnitude, between measurements of scrotal circumference and reproductive traits measured in females, when combined with results for correlated responses and indirect selection, suggest that selection for increasing scrotal circumference should result, at long-term, in improvements in heifer subsequent rebreeding rate.

The estimated heritability for NC53 shows that a small part of the variation is determined by additive gene action. However, considering the correlations between the traits, correlated responses and indirect selection efficiency, there are possibilities that the number of calvings at 53 months can be used as an alternative way of evaluate the stayability of the cow, resulting in anticipation of the genetic evaluation of bulls, based on the performance of their daughters, of 76 months, as it has been practiced by the breeding programs that make use of stayability as selection criterion, to 53 months.

It also should be taken into consideration that, in studied herds, the differences found for stayability can be largely attributed to environmental differences, indicating that improvements in animal management, in general, would assist in increasing the productive permanence of females in the herd.

The inclusion of reproductive traits measured directly in females as selection criteria in animal breeding programs can be an alternative to improve, gradually, sexual precocity and length of productive life of cows in studied herds.

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CHAPTER 3 - ESTIMATION OF GENETIC PARAMETERS FOR REPRODUCTIVE TRAITS MEASURED IN FEMALES AND SCROTAL CIRCUMFERENCE IN NELLORE CATTLE USING BAYESIAN INFERENCE

ABSTRACT – In order to have improvements in production efficiency and growth development in animals as possible goals to be achieved, it is necessary to have herds of high sexual precocity and good fertility. Thus, it increases the availability of animals in the herd, whether for sale or for selection, which generates a higher selective intensity and, consequently, higher genetic progress. The use of reproductive traits as selection criteria can be used to achieve such improvements, therefore studies related to such traits should be increased in order to determine important genetic parameters. This study aimed at estimating heritability for reproductive traits seeking the possibility of using these measures directly in females as selection criteria for genetic improvement in Nellore cattle, besides to establish genetic and phenotypic correlations between number of calvings at 53 months and other traits investigating whether it can be used as an alternative to evaluate the ability of cows to stay productive in herd. It was estimated the (co)variances and genetic parameters for the traits mentioned using Bayesian inference. The traits number of calvings at 53 months, heifers rebreeding, and stayability were analyzed assuming a threshold model that relates the observed response (in discrete scale) with an underlying scale, while the trait scrotal circumference was analyzed with a linear model. NC53 is moderately heritable (≈ 0.22) and strongly positively correlated with STAY, which means that selecting for this trait could improve productive longevity of Nellore cows. Correlations estimated between HR and STAY (≈ 0.97) and also between HR and NC53 (≈ 0.99) allows an improvement on heifers rebreeding rates if selection was applied for traits related to longevity. Genetic correlations between SC and females reproductive traits are positive but weak, suggesting the need to use reproductive traits measured directly in females to obtain improvements in sexual precocity and longevity.

Key-words: Bayesian inference, beef cattle, heritability, reproductive trait, threshold model.

1. INTRODUCTION

Reproductive traits in beef cattle, measured directly in females, has been little explored by researchers and animal breeding programs, which leads to a slower development of analyses methodologies and even lack a of the knowledge of such traits. According to Eler et al. (2010), the main reasons for this are: 1) the "pre-established" concept that reproductive traits have low heritability which would cause a difficult and slow genetic change; 2) the difficulty and inaccuracy of reproductive data collection, which decreases the reliability of the genetic merit of animals for such traits, and 3) the categorical (threshold) quality of the most important traits, which requires more complex statistical procedures, only recently developed, compared to analyses of continuous variables.

Reproductive efficiency and improvement in growth traits of animals have been considered as key targets in livestock breeding programs nowadays. To achieve these objectives, it is evident the importance of working with herds of high sexual precocity and fertility. Combining these factors means generating an increase in the availability of animals, both for sales and replacement, greater selective intensity and, consequently, higher genetic progress, resulting in an increase in the profitability of the production system.

The evaluation of scrotal circumference, for example, widely used in animal breeding programs as an indicator of fertility and sexual precocity in beef cattle due to its easiness measurement and, especially, the high heritability estimates, should not be regarded as an indirect selection criteria that targets the real objective, which is to increase the precocity of the herd.

Traits like pregnancy in heifers, heifers rebreeding and stayability, which are measured directly in females, even being of economic interest, since they consider the fertility of each female, are still little explored.

Brumatti et al. (2002) in a simulation study considering typical conditions of production systems for beef cattle in Brazil, reported that reproductive traits of females were 3.4 times more important economically than growth traits, when considered on a selection index. Furthermore, reproductive efficiency is shown to be

the most important economically feature in many production systems, strongly affecting the efficiency of livestock (MALHADO et al., 2013).

Traits related to longevity are of utmost importance in beef cattle evaluation, still, the main disadvantage of selecting for such traits is the increase in generation interval due to delay in phenotypic data collection (DUCROCQ et al., 1988). Therefore, selecting for correlated traits recorded early in lifetime would allow the selection for longevity to be performed without such problems.

The aim of this study is to investigate the genetic correlation of reproductive traits measured in females in order to evaluate longevity and verify the possibility of using such traits as selection criteria in cattle breeding programs.

2. MATERIAL AND METHODS

1. Description of the dataset

This study used a file formed by the dataset of herds belonging to different cattle breeding programs, in the North, Northeast, Southeast, Midwest and southern Brazil and Paraguay.

The animals were from 37 different farms belonging to the dataset *Aliança Nelore* (GENSYS, 2010). The feeding adopted in these farms consisted basically of tropical pastures, mineral salt and water *ad libitum*. In general, supplementation was not performed for any category of females. On some farms where there was no uniformity of quality and availability of forage, the breeding females were allocated in the best pastures.

The breeding season traditionally lasts 90 days and its onset must be determined by weather and nutrition conditions of each region. In order to identify early females, part of the herds adopted two breeding seasons: one anticipated that, in general, occurs from March to April, and the traditional season, usually between the months of November and February. The remaining herds adopted only the traditional breeding season. Females were mostly inseminated and, if the pregnancy was not detected, they were exposed to a breeding system with more than one sire for a group of cows. The natural mating was controlled, that is, a group of 30 to 50 females were placed with a single-sire.

Most participating herds exposed the primiparous to controlled natural mating or breeding groups, thus increasing the pregnancy rate in this category. Heifers that became pregnant early in the season were favored, since they had more time to recover and conceive at the beginning of the traditional breeding season.

2. Evaluated Traits

The scrotal circumference was obtained approximately at 18 months of age, by measurements made transversely in the region of larger diameter of the scrotum, with the use of specific scrotal tape measure.

The stayability records (STAY) were analyzed categorically, applying scores "1" for females that remained in the herd up to 76 months and that conceived at least three products until this age. Received "0", representing the failure, females that did not remain in the herd, in other words, were discarded for not becoming pregnant in previous breeding seasons. For this trait, the number of calvings could range from 0 to 5 for those cows with first service at 18 months and, for cows with first service at 24 months, the calvings could range from 0 to 4 .

Similarly, number of calvings at 53 months (NC53) was used as an alternative way of measuring the ability to stay in herd. Was computed the number of calvings that the cow had up to 53 months, ranging from 0 to 3.

Heifers rebreeding (HR) was also calculated using scores. If the heifer calved, since it had given birth in the first breeding season, it received a score of 1, indicating success. Otherwise, if the heifer failed, it received a score of 0.

For analyses of reproductive traits, a maximum interval of 15 months between first and second births was considered for females submitted to a normal breeding season and, for those submitted to an early breeding season, the maximum interval accepted was of 24 months.

3. Preliminary analyses

The editing of dataset were performed using the software SAS[®] (SAS Inst., Inc., Cary, NC).

For the analyses were carried out investigations concerning to the identifications of animal, sire, dam, sex, season of birth, age and number of calvings. Animals that did not have dates of birth and/or calving were not considered. To study the reproductive traits measured in females, were calculated age at first calving, calving interval, number of births and season of birth. The season of calving was

defined by two classes: raining, between October and March and dry, from April to September.

The inclusion of genetic groups assigned to individuals whose relationship information was incomplete in the pedigree file were also adopted, as described in the previous chapter.

The trait NC53 was defined as the number of calvings till 53 months of age, given the cow had performance records until yearling age and also had the opportunity to reach this age. Females whose ages at first calving were less than 20 months were erased from the dataset. Contemporary groups (CG) were defined based on concatenation of season and year of calving, farm of weaning to yearling and classification of precocity status. After being held previously described procedures, records for this trait varied between 0 and 3 calvings until the reference age.

To evaluate STAY, the consistency of the dataset was performed similarly as described to NC53. There were only births up to 76 months.

For NC53 and STAY, the models included the fixed effects of contemporary groups, defined by season and year of birth, farm of weaning to long yearling and classification of precocity status. In addition, for STAY analysis, the effects of mating system to which the cow was submitted in its last calving, was included as a covariate in the model, and it may be: artificial insemination, single and multiple sire.

The description of the dataset used in the analyses are presented in Table 9.

Table 9. Description of dataset used in the analyses of number of calvings at 53 months (NC53), stayability (STAY), heifers rebreeding (HR) and scrotal circumference (SC) of Nellore cattle.

Information	NC53	STAY	HR	SC
No. of observations	104,559	48,403	63,130	59,576
Period of calving	1984 to 2008	1984 to 2005	1984 to 2008	1984 to 2010
Contemporary groups	932	668	854	3789
No of animals in relationship matrix	116,766	90,195	116,558	134,638

Preliminary investigations were carried out on the significance of the variables used in contemporary groups (CG) and covariates included in the model by GLM procedure of SAS[®] software (SAS Inst., Inc., Cary, NC). Only variables that were statistically significant at the 5% level were included in the analyses.

CG without variability were eliminated, that is, those in which all animals showed the same response category and CG with less than 5 observations. The number of observations and the frequency of different values for STAY and NC53 are described in Table 10.

Table 10. Frequency of observation of stayability and number of calvings at 53 months of Nellore females.

Stayability	No. of observations	Frequency (%)
0	32,901	67.97
1	15,502	32.0
Total	48,403	100%
No. of calvings at 53 months	No. of observations	Frequency (%)
0	58,730	56.17
1	31,500	30.1
2	14,111	13.50
3	218	0.20
Total	104,559	100%

The definition of contemporary groups for scrotal circumference included year and season of calving, farm and group of management at calving, weaning and yearling beyond the dates when the animals were weaned and when measurements of scrotal circumference were taken. The scrotal circumference were previously adjusted for age and long yearling weight. The covariates were the linear and quadratic effects of age of dam at calving.

Heifers rebreeding (HR) was defined as success (1) or failure (0) for heifers that calved or not, respectively, since they had previously given birth. The contemporary groups for this trait included the classification of being precocious heifers or not, season and year of calving and farm from weaning to yearling. It was

included in the model, as a covariate, the age at first calving, the type of service that the female was submitted when it entered the breeding season and the sex of its first offspring.

A descriptive summary of the data of heifers rebreeding is shown in Table 11.

Table 11. Frequency of observation of heifers rebreeding of Nellore females.

Heifers rebreeding	No of observations	Frequency (%)
0	30,193	47.83
1	32,937	52.17
Total	63,130	100%

The percentage shown in Table 11 refers to the total of females that conceived or not, regardless of age that were exposed in the breeding season. The percentage of females that conceived were 75.14% and 50.11% for precocious and not precocious females, respectively.

2. Estimation of genetic parameters

In order to compare the results obtained with the analyses using Restricted Maximum Likelihood (REML) method and seek for procedures that provide more accurate estimates showing properties of interest in the estimation of variance components, we also performed analyses using Bayesian methods.

The Bayesian methodology differs from frequentist methodology because the parameters are viewed as random variables whose behavior is governed by a probability distribution that is assumed about its possible values, reflecting an initial information about the parameters, called *a priori* information, even before obtaining the data. Next, this *a priori* information is combined with that from the data, resulting in *a posteriori* information, that is used to make inferences about the parameters.

As the joint posterior distribution, in general, cannot be obtained in an accurate way due to integration involved, the inference is based on samples from the full conditional posterior distribution using simulation processes through iterations using Markov chain Monte Carlo methods (MCMC), as the Gibbs sampler algorithm

(CASELA & GEORGE, 1993). The full conditional distributions correspond to the distribution of a specific parameter, the other values of the parameters in the model are considered as known or fixed, and will be needed for each parameter to be estimated (VAN TASSEL & VAN VLECK, 1996).

One way to obtain samples from the posterior distribution, so that an inference about the parameters is possible, it's through the Gibbs sampling (GS). For this purpose, we used the software THRGIBBS2F90 (MISZTAL, 2010), to perform the calculation of the average posterior marginal distributions obtained from samples of GS chain, thereby estimating the (co)variance, which results in a chain of vectors (VAN TASSEL & VAN VLECK, 1998). However, not all vectors of this chain are suitable to be used in the calculation of the (co)variance components, therefore, an initial period of vector's discard, called burn-in, is adopted.

A priori information were taken as *flat prior* distributions for the fixed effects and direct additive genetic variance. Thus, it is expected that the data are dominant, in other words, the *priori* information has little influence on the estimates.

The (co)variance components and genetic parameters were estimated by single and bi-trait analyses (for all possible trait combinations) using an animal model. It was assumed a linear animal model for SC and a threshold model for NC53, HR and STAY. The linear model considered the CG as fixed effect and additive genetic effect of the animal as random and can be represented in matrix form by:

$$Y = Xb + Z_1a + Z_2Q_1c + e$$

Where Y is the vector of observations and X is the incidence matrix associating observations to the fixed effects of CG, b is the vector of fixed effects, Z_1 and Z_2 are the incidence matrices associating observations to direct genetic effect of animal, Q_1 is incidence matrix that relate animals to fixed effect of genetic groups and a , c and e are the random additive direct genetic effect of animal, the vector of fixed effects of genetic groups and the vector of random residuals, respectively.

The model considered the following assumptions:

$$\begin{bmatrix} a \\ e \end{bmatrix} \sim N \left\{ \begin{bmatrix} 0 \\ 0 \end{bmatrix}, \begin{bmatrix} G & 0 \\ 0 & R \end{bmatrix} \right\}$$

\mathbf{G} is a matrix of (co)variance of the random effect of vector \mathbf{a} and \mathbf{R} is matrix of residual (co)variance. The matrices \mathbf{G} e \mathbf{R} are described as $\mathbf{G} = \mathbf{A} \times \mathbf{G}_0$, where \mathbf{A} is the relationship matrix, \mathbf{G}_0 is the matrix of direct additive genetic (co)variances between studied traits and \times is the direct product between the matrices. $\mathbf{R} = \mathbf{I} \times \mathbf{R}_0$, where \mathbf{I} is an identity matrix, \mathbf{R}_0 is the matrix of residual (co)variance between the traits and $\mathbf{0}$ represents a null matrix.

Following Gianola (1979), when a threshold model was fitted, we assumed that an underlying continuous random variable \mathbf{g} could represent the liability for NC53. Because NC53 was defined by records falling into 4 mutually exclusive ordered categories, a set of 3 thresholds (t_1 , t_2 and t_3) correspond to the discontinuities in the observed scale (y), under the assumption that $t_0 = -\infty$ and $t_4 = +\infty$; such that: if $\mathbf{g} < t_1$, $y = 0$; if $t_1 < \mathbf{g} < t_2$, $y = 1$; if $t_2 < \mathbf{g} < t_3$, $y = 2$; and if $t_3 < \mathbf{g}$, $y = 3$.

In this way, the liability \mathbf{g} was modeled as:

$$\mathbf{g} = \mathbf{X}_1\mathbf{b} + \mathbf{Z}_1\mathbf{u} + \mathbf{Z}_2\mathbf{Q}_1\mathbf{c} + \mathbf{e}$$

In which \mathbf{g} is the vector with underlying liabilities for NC53, and \mathbf{b} , \mathbf{u} and \mathbf{c} are vectors of fixed effects of CG, genetic additive random effects of animal and the vector of fixed effects of genetic groups respectively. The \mathbf{X}_1 , \mathbf{Z}_1 and \mathbf{Z}_2 represent incidence matrices relating elements in \mathbf{b} , \mathbf{u} and \mathbf{c} to \mathbf{g} , respectively. \mathbf{Q}_1 is incidence matrix that relate animals to fixed effect of genetic groups. We assumed that: $E[\mathbf{g}] = \mathbf{X}_1\mathbf{b}$, $\mathbf{u} \sim N(\mathbf{0}, \mathbf{A}\sigma^2\mathbf{u})$ and $\mathbf{e} \sim N(\mathbf{0}, \mathbf{I}\sigma^2\mathbf{e})$, where \mathbf{A} is the additive genetic relationship matrix and \mathbf{I} is an identity matrix of order equal to the number of observations.

The traits related to longevity and heifers rebreeding (threshold traits) have underlying continuous distribution with a threshold, which makes the expression of these traits discontinuous (FALCONER & MACKAY 1996). Thus, it was used for the analyses of those traits a threshold model, assuming that the underlying distribution (U) is given by:

$$U \sim N(X\beta + Za, |\sigma_g^2)$$

As σ_{ϵ}^2 is not estimable (GIANOLA & FOULLEY, 1983), it was attributed to this parameter the arbitrary value 1 and set up uniform distributions *a priori* for the fixed effects ($b' = EF'$) and for σ_{α}^2 .

In single and bi-trait analyses, chains with length of 1,000,000 cycles were originated, in which the first 100,000 cycles were discarded (Burn-in). In the single-trait analyses, the samples were stored every 100 cycles and, for bi-trait, every 50 cycles. These values were set randomly in order to verify the convergence of chains

The convergence of Gibbs Sampling algorithm was verified by graphical visual inspection (sampled values versus iterations), using the package Bayesian Output Analysis (BOA) available for free software R[®] (CORE TEAM, 2013). It was assumed convergence when, after a certain point, the data presented behavior considered constant, which could be observed for all traits under study. It was also verified Welch & Heidelberger (1983) and Geweke (1982) tests results.

Estimates of average posterior heritability and correlations were estimated based on averages of the estimated posterior variances in single and bi-traits analyses.

Saying that two traits are genetically correlated, implies that the selection applied to one of them will cause a change in another. Thus, when the goal is to improve a trait based on the selection of another, there is indirect selection. According to Falconer and Mackay (1996), the magnitude of change in a trait when indirect selection applied to other traits, is used, can be obtained by knowing the heritability of the two traits and the correlation between them. The answer of the trait under selection, for example X, is equivalent to the average of the breeding values of the selected individuals. Thus, the response in the correlated trait, Y, is given by the regression of the genetic value of the trait Y in the genetic value of X:

$$b_{(a)yx} = \frac{COV_a}{\sigma_{\alpha_x}^2} = r_a \frac{\sigma_{\alpha_y}}{\sigma_{\alpha_x}}$$

The response of X, the trait that is under selection, can be described by:

$$R_x = ih_x \sigma_{\alpha_x}$$

Therefore, the correlated response of Y is:

$$R_y = (b_{(a)YX})(R_x) = i h_x \sigma_{ax} (r_a (\sigma_{ay} / \sigma_{ax})) = i h_x r_a \sigma_{ay}$$

Replacing σ_{ay} for $i h_y \sigma_{py}$, the response of Y is:

$$R_y = i h_x h_y r_a \sigma_{py}$$

In order to verify if the indirect selection would be advantageous over direct selection, we adopted the criteria described Falconer and Mackay (1996) that calculates the merit of indirect selection relative to direct selection (CR_x/R_x) using the following formula:

$$\frac{CR_x}{R_x} = \frac{i_y h_y r_A \sigma_{A_x}}{i_x h_x \sigma_{A_x}} = \frac{i_y h_y r_A}{i_x h_x}$$

Where:

R_x is the response of the primary trait;

CR_x is the response of trait X when selection is practiced on a secondary trait Y ;

$i_{x,y}$ is the intensity of selection applied to the traits;

$h_{x,y}$ is the heritability of the traits;

r_A is the correlation between traits;

σ_{A_x} is the standard deviation;

Therefore, it can be said that, the higher the ratio CR_x/R_x , greater the efficiency of selection, in other words, the indirect selection proves advantageous over direct selection.

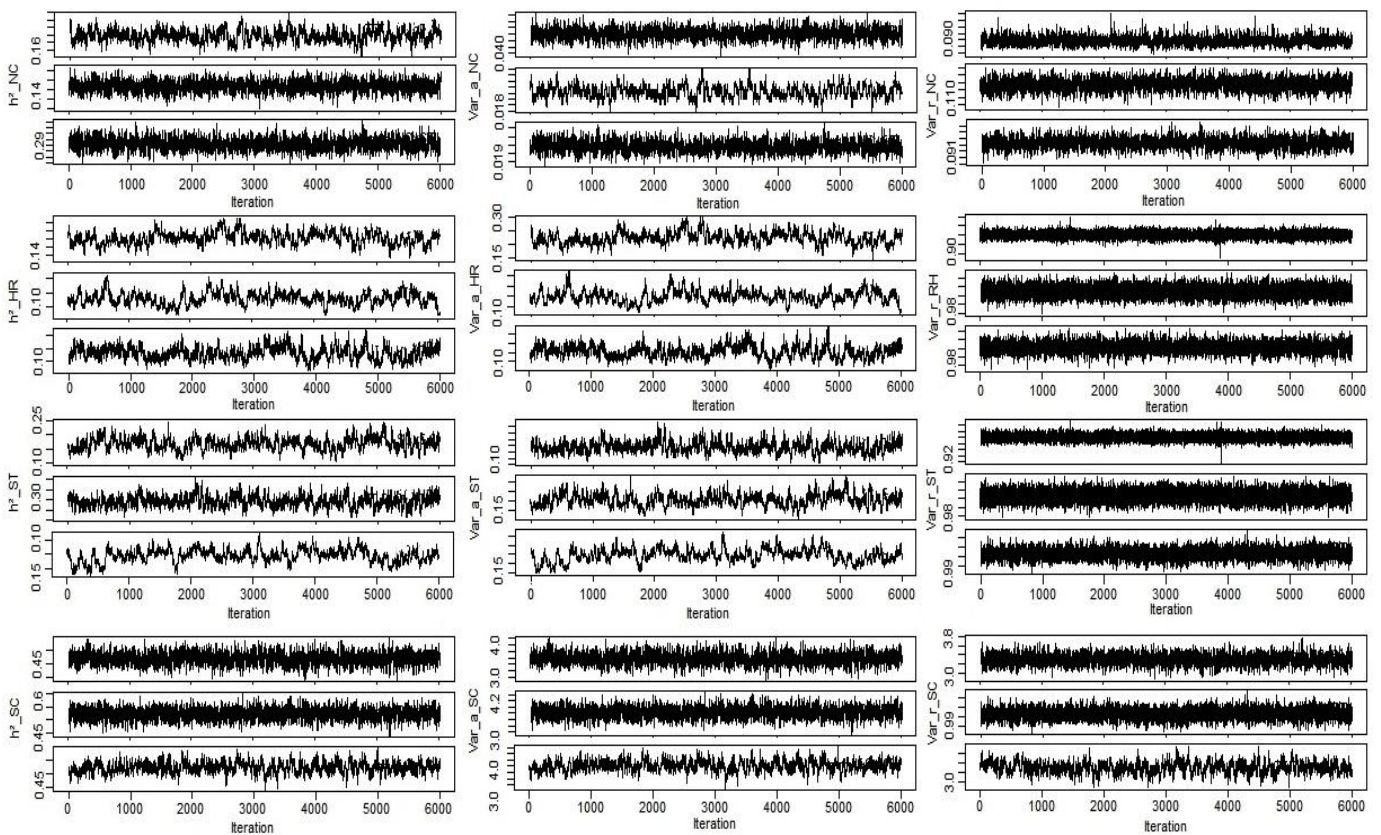
In order to know the effect of the selection of SC on other traits, it was assumed intensity of selection equal to 2.67 (selection of 1% of the animals) and direct selection for SC. For evaluation of longevity in females by analyzing the number of calvings at 53 months it was adopted selection intensities of 1.16 (selection of 30% of the animals).

2. RESULTS

1. Analysis of convergence of the Gibbs sampler

Visual inspections of the trace plots from the outputs of the Gibbs sampler were used to verify the convergence for the genetic parameters in the analysis between studied traits (Figure 1). All the traits have reached the stationary phase of the Gibbs chain, indicating that the sampling processes were appropriate.

Figure 1. Trace plots of estimated heritabilities, additive genetic variance and



residual variance for number of calvings at 53 months (NC), heifers rebreeding (HR), stayability (ST) and scrotal circumference (SC).

2. Estimates of parameters

Results for variance components and genetic parameters, obtained in bi-trait analyses, are presented in Table 12.

Table 12. Estimates of marginal posterior distributions of variance components and heritabilities for number of calvings at 53 months (NC53), heifers rebreeding (HR), stayability (STAY) and scrotal circumference (SC).

Marginal Posterior Distributions					
Traits	Parameters	Mean \pm SD	Mode	Median	HPD 95%
NC53	σ_a^2	0.029 \pm 0.001	0.029	0.029	0.027; 0.032
	σ_e^2	0.102 \pm 0.002	0.101	0.102	0.099; 0.105
	h^2	0.22 \pm 0.009	0.20	0.20	0.205; 0.240
HR	σ_a^2	0.175 \pm 0.028	0.177	0.174	0.120; 0.232
	σ_e^2	1.002 \pm 0.009	1.003	1.002	0.984; 1.020
	h^2	0.15 \pm 0.021	0.13	0.14	0.106; 0.188
STAY	σ_a^2	0.229 \pm 0.037	0.228	0.228	0.157; 0.305
	σ_e^2	1.002 \pm 0.007	1.002	1.002	0.989; 1.017
	h^2	0.19 \pm 0.025	0.20	0.19	0.133; 0.253
SC	σ_a^2	3.602 \pm 0.169	3.599	3.600	3.281; 3.938
	σ_e^2	3.306 \pm 0.116	3.305	3.306	3.077; 3.527
	h^2	0.52 \pm 0.019	0.50	0.52	0.482; 0.560

σ_a^2 : direct additive genetic variance in the underlying scale; σ_e^2 : residual variance in the underlying scale; h^2 : heritability in the underlying scale; HPD 95% = limits 95% for the highest density posterior interval.

In Figure 2 are presented the density plots of the estimates *a posteriori* of the studied parameters. For all chains, the distributions are symmetrical and slightly close to a normal distribution.

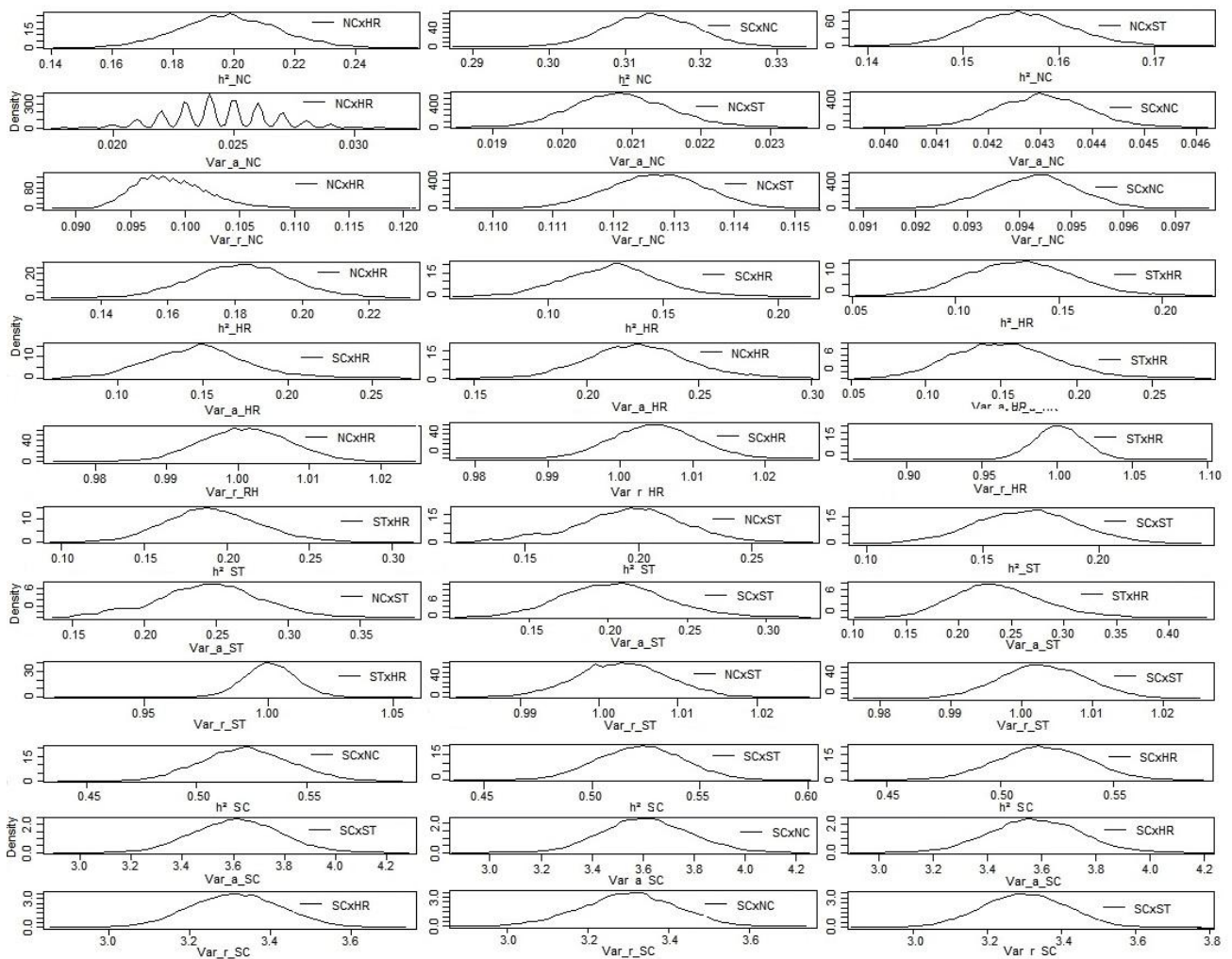


Figure 2. Posterior density of estimated heritabilities and variance components for number of calvings at 53 months (NC), heifers rebreeding (HR), stayability (ST) and scrotal circumference (SC).

Estimates of genetic correlations amongst the studied traits were positive, ranging from weak to strong values (Table 13). As expected, genetic correlations between the reproductive traits NC53, HR and STAY were similar and superior compared to those estimated between SC and these traits. For analysis purposes, residual correlations were fixed at zero.

Table 13. Estimates of genetic correlations, above the diagonal, between traits obtained in bi-trait analyses.

Parameters	NC53	HR	STAY	SC
NC53		0.99 ± 0.007	0.99 ± 0.051	0.07 ± 0.019
HR	-		0.97 ± 0.021	0.11 ± 0.069
STAY	-	-		0.12 ± 0.058
SC	-	-	-	

NC53: number of calvings at 53 months; HR: heifers rebreeding; STAY: stayability; SC: scrotal circumference.

3. Direct and correlated genetic responses to selection

To make possible that more accurate conclusions about the behavior and association between studied traits, when applied indirect selection, could be reached, it was not only considered the correlations estimated in this study. It was also calculated the correlated responses for each trait when indirect selection was applied.

As in the previous chapter, in order to know the effect of the selection of SC on other traits, it was assumed intensity of selection equal to 2.67 (selection of 1% of the animals) and direct selection for SC. Correlated and direct responses and indirect selection efficiency were, respectively, 0.022, 0.093 and 0.241 for NC53; 0.089, 0.188 and 0.471 for HR; and 0.112, 0.242 and 0.457 for STAY (Table 14).

Table 14. Effect of direct selection on scrotal circumference and the response on number of calvings at 53 months (NC53), heifers rebreeding (HR) and stayability (STAY).

Parameters	Correlated response	Direct response	Indirect selection efficiency
NC53	0.022	0.093	0.241
HR	0.089	0.188	0.471
STAY	0.112	0.242	0.457

For evaluation of longevity in females by analyzing the number of calvings at 53 mo it was adopted selection intensities of 1.16 (selection of 30% of the animals). Correlated and direct responses and efficiency of indirect selection were, in this case,

respectively, 0.261, 0.242 and 1.065 for STAY, 0.226, 0.188 and 1.199 for HR and, for SC, the values were 0.070, 3.654 and 0.019 (Table 15).

Table 15. Effect of direct selection of number of calvings at 53 months and the response on heifers rebreeding (HR), stayability (STAY) and scrotal circumference (SC).

Parameters	Correlated response	Direct response	Indirect selection efficiency
HR	0.261	0.242	1.065
STAY	0.226	0.188	1.199
SC	0.070	3.654	0.019

3. DISCUSSION

The estimate of heritability for NC53 (0.22 ± 0.009) was slightly higher than that estimated in other studies for traits related to longevity and can be considered of moderate magnitude, which means that it has a reasonable level of heritability. Neves et al. (2012) estimated 0.17 for heritability using the same definition of NC53. Van Melis et al. (2010) presented an estimate of heritability ranging from 0.17 to 0.20 in multivariate analysis for number of calvings until cow death, using a sequential threshold model.

Generally, most studies related to the evaluation of traits that measure longevity or length of productive life in cows, do it by adopting stayability using the following definition: probability of a cow remain in the herd until a specific age given the opportunity to reach that age. In the present research, stayability was evaluated at 76 months of age. At large, for this trait, estimates of heritability range from low to moderate and, in this work, the heritability obtained in bi-trait analyses, was moderate and equal to 0.19 ± 0.025 (Table 11).

In agreement with the findings achieved in this research, Martinez et al. (2005), Rasali et al. (2005) and Van Melis et al. (2007) also reported values of moderate magnitude: 0.25, 0.23 and 0.22, respectively for stayability using a threshold model.

Jamrozik et al. (2013) presented heritabilities for stayability to consecutive calvings in Canadian Simmental cows ranging from 0.12 to 0.36. The authors found a clear trend of reduction in heritability estimates proportional to the increase in the number of consecutive calvings.

Results found in literature with stayability measured in different ages show that estimates of heritability for this trait at younger ages are similar and correlated to those estimated for stayability at older ages. Jamrozik et al. (2013) concluded that stayability to second calving can be considered as a good indicator of stayability to later calvings due to the genetic correlation estimated between these traits (0.61).

Also, analyzing the efficiency of indirect selection values obtained between NC53 and STAY (1.065), it can be concluded that the selection applied on NC53 will

be more efficient to obtain results for longevity of animals compared to the selection applied directly on stayability.

The results found in the present study confirms that there is an advantage of selecting for stayability at younger ages or, as suggested in this study, for NC53, due to its strong correlation and greater heritability compared to stayability and also higher accuracy and consequently reduction in generation interval for being a trait evaluated earlier in lifetime.

The evaluation of stayability implies reducing costs related to replacement of animals due to discard. Furthermore, with a decrease in replacement and consequent increase in selection intensity, there is also a greater response to selection. However, due to the high time needed for evaluation of this trait, this practice could lead to an increase in the generation interval. This problem can be minimized by adopting NC53 as an indirect trait of evaluating the longevity of animals.

One of the major problems found in tropical countries herds is related to heifers rebreeding. Studies show that this trait is strongly influenced by environmental factors (PEREIRA, 2008 and BOLIGON & ALBUQUERQUE, 2012), since heifers have to conciliate pregnancy and subsequent lactation concomitant to their own growth. The heritability estimated in the present study for this trait was low (0.15 ± 0.021) and similar to the value of 0.14 reported by Boligon & Albuquerque (2012), confirming the influence of environmental effects on this trait.

However, the high genetic correlation estimated between HR and STAY (0.97 ± 0.021) and also between HR and NC53 (0.99 ± 0.007), combined with heritabilities of these traits obtained in bi-trait analyses (0.22 ± 0.009 and 0.19 ± 0.025 for NC53 and STAY, respectively), allows an improvement on heifers rebreeding rates if selection was applied for traits related to longevity.

This result can be confirmed by analyzing the value obtained for efficiency of indirect selection between NC53 and HR (1.199). This value suggests that, if applied selection on NC53 in order to achieve improvements in HR, the results would be more favorable than if directly selection on HR were performed.

As in the present study, Pereira (2008) possessed in its dataset cows that were exposed to early breeding season and those that were exposed to normal

breeding season. The author reported heritability estimates equal to 0.15 for rebreeding females that were exposed in the normal breeding season and 0.05 when all females were included (precocious and not precocious) in the analysis. Also according to this author, the inclusion of precocious animals in the analysis of HR would result in the reduction of genetic variance and, consequently, in heritability estimates for this trait. As described earlier, in this study we included both precocious and non precocious females, which may help explain the low estimated values of heritability on evaluation of heifers rebreeding.

The values estimated for genetic variance (3.602) and heritability (0.52 ± 0.019) for SC, as usually described in literature, indicates the existence of significant responses when selection is applied to this trait. No strong genetic correlations were estimated between females reproductive traits and SC, thus, genetic response in those traits through SC selection is not expected to be effective. These results indicate the need to include reproductive traits measured directly in females to obtain improvements in sexual precocity, in a more effective way, instead of considering only the inclusion of scrotal circumference.

4. CONCLUSIONS

The obtained results in this study allow us to conclude that:

The estimation presented using Bayesian inference, although computationally more demanding, was the most accurate for analyses considering reproductive traits measured directly in females.

As expected, the scrotal circumference is more heritable than traits measured in females, denoting the existence of sufficient additive genetic variability for obtaining genetic progress with the selection of young sires for this trait.

The number of calvings at 53 months, as a way of measuring the ability of the cow to stay productive in herd, is more efficient than the usual definition of stayability. The positive and strong estimates for genetic correlations between these traits, when combined with results obtained for correlated responses and indirect selection, confirm that selection performed earlier in life could be more advantageous for evaluation of longevity and animal breeding purposes.

The estimated heritability for NC53 shows that a considerable important part of the variation is determined by additive genes action. Also considering the correlations between the traits, correlated responses and indirect selection efficiency, there are possibilities that the number of calvings at 53 months could be used as an alternative criterion to evaluate the stayability of the cow, resulting in anticipating the genetic evaluation of bulls based on the performance of their daughters to 53 months, instead of 76 months, as it has been practiced by the breeding programs that make use of stayability as selection criterion.

Considering the positive and strong genetic correlations between NC53 and HR, selection for the trait measured early in lifetime would be recommended. However, the heritability estimate for NC53 is higher than that for HR, indicating more advantages in selecting for NC53 mainly due to greater genetic gain by its selection. Another advantage in selecting for NC53, instead of using binary traits such as STAY or HR, is that a trait with greater number of categories allows the threshold model resembles the linear model.

The inclusion of reproductive traits measured directly in females as selection criteria in animal breeding programs can be an alternative to improve, gradually, sexual precocity and length of productive life of cows in the herds studied.

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CHAPTER 4 - IMPLICATIONS

This study is related to reproductive traits measured in Nellore females as well as their relationship with scrotal circumference. Furthermore, it involves the study of different approaches of genetic parameters estimation for length of productive life of cows in the herd.

The evaluation of reproductive traits measured directly in females represents an improvement in the animal category of greater economics interest in breeding herds: the dams. The productive performance of a livestock breeding system depends, mainly, on the performance of the cows, since their function is, basically, to produce calves.

It is known that selection based on indices is more advantageous than selection applied individually for each interest trait. Thus, the development of an index that targets reproductive traits measured directly in females is the key to increase productivity in beef cattle.

Frequentist and Bayesian inference methods were applied for evaluation the number of calvings at 53 months (NC53), heifers rebreeding (HR), stayability (STAY) and scrotal circumference (SC). The Bayesian method was the most accurate for analyses considering females reproductive traits. However, the estimation presented using such approach required more time for processing the analyses and was also computationally more demanding.

Selection for number of calvings at 53 months is possible and could be more advantageous for evaluation longevity if compared to stayability, mainly, due to the estimated heritability of NC53 and correlations between these two traits. Another advantage in selecting for NC53, instead of using binary traits such as STAY or HR, is that a trait with greater number of categories allows the threshold model resembles the linear model.

Selection for NC53 results in anticipation of genetic evaluation of bulls based on the performance of their daughters, greater accuracy in predictions of genetic merit as a consequence of a larger number of observations available in the data file

and, besides this, a lower generation interval would also be expected compared to the usual definition of STAY.

Considering the positive and strong genetic correlations between NC53 and HR, selection for the trait measured early in lifetime would be recommended. However, the heritability estimate for NC53 is higher than that for HR, indicating more advantages in selecting for NC53 mainly due to greater genetic gain by its selection. Moreover, the threshold of 53 months accommodates this critical period of rebreeding of primiparous and also allows some emphasis on the sexual precocity of cows.

Low estimates of genetic correlations between females reproductive traits and scrotal circumference suggests that significant genetic responses in reproductive traits, when selecting for SC, are not expected, indicating the need to use reproductive traits measured directly in females as selection criteria for genetic improvement in Nellore cattle reproductive efficiency.