

LAIS COSTA BRITO

**CENSORED AND MULTI-TRAIT BAYESIAN MODELS FOR GENETIC
EVALUATION OF MILK, WEIGHT AND REPRODUCTIVE TRAITS IN
GUZERÁ CATTLE IN TROPICAL CONDITIONS**

Tese apresentada à Universidade Federal de Viçosa, como parte das exigências do Programa de Pós-graduação em Zootecnia, para obtenção do título de *Doctor Scientiae*.

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APROVADA: 13 de maio de 2016.

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BIOGRAFIA

LAIS COSTA BRITO, solteira, filha de Miguel Baia Brito e Cidia Maria Rosário da Costa, nasceu em 26 de abril de 1990, em Belém, Pará. Em março de 2007, iniciou o curso de Zootecnia na Universidade Federal Rural da Amazônia – PA. Em outubro de 2008 recebeu o Diploma de Reconhecimento e Estímulo pelo seu destaque e aproveitamento curricular nas disciplinas do curso de Zootecnia. Em julho de 2011 recebeu o diploma de Zootecnista e em agosto do mesmo ano iniciou o curso de Mestrado em Zootecnia pela Universidade Federal de Viçosa. Em março de 2013, obteve o título de *Magister Scientiae* em Zootecnia, sob orientação do prof. Ricardo Frederico Euclides (Bajá) e coorientação do prof. Robledo de Almeida Torres. Em abril do mesmo ano, iniciou o curso de Doutorado em Zootecnia na Universidade Federal de Viçosa com período *sandwich* pela *Universidad de Zaragoza* sob supervisão do prof. Luis Varona Aguado. Em maio de 2016, submeteu-se aos exames finais de defesa de tese para obtenção do título de *Doctor Scientiae* em Zootecnia, sob orientação do prof. Paulo Sávio Lopes e coorientação do prof. Fabyano Fonseca e Silva e Dr^a Maria Gabriela Campolina Diniz Peixoto.

SUMÁRIO

RESUMO.....	VI
ABSTRACT	VIII
GENERAL INTRODUCTION	1
LITERATURE CITED	3
CHAPTER 1.....	5
GENETIC EVALUATION OF AGE AT FIRST CALVING FOR GUZERÁ BEEF CATTLE USING LINEAR AND SURVIVAL CENSORED BAYESIAN MODELS	6
<i>ABSTRACT</i>	6
<i>INTRODUCTION.....</i>	7
<i>MATERIALS AND METHODS</i>	8
<i>RESULTS AND DISCUSSION</i>	14
<i>CONCLUSIONS.....</i>	24
<i>LITERATURE CITED</i>	24
CHAPTER 2.....	30
GENETIC PARAMETER ESTIMATES FOR BEEF, DAIRY AND REPRODUCTIVE TRAITS OF GUZERÁ CATTLE IN TROPICAL CONDITIONS.....	31
<i>ABSTRACT</i>	31
<i>INTRODUCTION.....</i>	31
<i>MATERIALS AND METHODS</i>	33
<i>RESULTS AND DISCUSSION</i>	36
<i>CONCLUSIONS.....</i>	43
<i>LITERATURE CITED</i>	43
GENERAL CONCLUSION	47

RESUMO

BRITO, Lais Costa, D.Sc., Universidade Federal de Viçosa, maio de 2016. **Modelos Bayesianos censurados e multicaracterística para avaliação genética de características de leite, peso e reprodutivas em bovinos Guzerá em condições tropicais.** Orientador: Paulo Sávio Lopes. Coorientadores: Fabyano Fonseca e Silva e Maria Gabriela Campolina Diniz Peixoto.

Objetivou-se com este trabalho estimar parâmetros genéticos para características de produção de leite (produção de leite em até 305 dias – PL305), peso (peso aos 120 – P120, aos 365 – P365 e aos 550 dias – P550) e reprodutiva (idade ao primeiro parto - IPP) em bovinos da raça Guzerá utilizando modelos multicaracterísticos e comparar metodologias que se baseiam na utilização de dados censurados de idade ao primeiro parto. Os dados foram cedidos pela Associação Brasileira dos Criadores de Zebu (ABCZ) e Embrapa Gado de Leite em parceria com o Centro Brasileiro de Melhoramento do Guzerá (CBMG²). O arquivo de pedigree (120.599 animais) incluiu animais com registros fenotípicos e todos os ancestrais conhecidos. Registros censurados foram definidos como dados de IPP que extrapolaram os limites de 740 e 1860 dias. Os registros de IPP (69.157 informações) foram analisados por meio de sete diferentes metodologias: método linear convencional (LM); de simulação (SM); de penalidade (PM); modelos bicaracterística limiar-linear em que se considerou (TLcens) ou não (TLmiss) informações prévias sobre os registros censurados; e a metodologia de análise de sobrevivência por meio do modelo de riscos proporcionais de Weibull segmentado em que se considerou (PWPHcens) ou não (PWPH) os registros censurados. Para as análises de sobrevivência, os valores para o critério de informação da *deviance* (DIC) sugerem o uso de 0 e 2 nós na função base para os métodos PWPH e PWPHcens, respectivamente. Os componentes de variância genética aditiva estimados para os métodos LM, PM e TLmiss foram similares. As estimativas de herdabilidade para IPP variaram de 0,19 (TLcens) à 0,28 (SM) e 0,40 (PWPH) e 0,46 (PWPHcens). De forma geral, as correlações entre os valores genéticos obtidos por meio das diferentes metodologias e a porcentagem de touros selecionados em comum variaram de -0,28 (SM x PWPH) à 0,99 (TLmiss x LM), indicando reordenamento moderado entre os animais. As comparações baseadas na metodologia de validação cruzada, indicam a metodologia TLmiss como a melhor opção para predição dos valores genéticos dos animais para a característica IPP na população Guzerá. Para estimação dos parâmetros genéticos utilizando modelos multicaracterísticos, foram considerados os efeitos

sistemáticos de sexo e idade ao parto. Os efeitos aleatórios genético aditivo e de grupo de contemporâneo (rebanho, ano e estação de parto) foram considerados. Adicionalmente, os efeitos aleatórios genético aditivo materno e de ambiente permanente materno foram considerados para a característica peso à desmama. As estimativas de herdabilidade foram 0,29 (PL305), 0,42 (P120), 0,49 (P365), 0,56 (P550) e 0,25 (IPP). As correlações genéticas entre as características de peso foram maiores que 0,83 e entre PL305 e as demais foram de 0,25 (PL305 x P205), 0,32 (PL305 x P365) e 0,36 (PL305 x P550). A característica IPP foi negativamente correlacionada com as características de leite e de peso. Os resultados sugerem que a seleção para a produção de leite não compromete a seleção para características de peso e reprodutivas, bem como é passível a inclusão de dados censurados de IPP na avaliação genética por meio do uso de um modelo de limiar-linear em bovinos da raça Guzerá.

ABSTRACT

BRITO, Lais Costa, D.Sc., Universidade Federal de Viçosa, May, 2016. **Censored and multi-trait Bayesian models for genetic evaluation of milk, weight and reproductive traits in Guzerá cattle in tropical conditions.** Advisor: Paulo Sávio Lopes. Co-advisors: Fabyano Fonseca e Silva and Maria Gabriela Campolina Diniz Peixoto.

We aimed to estimate genetic parameters for 305-d milk yield (MY305), growth (weaning – WW, yearling – YW and long yearling weights - LYW) and reproductive (age at first calving - AFC) traits in Guzerá cattle by using Bayesian multi-trait models and compare methodologies for handling censored data of age at first calving by Bayesian models. Data were provided by Brazilian Association of Zebu Cattle (ABCZ) and Embrapa Dairy Cattle Research Unit in partnership with the Brazilian Center of Guzerá Genetic Improvement (CBMG²). The pedigree file (120,599 animals) included animals with phenotypic records and their known ancestors. Censored records were defined as AFC records out of range of 740 and 1860 days. Data including 69,157 AFC records were analyzed using seven different methods: conventional linear method (LM), simulation method (SM), penalty method (PM), a bitrait threshold-linear model considering (TLcens) or not (TLmiss) any prior information about censored records; and piecewise Weibull proportional hazards methodology considering (PWPHcens) or not (PWPH) censored records. For survival analyses, deviance information criterion (DIC) values suggested 0 and 2 piecewise change points in the baseline function of PWPH and PWPHcens methods, respectively. The additive genetic variance components estimated from LM, PM and TLmiss were similar. Heritability estimates for AFC ranged from 0.19 (TLcens) to 0.28 (SM) in non-survival approaches, and 0.40 and 0.46 to PWPH and PWPHcens methods, respectively. In general, genetic breeding values correlations from different methods and the percentage of selected bulls in common indicated moderate reranking, ranging from -0.28 (SM x PWPH) to 0.99 (TLmiss and LM). Comparisons based on cross-validation analyses, indicated TLmiss as a suitable alternative for predicting breeding values for AFC in this Guzerá population. In second chapter, systematic effects included sex and age at calving. The additive genetic and contemporary group (herd, year and season of birth) were included as random effects. Additionally, maternal genetic and permanent effects were included as random effects for weaning weight trait. Heritability estimates were 0.29 (MY305), 0.42 (WW), 0.49 (YW), 0.56 (LYW) and 0.25 (AFC). Genetic correlations between weight measures were higher than 0.83 and 0.25 (MY305 x WW), 0.32 (MY305 x YW) and 0.36 (MY305 x LYW) for

other traits. AFC trait was negatively genetically correlated with milk and weight measures. These results suggest that selection for milk yield do not jeopardize selection for beef and reproductive efficiency and AFC censored data could be included in genetic evaluation considering a threshold-linear model in Guzerá cattle.

GENERAL INTRODUCTION

The unrestricted use of methods to increase yield due to demand for foodstuff, such as improvements in environment, management practices and animal breeding efforts, tend to be recently criticized. Sustainability of livestock farming systems, concept that includes animal welfare, biodiversity, food safety and events related to climate change as greenhouse gas emissions have become important issues in recent years. In general, these concerns may conflict with profitability and sustainability of animal production. Adequate resources to support climate changes without put in risk the farmer's revenue are necessary. One of them is to use adaptable and versatility breeds, such as Guzerá cattle (Khan et al., 2011; Flysjö et al., 2012; Zehetmeier et al., 2012; Koknaroglu and Akunal, 2013).

Originated from India, Guzerá cattle are considered a dual-purpose breed in Brazil and have been used in a flexible way to produce animal protein. Farms that use dual-purpose animals to milk production, meat production or both are commonly found in small and marginal farmers in tropical areas. The main attempt is to increase the system profit from the sale of milk, calves and decreasing the feeding costs due to their adaptability to several environmental conditions. Recently, concerns about the effect of selection for one type of production system on another one are motivating investigations to measure correlated responses in Guzerá cattle. These investigations are necessary to integrate the genetic evaluations for milk and meat production traits aiming to provide joint information about the potential of the animals to produce both milk and meat (Nava-Trujillo et al., 2010; Peixoto et al., 2010; McManus et al., 2011). The knowledge of genetic parameters and correlated responses for milk and beef traits is important for designing specific dual-purpose breeding programs and conduct mating plans. It is

crucial to choose selection criteria genetically and favorably related with the selection objectives of the herds and identify genetically superior animals.

Female fertility has been neglected in breeding programs for decades (Madalena, 2008). The inclusion of reproductive traits on selection criteria is fundamental due to predominant poor fertility in Zebu breeds, characterized by a long postpartum anestrous period (Nava-Trujillo et al., 2010). The attempt is to select for sexual precocity in one of the most important fertility trait, the age at first calving (AFC). Lower AFC values are associated with heifer precocity, high lifetime productivity, high number of calves in a same period and allows higher genetic progress rate. Despite of easiness of routine recording, AFC data is not always appropriate to be used in genetic evaluation because of recording mistakes and non-occurrence or delay in communication of the event (parturition) at the moment of genetic evaluation. Usually, animals without AFC phenotype are ignored in routine genetic evaluation. However, their records can be reconsidered as censored observations (Tarrés et al., 2006). However, the analysis of censored traits requires non usual methodologies to be implemented in current genetic evaluation programs.

Therefore, in this study we aimed to apply and compare different methodologies that deal with censored AFC records and to estimate genetic parameters for growth (weaning - WW, yearling – YW, and long yearling weights – LYW), 305-days milk yield (MY305) and reproductive (age at first calving - AFC) traits in Guzerá cattle by using Bayesian multi-trait models.

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Chapter 1

Genetic evaluation of age at first calving for Guzerá beef cattle using linear and survival censored Bayesian models

ABSTRACT: The purpose of this study was to estimate genetic parameters and compare models for handling censored data of age at first calving (AFC) in Guzerá Brazilian beef cattle. Censored records were defined as AFC records out of range of 740 and 1860 days. Data including information of 69,157 Guzerá cows were analyzed using 7 different methods: conventional linear method (LM), considering only uncensored records; simulation method (SM), which data are augmented by drawing random samples from positive truncated normal distributions; penalty method (PM), in which a constant of 21 days was added to censored records; a bitrait threshold-linear method (TLcens) considering or not (TLmiss) prior information about censored records; and piecewise Weibull proportional hazards methodology considering (PWPHcens) or not (PWPH) censored records. For survival analysis, deviance information criterion (DIC) values suggested 0 and 2 piecewise change points in the baseline function of PWPH and PWPHcens models, respectively. Survival variance components were different compared to non-survival approaches. Among non-survival approaches, the additive genetic variance components estimated from LM, PM and TLmiss were similar, whereas SM and TLcens provided different estimates. Heritability estimates ranged from 0.19 (TLcens) to 0.28 (SM) in non-survival approaches, and 0.40 and 0.46 to PWPH and PWPHcens methods, respectively. In general, genetic breeding values correlations from different methods and the percentage of selected bulls in common indicated moderate reranking, ranging from -0.28 (SM x PWPH) to 0.99 (TLmiss and LM). Comparisons based on cross validation analyses, indicated TLmiss as a suitable alternative for predicting breeding value for AFC in this Guzerá population.

Key words: age at first calving, censored data, Guzerá cattle, metropolis Hastings algorithm, survival analysis, threshold analysis

INTRODUCTION

Age at first calving (AFC) is one of the most important traits high related to fertility and reproductive efficiency in cattle. Lower AFC is associated with heifer precocity and also high lifetime productivity. Despite of easiness of routine recording, AFC data is not always appropriate to be used in genetic evaluation because of recording mistakes and non-occurrence or delay in communication of the event (parturition) at the moment of genetic evaluation. Also, selection schemes which involve reproductive tools such as multiple ovulation and embryo transfer (MOET) nucleus implemented in Guzerá breed programs in Brazil, should have some influence in AFC data. Consequently, these AFC records should not be considered. Usually, animals without AFC phenotype are ignored in routine genetic evaluation. However, their records can also be reconsidered as censored observations (Tarrés et al., 2006).

The analysis of censored traits requires non usual methodologies to be implemented in current genetic evaluation programs. Among them, stand out the simulation of censored records, augmentation of censored records by adding a penalty, threshold in a bitrait analysis and survival analysis.

Methods based on simulation of censored data records are augmented by drawing random samples from positive truncated normal taking into account the systematic effects in the model (Donoghue et al., 2004; Korsgaard et al., 2003). The penalty methodology was proposed by Johnston and Bunter (1996) and consists in estimate information by adding a constant (number of days) to an alternative data. For AFC, 21 days are included to these alternative data, based on the assumption that the

heifer should be fertile in the subsequent estrous cycle. Bitrait analysis uses the censoring status (threshold trait) as a correlated trait to improve the accuracy of genetic parameter estimates. It assumes that a correlation between AFC and the censoring status might reduce the problem of nonrandom censoring. Finally, survival analysis assumes a hazard function that provides the probability of parturition occurrence to estimate missing AFC values. The Weibull distribution is preferred to describe this probability (Roxström & Strandberg, 2002) because it is very flexible, but other distributions based on cut points are also desirable to enable temporal probability changes (Casellas, 2007).

In this context, we aimed to apply the mentioned methodologies (simulation, augmentation by adding a penalty, threshold in a bitrait analysis and survival analysis) under a Bayesian framework for genetic evaluation of AFC (un)censored records in Guzerá cattle. These comparisons were accessed by predictive performance via cross-validation and goodness-of-fit measures.

MATERIALS AND METHODS

Data

Guzerá fertility data were provided by Brazilian Association of Zebu Cattle (ABCZ), Embrapa Dairy Cattle Research Corporation and Brazilian Center for the Guzerá Genetic Improvement (CBMG²) partnership, Brazil.

In this study, AFC trait was defined as the interval between birth and first parity of the cows. Data from females with AFC out of the range of 2 standard deviations by GC were considered as censored observations. After editing, the dataset was composed by 69,157 AFC records during the period of 1991 and 2012. This dataset were used with 2 different approaches: DS1: with mean and standard deviation of $1,265.50 \pm 226.94$, included only uncensored phenotypes; DS2: with 76,180 records with mean and

standard deviation of $1,312.93 \pm 264.36$ included uncensored and censored phenotypes (7,023 AFC censored records). For censored records, an alternative AFC value were obtained. In a first step were identified the highest AFC value within each contemporary group and the date of parturition associated. In a second step, these dates of parturition were assumed to the censored records and a new AFC record were computed. In totality, 230 contemporary groups (CG) were formed as the combination of herd, year and season of birth. Each CG, had at least 4 uncensored records. The pedigree file (104,588 animals) included animals with phenotypic record and their known ancestors.

Methodologies

Age at first calving (AFC) data were analyzed using 7 Bayesian methodologies that deal with censored phenotypic records in different ways.

Linear Method (LM) was based on uncensored AFC data (DS1). The LM was used to evaluate the scenario when censored records were not used. For this, consider the standard animal model:

$$\mathbf{y} = \mathbf{1}\mu + \mathbf{W}\mathbf{d} + \mathbf{Z}\mathbf{a} + \mathbf{e} \quad [1]$$

where $\mathbf{y}$ is the vector of AFC records; μ is the general mean; $\mathbf{d}$ is the vector of contemporary group (herd-year-season) effects; $\mathbf{a}$ is the vector of additive genetic effects; $\mathbf{e}$ is the residual vector; and $\mathbf{W}$ and $\mathbf{Z}$ are the incidence matrices associated with $\mathbf{d}$ and $\mathbf{a}$, respectively. It was assumed that $\mathbf{d} \sim N(\mathbf{0}, \mathbf{I}\sigma_d^2)$, $\mathbf{a} \sim N(\mathbf{0}, \mathbf{A}\sigma_a^2)$ and $\mathbf{e} \sim N(\mathbf{0}, \mathbf{I}\sigma_e^2)$, being $\mathbf{A}$ the numerator relationship matrix, σ_d^2 the contemporary group variance, σ_a^2 the additive genetic variance, $\mathbf{I}$ an identity matrix, and σ_e^2 the residual variance.

Imputation Method (SM) was similar to Eq. [1] using DS1, but for heifers with censored record, the methodology considers data simulation. Thus, $\mathbf{y} = \begin{bmatrix} \mathbf{y}_{ur} \\ \mathbf{y}_{cr} \end{bmatrix}$ is a vector in which $\mathbf{y}_{ur}$ is the vector of uncensored records of AFC, and $\mathbf{y}_{cr}$ the vector of simulated values for censored records. Using Gibbs sampling approach (Sorensen et al., 1998; Guo et al., 2001), $\mathbf{y}_{cr}$ were sampled from their respective predictive distributions. It was assumed that $\mathbf{y}_{cr}$ values followed a Gaussian truncated distribution whose lower limit is defined by the maximum values of AFC within the corresponding contemporary group. Thus, the augmented data $\mathbf{y}_{cr}$ were considered within each iteration of the Gibbs sampler as an observation for each censored record (Donoghue et al., 2004; Korsgaard et al., 2003).

Penalty Method (PM) was equivalent to SM, but censored records were replaced by a set of augmented records by adding a constant of 21 days over the alternative AFC value (DS2). The penalty suggested that the cows failing to become pregnant would conceive if they have another opportunity, as an extra estrous cycle (Donoghue et al., 2004; Hou et al., 2009).

Threshold – Linear (TLmiss) methodology represented a bitrait analysis where one trait is continuous (censored records are treated as missing records – DS1) and the another one was a threshold binary trait which indicates the censored status. The binary records were associated to liability values representing latent continuous records (Sorensen and Gianola, 2002). At each MCMC iteration, the binary records generate a liability value below or over a given threshold. Considering the linear model [1], this model can be adapted considering $\mathbf{y}' = [\mathbf{y}_{ur} \quad \mathbf{0}]$:

$$\begin{bmatrix} \mathbf{y} \\ \mathbf{l} \end{bmatrix} = \mathbf{1}\mu + \begin{bmatrix} \mathbf{W}_y & \mathbf{0} \\ \mathbf{0} & \mathbf{W}_l \end{bmatrix} \begin{bmatrix} \mathbf{d}_y \\ \mathbf{d}_l \end{bmatrix} + \begin{bmatrix} \mathbf{Z}_y & \mathbf{0} \\ \mathbf{0} & \mathbf{Z}_l \end{bmatrix} \begin{bmatrix} \mathbf{a}_y \\ \mathbf{a}_l \end{bmatrix} + \begin{bmatrix} \mathbf{e}_y \\ \mathbf{e}_l \end{bmatrix} \quad [2]$$

where $\mathbf{y}$ is the vector of AFC records; $\mathbf{y}_{ur}$ representing uncensored records; $\mathbf{l}$ is the vector of liability predisposition of censored status; $\mathbf{W}, \mathbf{Z}, \mathbf{d}, \mathbf{a}$ and $\mathbf{e}$ as defined previously, but specific to AFC records or liability predisposition. The following distributions were assumed:

$$\begin{bmatrix} \mathbf{a}_y \\ \mathbf{a}_l \end{bmatrix} \sim N(\mathbf{0}, \mathbf{G}_0 \otimes \mathbf{A}), \begin{bmatrix} \mathbf{d}_y \\ \mathbf{d}_l \end{bmatrix} \sim N(\mathbf{0}, \mathbf{D}_0 \otimes \mathbf{I}) \text{ and } \begin{bmatrix} \mathbf{e}_y \\ \mathbf{e}_l \end{bmatrix} \sim N(\mathbf{0}, \mathbf{R}_0 \otimes \mathbf{I})$$

where $\mathbf{G}_0$ and $\mathbf{R}_0$ are the additive genetic and residual (co)variance matrix, respectively as proposed by Varona et al. (1999); and, $\mathbf{D}_0$ is the (co)variance matrix for CG effects.

Threshold – Linear censored (TLcens) methodology represents the same model described in Eq. [2], however despites of missing values, $\mathbf{y}' = [\mathbf{y}_{ur} \ \mathbf{y}_{al}]$, where y_{al} are the alternatives AFC records (DS2).

Piecewise Weibull Proportional Hazards (PWPH) methodology was included in the survival analysis context. The Weibull distribution was assumed as the baseline hazard function for the observed value. The data assumed (DS1) for the animal i are (t_i, δ_i) , where t_i is the vector of uncensored records and δ_i is a censure indicator random variable (Casellas, 2007). The baseline hazard function can be written as:

$$h_0(t) = \lambda \rho (\lambda t)^{\rho-1}. \quad [3]$$

Considering $\boldsymbol{\theta}' = [\mu', \mathbf{d}', \mathbf{a}']$ and $\mathbf{U}' = [\mathbf{W}', \mathbf{Z}']$, the Eq. [3] can be rewritten conditionally to $\boldsymbol{\theta}$ as follows:

$$h(t|\boldsymbol{\theta}) = h_0(t) \exp(\boldsymbol{\theta} \mathbf{U}) \quad [4]$$

where $\mathbf{h}(\mathbf{t}|\boldsymbol{\theta})$ is the vector of hazard functions which compute the limiting probability of the parturition at time t for a heifer given $\boldsymbol{\theta}$; $\mathbf{h}_0(\mathbf{t})$ is a Weibull baseline hazard function of time t with a positive scale parameter λ and a shape parameter ρ .

This Weibull model was modified allowing the baseline to assume several unknown change points along the parametric space. The number of change points is predefined and are estimated simultaneously with the other parameters under a Bayesian framework (Yazdi et al., 2002; Tarrés et al., 2005; Casellas, 2007).

The Bayesian inference on PWPH is accessed by multiplying the likelihood function by the prior distributions of all parameters as follows:

$$p(\mathbf{b}, \mathbf{d}, \mathbf{a}, \sigma_a^2, \sigma_d^2, \rho, \lambda, \boldsymbol{\tau} | \mathbf{y}) \propto p(\mathbf{y} | \mathbf{b}, \mathbf{d}, \mathbf{a}, \rho, \lambda, \boldsymbol{\tau}) \quad [5]$$

$$\times p(\mathbf{b})p(\mathbf{d} | \sigma_d^2)p(\sigma_d^2)p(\mathbf{a} | A, \sigma_a^2)p(\sigma_a^2)p(\rho)p(\lambda)p(\boldsymbol{\tau}),$$

where $\boldsymbol{\tau}$ is the vector of c change points ($c \geq 2$) homogeneously distributed by quantiles, assuring the same number of sorted phenotypic records between two adjacent change points. The τ_1 was fixed to 0, τ_c equaled the maximum value in vector $\mathbf{y}$, and $\tau_j < \tau_{j+1}$.

Following Damgaard and Korsgaard (2006), bounded uniform priors were assigned to ρ, λ and τ , whereas remaining prior distributions were defined as for the other methodologies. The PWPH methodology was implemented by assuming an increasing number of change points ($0 \leq c \leq 4$) and the most desirable number of c was selected according to Deviance Information Criterion (DIC), defined by Spiegelhalter et al. (2002).

Piecewise Weibull Proportional Hazards Censored (PWPHcens) methodology

represents the same previously methodology, however includes censored data by adding prior information, $\mathbf{t}' = [\mathbf{t}_{ur} \quad \mathbf{t}_{al}]$, where $\mathbf{t}_{al}$ are the alternative AFC records (DS2).

Markov Chain Monte Carlo (MCMC) Sampling

Inferences about all unknown parameters were done from the marginal posterior distributions. Gibbs Sampler (Gelfand and Smith, 1990) with Metropolis-Hastings (Metropolis et al., 1953; Hastings, 1970) steps in PWPH methodology were used implemented in SAC 1.5 software (Casellas, 2007). For other methods, only Gibbs sampling algorithm was used through TM software (Legarra et al., 2008). More specifically, a unique MCMC process with 100,000 iterations was launched for each analysis, and the first 20,000 iterations were discarded as burn-in keeping every 50th sample for inference of posterior features. Convergence was monitored by graphical inspection and R package BOA (Smith, 2005).

Methods Comparisons

Due to a difference in scale between estimated breeding values (EBV) of survival analysis and other methods, the observed and predicted uncensored phenotypes were used to compare them. The cross-validation approach was used. Training population was composed by censored and uncensored records. 30% of uncensored records were set to missing and their predicted phenotypes were compared with observed phenotypes. These populations were randomly redefined 10 times within contemporary groups. The predicted phenotype value of animal i for age at first calving was calculated as $\hat{Y} = X\hat{\beta} + Z\hat{u}$. Pearson correlations, mean square errors and regression analyses between observed and predicted uncensored phenotypes were estimated to access the predictive ability of methodologies.

Spearman's rank correlation coefficients between estimated breeding values from several methodologies (using the complete data record) were computed to

compare differences in the ranking of animals provided by each method. In addition, the percentage of sires (with at least one daughter) selected in common at different percentiles (TOP1% and TOP10%) based on the compared methods were also calculated.

RESULTS AND DISCUSSION

PWPH models comparison

Goodness-of-fit analyses for 5 alternative parametrizations ($0 \leq c \leq 4$ change points) of PWPH and PWPHcens methods were evaluated using deviance information criterion (DIC). The DIC values for PWPH analysis from 0 to 4 change points were 1,247,055; 1,251,001; 1,246,580; 1,248,432 and 1,257,111, respectively. For PWPHcens methodology the DIC values from 0 to 4 change points were: 1,646,395; 1,659,998; 1,663,677; 1,659,015 and 1,663,660, respectively. When using censored data (PWPHcens approach), the DIC values suggested that no additional change points in the baseline function were required, only the boundaries points (i.e., 0 and 1860 d). However, for PWPH approach without censored records, a more parametrized model was necessary to properly fit the distribution of AFC data (2 number of change points).

Baseline Function Parameters for AFC Data

At least two parameters, ρ and λ , were required to characterize the piecewise Weibull function and are summarized in Table 1. The ρ parameter modulates the shape of the distribution and was higher for PWPH₀cens method than PWPH₂, evidence of the influence of trait distribution patterns in survival analysis. According to Casellas and Bach (2012), higher values of ρ were related with asymmetric curves, as observed for DS2 (APPENDIX). When $\rho > 1$, as observed in this study, the hazard increases with

time (Boettcher et al. 1999), meaning that older the heifers become, higher the chance of reaching sexual maturity and become pregnant.

Table 1. Posterior mean, standard deviation and highest posterior density region (95%) for the parameters of the piecewise Weibull proportional hazard models

Parameter ¹	PWPH ₂ ²	PWPH _{0cens} ²
ρ	6.94 (0.05)	7.05 (0.05)
	[6.84, 7.05]	[6.94, 7.13]
$\lambda \times 1000$	0.60 (0.01)	0.54 (0.01)
	[0.59, 0.62]	[0.52, 0.55]
τ_2	1,020 $\pm$ 1.30	-
	[1,018, 1,022]	
τ_3	1,572 $\pm$ 0.21	-
	[1,571, 1,573]	

¹ ρ and λ : Weibull-specific parameters; τ_k : kth change points. All models included two additional points, $\tau_1 = 0$ and $\tau_{k+1} = 1980$ days.; ²the number of change points was fixed to 0 (PWPH) and 2 (PWPHcens) change points according to DIC results.

It is important to emphasize that these values provide the first estimates about proportional hazards analysis for AFC data in Guzerá cattle. The PWPH methodology had not been tested in cattle fertility traits. Lambing interval in ewes (Casellas and Bach, 2012), sow longevity (Casellas et al., 2008) and simulated dataset (Casellas, 2007; Casellas, 2011) are some of examples dataset which applied PWPH methodology. Theoretically, the piecewise reparametrization in survival analysis based on Weibull baseline increases the flexibility of the model to fit real survival data.

Others survival approaches were used in reproductive simulated dataset (Schneider et al., 2005). Pereira et al. (2007) found lower values of ρ for AFC trait in Zebu Nellore cattle in comparison with the present study.

Variance components

Posterior means, standard deviation and highest posterior density (HPD95%) interval for genetic parameters under the different methods of handling censored data are presented in Table 2. Estimates of genetic parameters provided the first comparison of the used models. The LM only considers AFC uncensored values and its results should be used as reference (simplest model). The HPD95% interval exclude the null value in all parameters, highlighting the statistical relevance of the random sources of variance, as contemporary group effect.

Table 2. Posterior means, standard deviation and highest posterior density interval (HPD95%) of genetic parameters for AFC trait

Method ²	CVC ¹			
	h^2*	σ_a^2	σ_d^2	σ_e^2
LM	0.26 (0.01) [0.25, 0.28]	19,617.46 (568.70) [18,578.95, 20,790.14]	6,277.02 (644.16) [5,067.28, 7,604.48]	48,900.01 (435.65) [48,041.00, 49,712.81]
SM	0.28 (0.01) [0.27, 0.30]	49,370.57 (1,108.85) [47,195.50, 51,540.91]	32,233.76 (2,601.06) [27,527.90, 37,615.27]	91,999.26 (830.59) [90,288.76, 93,588.29]
PM	0.25 (0.01) [0.23, 0.26]	21,299.24 (563.69) [20,119.11, 22,337.36]	12,102.18 (1,140.93) [11,024.03, 15,420.95]	53,370.49 (459.02) [52,491.59, 54,321.55]
TLmiss	0.25 (0.01) [0.24, 0.27]	18,720.01 (567.00) [17,662.69, 19,872.40]	6,019.29 (630.42) [4,809.97, 7,332.29]	49,488.00 (463.42) [48,536.51, 50,428.08]
TLcens	0.19 (0.01) [0.18, 0.20]	15,999.64 (410.55) [14,145.28, 16,757.71]	13,800.89 (1,131.05) [11,431.68, 15,777.33]	54,000.91 (371.43) [53,618.95, 55,086.87]
PWPH ₂	0.40* (0.01) [0.38, 0.42]	1.38 (0.04) [1.28, 1.43]	0.26 (0.03) [0.22, 0.32]	-
PWPH ₀ cens	0.46* (0.01) [0.47, 0.52]	2.30 (0.06) [2.17, 2.42]	1.1 (0.11) [0.91, 1.30]	-

*heritability on the original scale calculated as proposed by Korsgaard et al. (1999) as $h^2 = \sigma_a^2 / [\sigma_a^2 + \sigma_d^2 + (\pi^2/6)]$; ¹CVC=(co)variance components: h^2 = heritability, σ_a^2 , σ_d^2 and σ_e^2 = additive genetic, contemporary group and residual variance, respectively; ²methods: LM, SM, PM, TLmiss, TLcens, PWPH₂, PWPH₀cens: linear, simulation, penalty, threshold-linear, threshold-linear censored, piecewise Weibull proportional hazard (fixed $c = 2$) and piecewise Weibull proportional hazard censored (fixed $c = 0$) methodologies.

Clearly, parameter estimates could be classified in two main groups: non-survival and survival approaches. This is due to the method nature, because PWPH is a class of survival analysis models and the parameters are based on a hazard rate scale. Among non-survival approaches (LM, SM, PM, TLmiss and TLcens), posterior means of the additive variance under LM, PM and TLmiss were similar, because estimates were within the highest posterior density interval of the other method. The corresponding estimate for SM and TLcens methods, however, was significantly higher and lower than these estimates, respectively, and was outside the HPD95% interval for both LM, PM and TLmiss methodologies. Because the SM method was based on obtain random numbers obtained in a a truncated normal distribution, includes an important source of variation, it was expected that this method would produce higher estimates for additive variance. Urioste et al. (2007a) found similar additive genetic and residual variances estimates between SM and PM for other reproductive trait. Probably, the correlation generated by trivariate analysis used for this author could have influenced the variance estimates. Posterior means of the residual variance for LM and TLmiss were the smallest, whereas the estimate under SM was the highest value. These results imply that LM and TLmiss methods provide a better fit to the data than the other non-survival methods when censored records are presented. For all parameters presented, LM and TLmiss were similar, representing the correspondence among the simplest method and threshold analysis. The TLmiss and TLcens model had genetic correlation of 0.42 ± 0.10 and 0.42 ± 0.03 , between the trait representing in linear or threshold way. Genetic correlation considered between data and censored status could be influencing in results, providing low estimates of additive genetic variance in the TLcens model. It clarifies the influence of values assumed for censored records in a threshold analysis. The advantage using models that included censored data in

threshold methods and their correspondence to uncensored predicted phenotype, should be considered in a genetic evaluation.

The non-survival approaches showed similar estimates of heritability, except for TLcens method. Heritability estimates for AFC trait from field data reported in the literature also oscillate as observed in the present study, ranging from 0.10 to 0.37 in Brazilian Zebu cattle (Boligon and Albuquerque, 2011; Barrozo et al., 2012; Moreira et al., 2015). Van Melis et al. (2010) indicates that the high genetic variability observed appears to be a characteristic of *Bos indicus* cattle population, because the breed has rarely been selected for sexual precocity. The heritability results under threshold analysis conflicts with some authors (Johnston and Bunter, 1996; Morris et al., 2000; Phocas and Sapa, 2004). They affirm that the use of threshold models generate higher estimated heritability than those obtained by linear models. However, in the present study TLcens method were significantly lower to the other methods and TLmiss heritability estimate were within the range for this parameter to the other methods.

The interpretation of heritability in the case of survival analysis has been in discussion (Yazdi et al., 2002; Pereira et al., 2007), because there is no linear decomposition of phenotypic variance in the survival model (Guo et al., 2001). It must be noted that heritability on the original scale for PWPH models proposed by Korsgaard et al. (1999) were not appropriate in this population, due to high values of heritability, mainly to a reproductive trait. Pereira et al. (2007) using a sire model, also find high values of heritability while using survival approach for Nellore cattle in the same trait (0.51). Among PWPH methods, highest value of heritability were observed in PWPH_{0cens} method. Pereira et al. (2006) affirms that this is a result of using additional information for censored data.

The predictive ability was validated by correlation coefficients, mean square error and bias (regression between observed and predicted phenotype) using cross-validation approach (Table 3). Standard deviations across models suggest precise inference for these results.

Table 3. Average mean square error (MSE), correlation coefficient and bias with respective standard deviation obtained from cross-validation analysis

Comparison method			
Method ¹	MSE	Correlation	Bias
LM	63,087.19 (294.32)	0.43 (0.0033)	0.99 (0.0141)
SM	110,903.6 (961.42)	0.40 (0.0047)	0.43 (0.0047)
PM	65,277.25 (479.21)	0.43 (0.0037)	0.81 (0.0105)
TLmiss	62,987.62 (293.64)	0.44 (0.0034)	1.01 (0.0156)
TLcens	67,816.38 (256.00)	0.39 (0.0047)	0.80 (0.0114)
PWPH ₂	71,176.51 (293.64)	0.40 (0.0031)	0.92 (0.0562)
PWPH ₀ cens	81,120.18 (479.09)	0.30 (0.0051)	0.55 (0.0067)

¹methods: LM, SM, PM, TLmiss, TLcens, PWPH₂, PWPH₀cens: linear, simulation, penalty, threshold-linear, threshold-linear censored, piecewise Weibull proportional hazard (fixed $c = 2$) and piecewise Weibull proportional hazard censored (fixed $c = 0$) methodologies, respectively.

Higher correlations and lower MSE and bias were found to TLmiss method, indicating that this is recommended to be used in AFC genetic evaluation with censored records in Guzerá cattle. The absence of previous information about AFC censored records and the genetic correlation among AFC data and censored status provide a slightly

advantage compared to others approaches. These results corroborates with Alison (2010), who affirms that for predictors been adequately obtained, missing data should be influenced by observed values and not depend on any prior information, and this relation between real and censored values should be done by a censoring indicator variable, as well as in threshold analysis. However, Urioste et al. (2007b) found higher computational requirements for threshold analysis compared to linear models and convergence problems while using large data sets with threshold analysis could be a difficulty to transpose.

The survival analysis was not the best choice when handling AFC trait in Guzerá cattle, because PWPH models had predictive ability worse than others methods. However, the literature affirms that PWPH model provides a more flexible framework to accommodate both positive and negative asymmetry in the data (APPENDIX 1). Casellas and Bach (2012) in their study indicate PWPH method as the best for lambing interval in Ripolesa ewes. In this study, high values of heritability observed in PWPH models were not a sign of better adjustment of the data to survival model, as proposed by Pereira et al. (2007). Probably, heritability formula should be reviewed and depends on each genetic model and trait dataset used.

Within-methods Spearman correlation coefficients and percentage of selected bulls in common (considering different percentiles, TOP1% and TOP10%) between genetic breeding values predicted from survival and non-survival methodologies are shown in Table 4.

Table 4. Spearman correlation of all animals (above diagonal) and sires (below diagonal) predicted breeding values of AFC trait and percentage of sires in common between models at 1% (above diagonal) and 10% (below diagonal) selection percentages

Method ¹	LM	SM	PM	TLmiss	TLcens	PWPH ₂	PWPH ₀ cens
Spearman correlations							
LM	-	0.88	0.98	0.99	0.96	-0.61	-0.59
SM	0.82	-	0.92	0.90	0.88	-0.55	-0.70
PM	0.96	0.88	-	0.98	0.94	-0.59	-0.61
TLmiss	0.99	0.87	0.98	-	0.96	-0.60	-0.63
TLcens	0.96	0.85	0.93	0.98	-	-0.57	-0.58
PWPH ₂ ²	-0.30	-0.28	-0.29	-0.30	-0.30	-	0.77
PWPH ₀ cens ²	-0.34	-0.35	-0.33	-0.34	-0.36	0.45	-
Percentage of sires in common							
LM	-	37.21	86.04	93.02	67.44	2.32	6.98
SM	65.27	-	39.53	41.86	30.23	0.0	2.32
PM	89.12	69.91	-	90.70	65.11	2.33	6.98
TLmiss	94.44	69.68	90.74	-	67.44	2.32	6.98
TLcens	85.88	62.5	80.79	84.72	-	2.32	9.30
PWPH ₂ ²	26.62	21.76	27.08	25.93	27.55	-	41.86
PWPH ₀ cens ²	19.44	18.52	19.91	18.98	19.44	45.60	-

¹method: LM, SM, PM, TLmiss, TLcens, PWPH₂, PWPH₀cens: linear, simulation, penalty, threshold-linear, threshold-linear censored, piecewise Weibull proportional hazard (fixed $c = 2$) and piecewise Weibull proportional hazard censored (fixed $c = 0$) methodologies; ²EBV's on original survival scale.

The use of rank rather than Pearson correlation solves the scale issue of PWWP models and EBVs could be compared. However, the comparison of non-survival methods with PWWP methods provided negative correlations estimates, due to the inverted interpretation necessary to PWWP methods as consequence of the relative risk scale presented by EBV results. Low values of EBV are desirable for AFC trait in non-survival methods and the opposite happens with survival methods.

Despite of different predictive abilities and parameter estimates observed, the Spearman correlations among non-survival methods were similar, indicating that no major reranking would be expected across these methodologies. These similarities and another previously results suggests that either approaches (PM and TLmiss) could be used for genetic evaluations of AFC trait. Simulation method appears to be the only one among non-survival methods that present some difference in comparison to others non-survival methods. The correlations between non-survival and PWWP models were moderate, ranged from -0.70 to -0.55. These results indicate moderate reranking of animals in PWWP analysis versus non-survival methodologies. Similar results were found by Casellas and Bach (2012), which also assessed the agreement between models. Higher correlations were found by Pereira et al. (2007) studying age at first conception in Nellore cattle population. Considering just the sires, the correlation was even lower, as expected. However, the same author affirm that it is necessary to remember that the lower the number of animals considered, the more sensitive is the Spearman correlation to slight changes in classification.

The percentages of sires in common were higher between LM and PM, LM and TLmiss and PM and TLmiss. Among the other methods, it was observed a remarkable loss in efficiency of selection when the censoring models were applied. These percentages were even smaller when only TOP1% of sires were considered, showing a greater change in the

position. We can infer that the choice of methodology in the present study had large effect in the identification of the best animals in this population.

CONCLUSIONS

A threshold linear method was the more accurate for genetic evaluation of age at first calving trait in Guzerá cattle. Presented more consistent predictions of breeding values, enabling the use of all missing records without any previous information about censored records. Penalty method is also an alternative method to genetic evaluations for age at first calving data.

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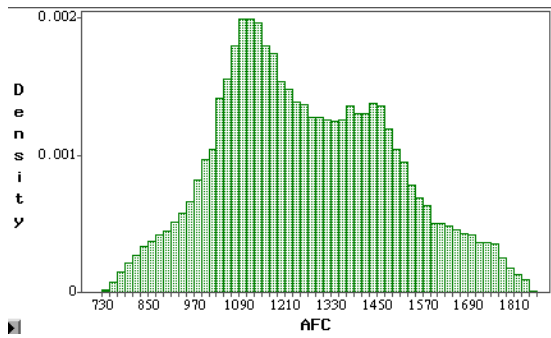
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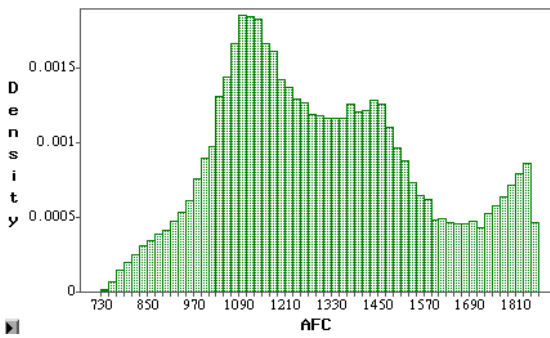
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APPENDIX 1: Distribution of datasets

DS1



DS2



Chapter 2

Genetic relationship estimates among milk, weight and reproductive traits of Guzera cattle in tropical conditions

ABSTRACT: We aimed to estimate genetic parameters for milk (305-days milk yield - MY305), weight (weaning - WW, yearling - YW and long yearling weights - LYW) and reproductive (age at first calving - AFC) traits in Guzera cattle by using Bayesian multi-trait models. Systematic effects included sex and age at calving for weight and milk traits, respectively. The additive genetic and contemporary groups (herd-year-season of birth) were included as random effects. Additionally, maternal genetic and permanent effects were included as random effects for weaning weight trait. Heritability estimates were 0.29 (MY305), 0.42 (WW), 0.49 (YW), 0.56 (LYW) and 0.25 (AFC). Genetic correlations among weight measures were higher than 0.83 and between MY305 x WW was 0.25, MY305 x YW was 0.32 and MY305 x LYW was 0.36. Age at first calving was negatively correlated with milk and weight measures. These results suggest that selection for milk yield do not jeopardize selection for growth and reproductive traits.

Key words: age at first calving, Bayesian inference, genetic correlation, Guzera cattle, growth, milk yield

INTRODUCTION

Dual-purpose production systems allow profits both from sale of milk and calves, characterizing a flexible and attractive production system. Dual-purpose cows are important because these animals serve as the main source of animal protein (milk and meat) in many tropical countries (Nava-Trujillo et al., 2010; McManus et al., 2011). In this context, Guzera breed is considered a dual-purpose cattle in Brazil, since it has been

selected for economically important traits for beef, dairy or both production systems traits over the years. Guzerá breeding programs for beef and milk purposes were independently implemented in 1993 and 1994, respectively and continue to be conducted separately in Brazil, despite being connected genetically.

Recently, concerns about the effect of selection for each production system traits are motivating investigations to measure correlated responses in Guzerá cattle. These investigations are necessary not only to access the relationship among traits, but mainly to integrate the genetic evaluations for milk and beef purposes. This joint evaluation is feasible due to the genetic connection that exists between pedigree datasets of Guzerá breed programs (Bruneli et al., 2014; Peixoto et al., 2010). The knowledge of genetic parameters and correlated responses for milk and weight traits is important for designing specific dual-purpose breeding programs and conducting mating plans. It is crucial to choose selection criteria genetically and favorably related with the selection objectives of the herds and identify genetically superior animals.

The inclusion of reproductive traits on selection criteria is also fundamental due to poor fertility and reproductive efficiency observed in Zebu breeds (Nava-Trujillo et al., 2010). One attempt is to improve sexual precocity by selection on age at first calving (AFC), one of the most important and usual trait related to fertility and reproductive efficiency. Lower AFC values are associated with heifer precocity, high lifetime productivity and allows higher genetic progress rate (Bazzoli et al., 2014).

Considering these, we aimed to estimate genetic parameters for growth (weaning - WW, yearling - YW, and long yearling weights - LYW), 305-days milk yield (MY305) and reproductive (age at first calving - AFC) traits in Guzerá cattle by using Bayesian multi-trait models.

MATERIALS AND METHODS

Data

The phenotypic measurements and pedigree information used in this study were from the database of the Brazilian Breeding Program for the Guzará Cattle carried out by a partnership between Brazilian Association of Zebu Cattle (ABCZ), Embrapa Dairy Cattle and Brazilian Center for the Guzará Genetic Improvement (CBMG²). The pedigree file (120,599 animals) included animals with phenotypic records and their known ancestors. The following traits were analyzed: 305-days milk yield (MY305) at first lactation, weaning weight (WW), yearling weight (YW), long yearling weight (LYW) and age at first calving (AFC).

The 305-day lactation records were previously adjusted for mature age. Ongoing lactation records over 140 days before the evaluation date were extrapolated to the mean of the breed lactation length of 278 days using projection factors, conventionally used in the genetic evaluations of the breeding program. Body weights were adjusted to 120 (WW), 365 (YW) and 550 (LYW) days of age considering the age at measurement, age of dam and previously weight, according to BIF Guidelines (2010). The age at first calving, in months, was obtained by calculating the difference between the date of the first calving and the cow birth date. The contemporary groups were formed by herd + year of birth + season of birth for weight and AFC traits. The contemporary groups for MY305 trait were formed by herd + year of calving + season of calving. Birth or calving season was defined as 1 (from April to September – dry season) and 2 (from October to March – rainy season). For all traits, records outside the range determined by the mean of the contemporary group plus or minus two standard deviations, and contemporary groups fewer than four

observations were excluded. After constrains, records of Guzerá animals born between 1991 and 2014 were used.

Multi-trait Analysis

The (co)variance components were estimated by Bayesian inference and the traits were analyzed in pairs using two-trait analysis in which $Q = f(f - 1)/2$, where Q is the number of realized analyses ($Q=10$) and f is the number of traits ($f=5$). The contemporary groups ($\mathbf{h}$) and direct additive genetic ($\mathbf{a}$) effects were considered for all traits; and extra effects of maternal genetics ($\mathbf{m}$) and maternal permanent environmental ($\mathbf{p}$) were assumed only for weaning weight. The age of dams at calving were considered as systematic covariate for 305-days milk yield and for weight traits (WW, YW and LYW), while sex was included only for weight traits. In this context, the following full model [1] was assumed:

$$\mathbf{y} = \mathbf{X}\boldsymbol{\beta} + \mathbf{W}\mathbf{h} + \mathbf{Z}_1\mathbf{a} + \mathbf{Z}_2\mathbf{m} + \mathbf{Z}_3\mathbf{p} + \mathbf{e}, \quad [1]$$

where $\mathbf{y}$ is a vector of observations for both traits; $\boldsymbol{\beta}$ is a vector of systematic effects; $\mathbf{X}$ is an incidence matrix for systematic effects; $\mathbf{W}$, $\mathbf{Z}_1$, $\mathbf{Z}_2$ and $\mathbf{Z}_3$ are incidence matrices to contemporary group, direct additive genetic, maternal additive genetic and maternal permanent environmental effects, respectively; $\mathbf{h}$, $\mathbf{a}$, $\mathbf{m}$ and $\mathbf{p}$ were defined previously; and $\mathbf{e}$ is a vector of residual effects.

Uniform prior distribution was defined for systematic effects ($\boldsymbol{\beta}$). Multivariate Gaussian distributions (MVN), inverted Wishart (IW) and inverted chi-square (χ^{-1}) were defined as prior distributions for effects and (co)variance components, as follows:

$$\begin{aligned}
\mathbf{h} &\sim MVN(\mathbf{0}, \mathbf{H} \otimes \mathbf{I}_n) & \sigma_m^2 | S_m, n_m &\sim \chi^{-1}(S_m, n_m) \\
\mathbf{H} | V_h, \mathbf{v}_h &\sim IW(V_h, \mathbf{v}_h) & \mathbf{p} | \sigma_p^2 &\sim MVN(\mathbf{0}, \sigma_p^2 \mathbf{I}) \\
\mathbf{a} | \mathbf{G}_0, \mathbf{A} &\sim MVN(\mathbf{0}, \mathbf{G}_0 \otimes \mathbf{A}) & \sigma_p^2 | S_p, n_p &\sim \chi^{-1}(S_p, n_p) \\
\mathbf{G}_0 | V_g, \mathbf{v}_g &\sim IW(V_g, \mathbf{v}_g) & \mathbf{e} | \mathbf{R}_0 &\sim MVN(\mathbf{0}, \mathbf{R}_0 \otimes \mathbf{I}_n) \\
\mathbf{G}_0 = \begin{bmatrix} \sigma_{a1}^2 & \sigma_{a12} \\ \sigma_{a12} & \sigma_{a2}^2 \end{bmatrix} & & \mathbf{R}_0 | V_r, \mathbf{v}_r &\sim IW(V_r, \mathbf{v}_r) \\
\mathbf{m} | \sigma_m^2, \mathbf{A} &\sim MVN(\mathbf{0}, \sigma_m^2 \mathbf{A}) & \mathbf{R}_0 = \begin{bmatrix} \sigma_{e1}^2 & \sigma_{e12} \\ \sigma_{e12} & \sigma_{e2}^2 \end{bmatrix} &
\end{aligned}$$

where $\mathbf{H}$ is a known diagonal matrix with values $1e+10$ (large variances) to represent vague prior distributions knowledge; $\mathbf{I}_n$ is the identity matrix whose order is the number of observations; $\mathbf{G}_0$ is the additive genetic (co)variance matrix; $\mathbf{A}$ the additive relationship matrix among the animals; σ_{ai}^2 and σ_{ei}^2 are the additive genetic and residual variance for trait $i, i = 1, 2$; σ_{a12} and σ_{e12} are the additive genetic and residual covariance between trait 1 and 2; σ_m^2 and σ_p^2 are the variance for maternal genetics and maternal permanent environmental effects, respectively; S_m, S_p, V_h, V_g and V_r are the hyperparameters values of the variances; $n_m, n_p, \mathbf{v}_h, \mathbf{v}_g$ and $\mathbf{v}_r$ are their corresponding prior “degrees of belief”; $\mathbf{R}_0$ is the residual (co)variance matrix; and $\mathbf{I}$ an identity matrix of appropriate order.

Parameter estimation

(Co)variance components and genetic parameters were estimated via MCMC Bayesian approach using the Gibbs Sampler algorithm with GIBBS3F90 software (Misztal, 2012). A total of 100,000 samples were generated in the analyses and a burn-in period of 10,000 samples was used with samples taken each 10 cycles. Convergence was verified through graphical inspection (trace-plots) and also using R package BOA (Smith, 2005).

The descriptive statistic (mean) of posterior distribution for each parameter was obtained from effective samples. The highest posterior density (HPD95%) region provides the interval that includes 95% of samples. The posterior marginal distribution samples for heritability and genetic correlations were obtained from the variance components estimates generated in each MCMC iteration (k) as follow: $h_1^{2(k)} = \sigma_{a1}^{2(k)} / (\sigma_{a1}^{2(k)} + \sigma_{h1}^{2(k)} + \sigma_{m1}^{2(k)} + \sigma_{p1}^{2(k)} + \sigma_{e1}^{2(k)})$ and $r_{a12}^{(k)} = \sigma_{a12}^{(k)} / \sqrt{\sigma_{a1}^{2(k)} \sigma_{a2}^{2(k)}}$.

RESULTS AND DISCUSSION

Descriptive Statistics

The descriptive statistics and number of individuals for the studied traits are shown in Table 1. The small number of yearling and long yearling records compared to weaning records is expected because generally in beef herds, culling generally occurs at weaning and the number of records measured in advance ages are lower than in previously ages (Mota et al., 2013). Despite of that, for weaning weight more than 51% of animals were also evaluated for long yearling weight. The recently phenotypic evaluation for dual-purpose is verified by the number of conjoint records for weight and milk traits. It should be highlighted the importance of this type of data to accurately estimate genetic parameters and consequently assist in selection decisions. It is necessary to reinforce the importance of data collection and to encourage dual-purpose herds to participate and provide data to dairy and beef Guzerá breed programs (Peixoto et al., 2010; Bazolli et al., 2014; Peixoto et al., 2014).

The decrease on AFC phenotypic value allows an increase in genetic progress rate in any cattle production systems. It should be highlighted that in some regions in Brazil (e.g. in northeast) it is known that AFC values in Guzerá cattle are normally higher than

others due to management system adopted and the adversity of environmental conditions. Improvements in cattle fertility, as the decrease in AFC phenotypic values, could increase income from meat production due to surplus calves and culled cows (Bazzoli et al., 2014).

Table 1. Number of records (N), means and standard deviation (SD), number of contemporary groups (CG) and number of animals with records in common in traits (n) in Guzerá cattle.

Traits ¹	N	Mean ± SD	CG
WW (kg)	35,020	172.94 ± 34.79	225
YW (kg)	22,513	223.75 ± 52.69	210
LYW (kg)	18,113	291.82 ± 68.34	198
AFC (days)	69,157	1265.50 ± 226.94	230
MY305 (kg)	2,968	1997.75 ± 1084.83	121
Traits ²	n	Traits ²	n
WW x YW	22,513	YW x AFC	21,875
WW x LYW	18,113	YW x MY305	657
WW x AFC	15,406	LYW x AFC	9,388
WW x MY305	798	LYW x MY305	563
YW x LYW	18,095	MY305 x AFC	2,145

¹ WW, weaning weight; YW, yearling weight; LYW, long yearling weight; AFC, age at first calving; MY305, 305-days milk yield.

² traits combination

Heritabilities, Genetic and Phenotypic correlations

From bi-trait analysis, average posterior means of variance components, heritability coefficients, genetic and phenotypic correlation among weaning, yearling and long yearling weights, age at first calving and first lactation 305-d milk yield are presented in Table 2. To our knowledge literature does not report genetic correlation among weight traits and milk yield in Guzerá breed. Results of the present study can be considered an original set of knowledge useful for genetic selection in dual-purpose systems.

Table 2. Average posterior means and 95% highest posterior density region of direct heritability (diagonal), genetic correlations (above the diagonal) and phenotypic correlations (below the diagonal) estimates among WW, YW, LYW, AFC and MY305 and variance components.

Traits ¹	WW	YW	LYW	AFC	MY305
WW	0.42 (0.39; 0.45)	0.85 (0.83; 0.87)	0.83 (0.81; 0.86)	-0.58 (-0.62; -0.54)	0.25 (0.1; 0.38)
YW	0.61 (0.6; 0.62)	0.49 (0.46; 0.52)	0.94 (0.92; 0.95)	-0.62 (-0.66; -0.57)	0.32 (0.18; 0.47)
LYW	0.59 (0.57; 0.6)	0.75 (0.74; 0.77)	0.56 (0.53; 0.59)	-0.61 (-0.66; -0.57)	0.36 (0.23; 0.5)
AFC	-0.04 (-0.05; -0.04)	-0.06 (-0.062; -0.05)	-0.07 (-0.074; -0.06)	0.25 (0.20; 0.28)	-0.14 (-0.24; -0.03)
MY305	0.007 (-0.003; 0.018)	0.06 (-0.003; 0.133)	0.06 (-0.01; 0.14)	-0.00005 (-0.00572; 0.00568)	0.29 (0.22; 0.36)
Variance Components ²					
Traits ¹	σ_a^2	σ_e^2	σ_h^2	σ_m^2	σ_p^2
WW	435.3 (405.38; 466.08)	429.46 (408.60; 449.57)	98.08 (73.68; 122.93)	47.14 (34.82; 59.25)	18.72 (8.48; 29.45)
YW	1095.06 (1022.4; 1166.5)	1002.07 (950.43; 1051.25)	152.75 (105.87; 202.6)	-	-
LYW	2008.61 (1884.25; 2128.5)	1321.26 (1237.0; 1401.5)	262.98 (179.75; 356.25)	-	-
AFC	45.01 (44.12; 45.90)	35.82 (35.09; 36.5)	100.98 (75.84; 130.14)	-	-
MY305	42.22 (34.64; 49.4)	30.98 (26.36; 35.47)	72.46 (52.58; 94.23)	-	-

¹ WW, weaning weight (205 d); YW, yearling weight (365 d); LYW, long yearling weight (550 d); AFC, age at first calving; MY305, 305-days milk yield.

² σ_a^2 , direct additive genetic variance; σ_e^2 , residual variance; σ_h^2 , contemporary group variance; σ_m^2 , maternal genetic, σ_p^2 , maternal permanent environmental.

The heritability were superior to 0.25 (AFC) and the most heritable trait were long yearling weight (0.56). The heritability estimate for AFC is considered high. Usually, reproductive traits are reported as influenced by environmental component (i.e. nutritional and management conditions). Afroz et al. (2011) reported heritability value for weaning and yearling weight of 0.50 in a selected for dual-purpose *Bos indicus* breed (Red Chittagong breed). Direct heritability of 0.40 and 0.08 for WW and AFC in dual-purpose Brown Swiss cattle were reported by Segura-Correa et al. (2012). Eaglen et al. (2013) studying an unselected dual-purpose Murboden cattle found heritability of 0.49 for 200-d weight trait. Heritability estimate of MY305 was equal to 0.29, within the range reported in previous studies for this population (Peixoto et al., 2006; Santos et al., 2013). Koeck et al. (2010) reported a heritability of 0.19 for MY in dual-purpose Austrian Fleckvieh cows. Despite of MY305 heritability result, Guzerá breeding program still does not have the expected impact on milk yield in Guzerá dual-purpose herds (Peixoto et al., 2006; Peixoto et al., 2010). However, heritability results indicate that milk and weight traits should respond to the direct selection process due to genetic variability observed, mainly for weights traits. Consequently, their adoption as selection criteria will be effective in this population and expressive genetic gain could be achieved in breeding programs.

Despite of low influence of maternal effect at weaning weight, the results indicate that these effects needed to be taken into account in genetic evaluations. Segura-Correa et al. (2012) estimated maternal heritability of 0.05 for 200-d weight trait in Brown Swiss cattle and Eaglen et al. (2013) estimate a heritability of 0.17 for the same trait in dual-purpose Murboden cattle.

In general, genetic correlation estimates were higher for adjacent weights, ranging from 0.83 (WW x LYW) and 0.94 (YW x LYW). Therefore, considerable proportion of the variation in these traits was explained by additive action of the same genes. Selection for

one of these traits would result in favorable correlated responses for the others, i.e., similar selection at mature ages could be achieved by earlier selection of sires, reducing costs in animal breeding programs.

The genetic correlations among weight traits and AFC were negative and favorable, indicating that selection on AFC (heifers which initiated reproductive life earlier) could cause positive changes in animals average weight performance. Dual-purpose Guzerá herds would be able to capitalize on the benefits of increased meat production if advances in genetics lead to improvement of reproductive performance. In Brown Swiss dual-purpose cattle, Segura-Correa et al. (2012) reported genetic correlation of -0.02 between weaning weight and age at first calving. Additionally, genetic correlation was negative but low between MY305 and the reproductive trait (-0.14), indicating that heifers that were younger when covered tended to have a slightly better performance in first lactations milk yield.

Noticeable are the positive genetic correlations among milk yield of related first calves females and weight traits measures (0.25-0.36). The absence of any antagonism among milk and weight traits suggests the effectiveness of simultaneous selection for both objectives and the viability of dual-purpose systems. It can be considered a favorable result for the possibility of joint selection in dual-purpose herds. The selection practice during the years of implementation of breeding programs can be working well, despite of independently conduction of breeding programs. If the breeding goal is to select animals with an adequate genetic balance for milk and meat production traits, a selection index should be establish for sire evaluation, when two or more traits constitute the breeding goal of a breeding program. One of the reasons for positive correlations can be the maintenance of an open-MOET nucleus. Constantly, new sires generally originated from beef herds and dams are introduced to constitute new families in the MOET nucleus, an attempt to not

only control the inbreeding rate but also to increase genetic variation (Peixoto et al., 2006). In a previous study, Peixoto et al. (2014) found positive Pearson correlations between PTA for milk (MY305) and weight traits (weaning and post-yearling weight - PYW) for the same breed using restricted dataset (all cows and sires with negative or positive PTA, only sires with positive PTA for milk traits regardless PTA sign's for beef traits or sires with positive PTA for both traits). In this study, the correlation estimates range from 0.14 (WW x MY305) and 0.26 (PYW x MY305). Other possibility for the positive correlations observed may be caused by some genetic common base in physical and physiological aspects, e.g., feed intake ability and growth hormone levels. In a study of the using of crossbreeding in Italy, Dal Zotto et al. (2009) found that dual-purpose dam breeds produced calves with better commercial values than specialized dairy cows, due to greater price at sale, market value and better weight performance, counterbalancing the decrease in milk production. However, some studies (Lôbo et al., 2000; Madalena, 2008; Dal Zotto et al., 2009; Caetano et al., 2013; Mazza et al., 2014) alert for the fact that direct selection for weight traits could change female size: heavier animals could result in greater dry matter intake and, consequently, greater nutritional requirements. These authors additionally emphasize the advantages of lighter cows: this fact leads to more cows, calves and lactations per hectare of cultivated land.

The phenotypic correlations among weight, milk and reproductive traits were, in general, weaker than the respective genetic correlations among the same traits. The strongest positive phenotypic correlations were observed among weight traits. No evidence of phenotypic association was found among MY305 and the other traits. Consequently, joint selection for dairy and beef purposes induces a favorable genetic relationship among the traits studied without necessarily expressing a phenotypic association. Weak phenotypic correlations were evident among AFC and all traits, ranging from -0.07 (AFC x

LYW) to -0.00005 (AFC x MY305). Phenotypically is not possible to verify the effect of selection in one type of trait into another, certifying the importance to participate and include a crescent number of animals in breeding programs. Consequently, animal selection would be made due to their genetic merit would be effective.

It is important to be aware that adequate parameter estimation requires a well structured and informative datafile. As data for Guzerá breed become available, new and more complex studies will be possible for the accurate evaluation and comparison of selection responses to different traits. Results for this study will be useful to lead the breeding strategies and mating plans in Guzerá breed. Further studies should be performed to evaluate the continued progress on selection for both milk yield and weight traits and its consequences on reproductive performance. Also, correlations among other reproductive and weight traits in later lactations may be different from those found here in first lactation and should be further investigated.

CONCLUSIONS

Given the heritability estimates, individual selection should imply in genetic gains for all traits. The favorable genetic correlations estimates among milk yield, weight and age at first calving traits suggest the viability and potential of joint selection for dairy, beef and reproductive purpose objectives in the Guzerá cattle.

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GENERAL CONCLUSION

Age at first calving censored data in Guzerá cattle could be incorporated in genetic evaluations through a threshold linear model. Given the heritability estimates, individual selection should imply in genetic gains for weight traits (weaning, yearling and long yearling weight), as well as 305-days milk yield and age at first calving. The favorable genetic correlations among dairy, weight and reproductive traits studied suggest the viability of dual-purpose breeding objectives in Guzerá cattle.