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Estimation of genetic parameters for longevity considering the cow's age at last calving

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Abstract The aim of this study was to estimate heritability and predict breeding values for longevity among cows in herds of Nellore breed, considering the trait cow's age at last calving (ALC), by means of survival analysis methodology. The records of 11,791 animals from 22 farms were used. The variable ALC has been used by a criterion that made it possible to include cows not only at their first calving but also at their ninth calving. The criterion used was the difference between the date of each cow's last calving and the date of the last calving on each farm. If this difference was greater than 36 months, the cow was considered to have failed and uncensored. If not, this cow was censored, thus indicating that future calving remained possible for this cow. The survival model used for the analyses was the proportional hazards model, and the base risk was given by a Weibull distribution. The heritability estimate obtained was equal to 0.25. It was found that the ALC variable had the capacity to respond to selection for the purpose of increasing the longevity of the cows in the herds.

Introduction

The cow's age at last calving (ALC), i.e. each cow's last calving recorded in the database, was used in the present study to evaluate longevity in the herd (Caetano et al. 2013). This trait is easy to obtain, already forms part of the database on most farms and, moreover, makes it possible to assess whether the animal presents reproductive viability or not. After some time without calving, cows are commonly discarded and, in such cases, the ALC record is assumed complete (uncensored data). Other cows still continue in the herd and might calve in the future; thus, these animals are also taken into consideration, although their information may be incomplete (censored data). However, to analyse data of this type, survival analysis is the appropriate methodology.

Application of survival analysis to animal breeding has been considered since the initial study by Smith (1983). The main steps in developing it have been: extension of the Cox model (Cox 1972) to a mixed model for evaluating bulls (Smith 1983; Smith and Quass 1984), use and justification of the Weibull model with time-dependent covariables (Ducrocq 1987) and software involving mixed models for survival analysis on large datasets made available and routinely implemented for genetic evaluation (Ducrocq and Casella 1996; Korsgaard et al. 1998). This methodology estimates the likelihood of cow's survival in the herd, according to the covariables included in the model.

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The aim of this study was to estimate genetic parameters (heritability and breeding values) for longevity among cows in herds of Nellore breed, from the ALC, by means of survival analysis methodology, taking into the consideration the proposed criterion and the covariables involved.

Materials and methods

The records of 11,791 animals from 22 farms, located in the states of Goiás, Mato Grosso do Sul and Minas Gerais e São Paulo, participating in the Nellore Breed Genetic Improvement Program ("Nellore Brazil"), which is coordinated by Associação Nacional dos Criadores e Pesquisadores (ANCP), a Brazilian association that conducts genetic evaluation of zebu cattle, were used. On these farms, the animals are reared on pasture. Weaning takes place at around 6–8 months of age. The reproduction management consists of a mating season lasting 90–130 days, using artificial insemination or controlled natural mounting using cleanup bulls after the first or second service.

Table 1 contains descriptive statistics on the ALC. The number of censored records was large after the cows analysed were born starting in 1998, such that most of them continued to be present in the herds and indicating that the interval of 36 months for cows to calve again was not exceeded. The number of records was 11,791 because the cows that had unknown parents and the contemporary groups only containing information on censored animals were deleted. The pedigree contained 11,791 cows, 987 bulls, with 12 female offspring per bull on average.

The variable used to assess the likelihood that cows would remain in the herd was calculated by taking into consideration the cow's ALC. The time-independent effects of the cow's age at first calving, farm, year of birth and season of birth on the

Table 1 Descriptive statistics on data relating to the trait cow's age at last calving (ALC) for calves of Nellore breed

Item	
Number of records	11,791
Number of censored records	7248
Minimum censoring time (months)	29
Maximum censoring time (months)	129
Mean censoring time (months)	71.8
Number of uncensored records	4543
Minimum failure time (months)	21
Maximum failure time (months)	95
Mean failure time (months)	45.9
Percentage of records censored	61.5
Number of contemporary groups	226

ALC have already been analysed (Caetano et al. 2013) using Kaplan–Meier (Kaplan and Meier 1958) estimators and the Cox model (Cox 1972), without verification of the base risk. There were two seasons of birth: dry (for births that occurred between April and September) and wet (between October and March). In this work, the contemporary group was composed of the farm, year of birth and season of birth effects. There were 226 contemporary groups with 52.17 ± 60.49 cows per group on average. The contemporary group and the age at first calving constituted the fixed-effect variables in the model. The random effect was constituted of the bulls and cows entries, thus forming the frailty term (Eq. 1).

The response variable was the ALC and it took into consideration whether the observations were censored or not. Criterion of censoring for each animal was based on the difference between the date of the last calving of a particular cow and the date of the last calving on the farm of that particular cow at the time of data collection. A productive farm must have cows in constant production, i.e. calving cows. If the interval between two calvings were too long, it would be a sign of low production on the farm. Thus, with the criterion of censoring specified, it is possible to calculate the risk of a cow not to give a birth within the chosen criterion (time interval). Thus, if the interval between the last calving of a cow and the last calving of the farm of this cow were too long, then probably the chances of that cow to not give birth would be great. If this difference was greater than 36 months, the cow was considered to have failed and uncensored. If not, the cow's record was censored, thus indicating that it might still have more calves in the future. The criterion of 36 months was taken because thus would be enough time for calving to occur again. In addition, it was seen from the dataset that this difference would allow the cow to remain in the herd, and that the intervals between calvings were not greater than 36 months. The mean ALC was 61.8 months, with a standard deviation of 5.1 months, and the minimum and maximum values were 21 and 129 months, respectively. The mean number of calvings was 2.52 per cow.

The Cox model has been used to estimate the fixed-effect and random-effect covariables. The random-effect estimates relating to bull identification records generated the expected progeny difference (EPD) for the ALC. The estimates relating to cow identification records generated the breeding values for ALC. Through the EPD and breeding values, the bulls and cows could be classified according to greatest risk of failure. The Cox risk model is given by:

$$\lambda(t;x;z) = \lambda_0(t)exp\{x'\beta + z'\alpha\} \tag{1}$$

in which $\lambda(t;x;z)$ is the risk function for the cow, depending on its ALC, $\lambda_0(t)$ is the base risk function, β is the fixed-effect vector of the contemporary group and age at first calving, α is the random-effect vector of animal (bulls and cows) and x and

z are the incidence vectors of β and α, respectively.

The dispersion of the ALC records was investigated for choosing the base risk function. The Kaplan–Meier survival function $\hat{S}_{KM}(t)$ (Kaplan and Meier 1958), in which t is the cow's ALC, was used. The estimate of the Kaplan–Meier survival function plays a fundamental role when there is a need to determine whether the density of the time variable belongs to a particular parameter family or not. Thus, if the graph of $-\log \hat{S}_{KM}(t)$ versus t (Fig. 1a) presents an approximation to a linear model of slope λ and going through the origin, it can be concluded that an exponential distribution with parameter λ can be used to fit the base risk function to the data. Likewise, fitting a Weibull distribution consists of determining from the graph (Fig. 1b) whether $\log[-\log \hat{S}_{KM}(t)]$ versus $\log t$ presents an approximation to a linear model, with slope and intercept correlated with the two parameters of the Weibull distribution (λ and ρ, respectively). To calculate the estimates for $\hat{S}_{KM}(t)$ and construct the graphs, the R software was used (R version 2.11.1; Copyright© 2010, The R Foundation for Statistical Computing).

From Fig. 1, it was observed that the dispersion that best approximated a linear model was the Weibull distribution. Thus, the base risk $\lambda_0(t)$ is given by:

$$\lambda_0(t) = \lambda \rho (\lambda t)^{\rho - 1}$$

in which λ is the scale parameter and ρ is the parameter for the form of the distribution. For $\rho > 1$, the risk function is higher, i.e. the greater the cow's ALC, the greater the chances are that the cow will be failed. On the other hand, for $\rho < 1$, the risk function is lower, thereby indicating that the greater the ALC, the lower the chances are that it will be failed. For $\rho = 1$, the base risk function is constant and the Weibull model is reduced to an exponential regression model. This last case did

not apply to the data in the present study, as can be seen in Fig. 1. Estimation of the random and fixed effects is much less demanding with the Weibull model than with a semi-parametric model like the Cox model, when the base risk function is arbitrary, according to Yazdi et al. (2002). These authors stated that, when the data present a Weibull distribution, the data analysis method does not significantly affect the results in terms of bull classification or response to selection.

The investigation of dispersion of the ALC records suggests that the Weibull sire model is the most adequate to study the ALC. All the random- and fixed-effect covariables included in the model were considered to be time-independent. Sire effects were assumed to be independent and to follow a normal distribution. The sires' variance component that was obtained was multiplied by four to obtain the additive genetic variance (σ_a^2). Thus, this was also fixed in order to obtain the genetic values according to the animal model. The Survival Kit v6.0 software was used (Ducrocq et al. 2010) in the survival analysis. This uses an empirical Bayesian approximation to estimate the parameters. According to Yazdi et al. (2002), an alternative derivation using the basic reliability expression in the sire model suggests a simple equation for heritability on the original scale that does not depend on the Weibull parameters. Thus, heritability is given by:

$$h^2 = \frac{4\sigma_S^2}{(\sigma_S^2 + 1)}.$$

The reliability of the Weibull model is calculated using the number of uncensored observations: (n_{ncens}), $R_{Wei} = (n_{ncens}) / \left(n_{ncens} + \frac{1}{\sigma_S^2} \right)$. From the expression given for calculating the reliability, it can be seen that it is directly related to the number of uncensored observations. If this number is large, the reliability will only be low in situations in
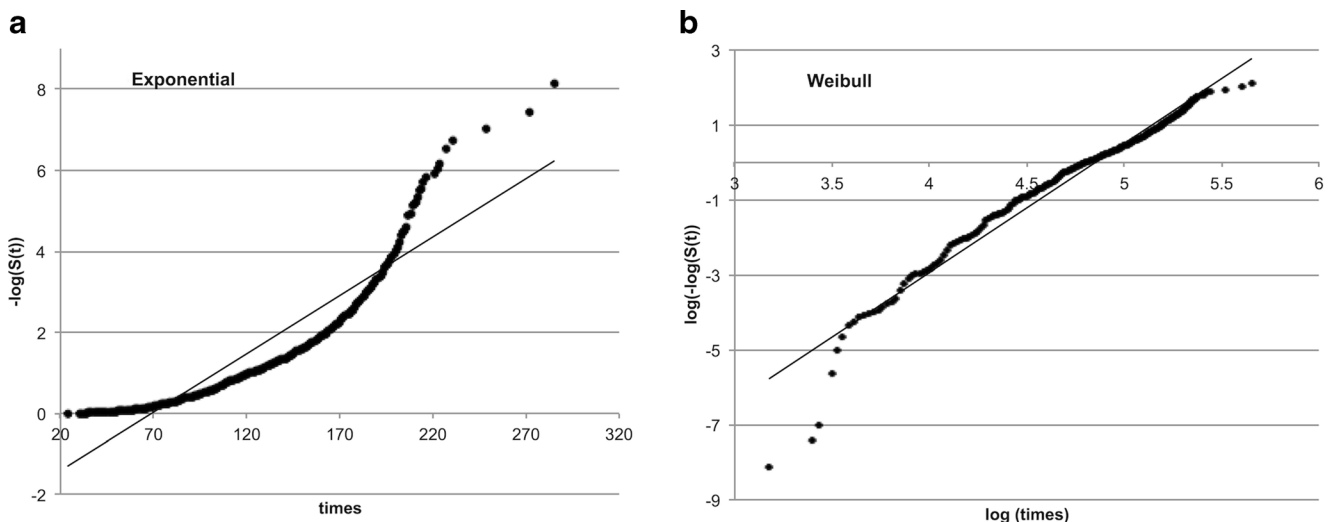
Fig. 1 Dispersion of $-\log \hat{S}_{KM}(t)$ as a function of the cow's age at last calving (ALC) (times in months), in which $\hat{S}_{KM}(t)$ is the survival function from the Kaplan–Meier estimator and the dispersion of $\log[-\log \hat{S}_{KM}(t)]$ is a function of $\log t$ (time in months)

which the variance of σ_S^2 is very small. An assessment of the estimated breeding values for the ALC of the cows was done in relation to the number of calves per cow and in relation to the ALC. The genetic trend among the cows was also calculated in relation to their year of birth. This was done by means of a regression model that made it possible to evaluate the change caused by a selection process over the years.

Results and discussion

The mean age at first calving in this study was 35.4 months, with a standard deviation of 5.1 months. Bertazzo et al. (2004) found a mean of 38.7 months and a standard deviation of 4.5 months. Boligon et al. (2010) obtained a mean of 1050 days (35 months), i.e. close to what was found in the present study. According to Forni and Albuquerque (2005), this trait reflects the genetic variability of the females in presenting estrus activity during the breeding season, the number of services required to achieve pregnancy, the duration of the pregnancy and the date of calving. This also made it possible to identify the animals presenting greater fertility within the herd, the females that became pregnant early during the breeding season and the bulls that produce female offspring that become pregnant earlier within the breeding season. The estimated age at first calving determined using the Weibull model was −0.015, with a standard error of 0.004. These values were close to those found by Caetano et al. (2013), which were −0.0218 ± 0.003.

The effect of the contemporary groups on the ALC was significant ($P < 0.0001$). The proportional hazard rates in relation to the base group (the group that had the greatest number of uncensored observations) indicated the contemporary groups in which the cows had greater or lower chances of being discarded, i.e. from 0.017 to 6.21. This result indicated that, in relation to the contemporary group with a risk of one (the base group), the cows in the group with the highest risk rate had around a six-fold greater chance of leaving the herd at the same age. For those in the group with the lowest risk rate, the chance of being discarded was around 58 times lower (1/0.017). According to Van Melis (2005), this variation, which was also seen in his work, indicated that modifications to the environment could lead to increased or decreased length of stay in the herd.

The estimates for the parameters of the survival model for the cows' ALC are described in Table 2. The value of the parameter in the Weibull distribution form (2.45), compared with the base value of one, indicated that the greater the cow's ALC, the greater the cow's chance of failure would be. The reliability of the Weibull model was high (0.997), given that its range is from 0 to 1, thus indicating that the estimates for the random- and fixed-effect parameters were accurate. The heritability estimate for the ALC variable was moderate, thus

Table 2 Estimates of parameters* for the cow's age at last caving (ALC), with regard to females of Nellore breed, obtained by means of survival analysis

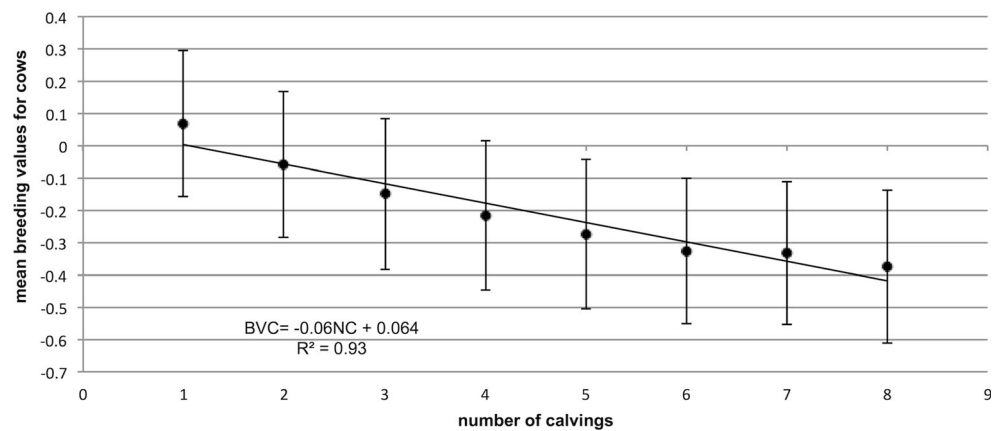| Estimates	ALC
Weibull format parameter ρ and standard deviation	2.45 (0.03)
Weibull scale parameter λ and standard deviation	−10.02 (0.11)
Heritability	0.25
Reliability (R_{Wei})	0.997

*Convergence criterion 10^{-9}

indicating that 25 % of the variation among the cows regarding the ALC trait was due to additive genetic variation. It is important to emphasise that the heritability parameter corresponds to the additive proportion of the total variability that is of genetic nature, or the quotient between the additive genetic variance and the phenotypic variance adjusted for fixed effects. The most important function of heritability is its predictive role, thereby expressing the reliability of the phenotypic values as a guide for the breeding values, or the degree of correspondence between the phenotypic value and the breeding values (Van Vleck et al. 1987), as well as enabling prediction of the response to selection.

No studies with estimates for genetic parameters for the variable of the cow's ALC, as the longevity trait, using survival analysis methodology were found in the literature. However, previous studies using other traits that also measure the capacity to remain in the herd have reported heritability estimates close to those obtained in the present study. Van Melis et al. (2010) and González-Recio and Alenda (2007) used a sequential threshold model for longevity traits and estimated heritabilities of, respectively, between 0.17 ± 0.01 and 0.20 ± 0.01 for beef cattle and 0.11 ± 0.01 for dairy cattle. Silva et al. (2006) and Van Melis et al. (2007) analysed the capacity to remain in the herd at the age of 6 years by means of a threshold model and obtained estimates of 0.24 ± 0.03 and 0.22 ± 0.03, respectively. Martínez et al. (2004) estimated genetic parameters for the duration of productive life (considering six groups) among Hereford cattle

Table 3 Frequency table of expected progeny differences (EPDs) for cow's age at last calving (ALC) and average daughters per bull of each frequency class

Class number	Lower limit of EPD for ALC	Upper limit of EPD for ALC	Absolute frequency	Average daughters per bull
1	−1.25	−0.75	5	47.2
2	−0.75	−0.25	44	26.41
3	−0.25	0.25	867	9.87
4	0.25	0.75	66	23.11
5	0.75	1.55	5	62.40

Fig. 2 Mean breeding values for cows, for their age at last calving (ALC), with the respective confidence interval, taking into consideration the standard deviation, in relation to the number of calvings

and obtained heritability estimates of between 0.05 and 0.15. Finally, Caraviello et al. (2005), also using a Weibull proportional hazards model, estimated a heritability of 0.18 among Jersey cattle.
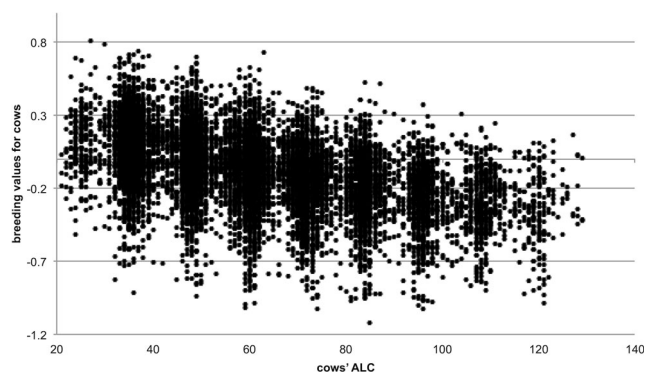
The distribution of the cows' breeding values for their ALC showed a symmetrical distribution, with a mean of −0.03 and minimum and maximum of −1.585 and 1.04, respectively. The mean rate for the risk of failure was 0.98, which means that there was a decrease in risk of 2 % in comparison with the base group, for which the risk was one. The 95 % confidence interval of the breeding values for the risk of failure was −0.46 to 0.26, which represents a 46 % lower chance and 26 % greater chance of failure. Therefore, the use of females with lower breeding values for failure (i.e. exceeding 36 months after the last calving without becoming pregnant) might cause an improvement in their continuation in the herd.

According to the frequency table (Table 3), many bulls presented an EPD next to zero for the ALC and they did not present a great number of female offspring (class 1, Table 3) compared to the other classes. The bulls that presented EPDs in classes 1, 2, 4 and 5 had a greater number of female offspring. This may be associated with the bull's age, or these bulls may have been selected for some traits of economic interest, thus presenting greater numbers of descendants and breeding values for the ALC

that differed from zero. Therefore, at the same time the selection favoured other traits of economic importance may have been occurring, this process also affected the ALC. Bulls with lower EPD can be selected as the fathers of future generations when the objective is to increase their descendants' longevity.

The relationship between the mean breeding values for the ALC as a function of the number of calvings per cow (Fig. 2) was shown to be a decreasing linear trend ($P < 0.05$). Lower mean breeding values for the chance of failure relating to the ALC were estimated for cows that had a greater number of calvings. Although it had been previously found that every additional month for age at first calving diminished the cows' risk of failure by 1.5 %, this did not imply that animals with lower age at first calving would be less long-lived. Cows with greater numbers of calvings were more precocious than those with fewer calvings. This was found through a significantly decreasing linear regression for which the equation was: age at first calving = 36.46 − 0.41*ND; $P < 0.001$; where ND = number of calvings.

The cows with greater breeding values for the risk of failure relating to the ALC were also the ones with lower numbers of calvings (Fig. 2). On the other hand, the cows with lower numbers of calvings and greater breeding values for the risk of failure relating to the ALC could

Fig. 3 Breeding values for cows, for their age at last calving (ALC), in relation to cows' ALC
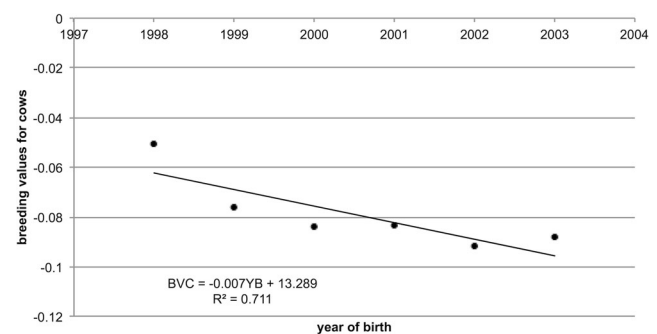
Fig. 4 Genetic trends of the cows' age at last calving (ALC) variable obtained through regression of the breedingvalues for cows, predicted as a function of the cows' year of birth

be the ones with larger intervals between calvings. After the first calving, cows take longer to conceive again, in relation to the situation after subsequent calvings (Andrade et al. 1990).

From Fig. 3, it can be seen that the greater the cow's ALC, the lower the breeding values for the ALC. Thus, cows with lower ALCs go beyond the 36-month limit that was taken as the censoring criterion more frequently than do cows with greater ALCs. The concentration of breeding values for the ALC around some ages of calving reflects the greater numbers of births at certain times of the year, resulting from the way in which the breeding season was managed on the farms.

Figure 4 presents the genetic trends of the ALC variable as a function of the risk of leaving the herd, obtained by means of regression on the predicted breeding values as a function of the cows' year of birth. The trend was negative (−0.0067), thus indicating that, every year, there was a decrease of 0.67 % in the chance of the cows leaving the herd, i.e. the risk of failure diminished. Furthermore, since the effect is multiplicative, the chance of the cows leaving the herd would be −6.9 % over a 10-year period. This trend might be improved if the ALC were to be included in the selection indexes applied in animal genetic improvement programmes.

It was found that the ALC variable had the capacity to respond to selection for the purpose of increasing the longevity of the cows in the herds. In addition, it is easy to measure and already forms part of most farms' databases. Thus, it can be used as a selection criterion in genetic improvement programmes. Bulls with lower breeding values for the risk of cow failure, according to the 36-month criterion adopted, can be used as the fathers of future generations. This may enable gains in reproductive longevity among their female offspring. Cows with lower breeding values can also be selected.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All applicable international, national and/or institutional guidelines for the care and use of animals were followed.

Informed consent Informed consent was obtained from all individual participants included in the study.

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