

Quantitative genetic study of age at subsequent rebreeding in Nellore cattle by using survival analysis

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ABSTRACT. The continuous trait age at subsequent rebreeding (ASR) was evaluated using survival analysis in Nellore breed cows that conceived for the first time at approximately 14 months of age. This methodology was chosen because the restricted breeding season produces censored data. The dataset contained 2885 records of ASR (in days). Records of females that did not produce calves in the following year after being exposed to a sire were considered censored (48.3% of the total). The statistical model used was a Weibull mixed survival model, which included fixed effects of contemporary groups (CG) and period and a random effect of individual animal. The effect of contemporary groups on ASR was significant (P < 0.01). Heritabilities obtained for ASR were 0.03 and 0.04 in logarithmic

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and original scales, respectively. These results indicate that the genetic selection response for subsequent reproduction of 2-year-old Nellore breed females is not expected to be effective based on survival analysis. Furthermore, these results suggest that environmental improvement is fundamental to this important trait. It should be highlighted that an increase in the average date of birth can produce an adverse effect in the future, since this cannot be compensated by genetic improvement.

Key words: Beef cattle; Censored records; Fertility; Heritability; Reproduction

INTRODUCTION

Reproduction is a component of great importance for profitable economic performance in beef cattle production or beef cattle breeding programs. In several studies, reproductive traits were shown to be the main economically relevant factors when compared with growth and final product traits (Newman et al., 1992; MacNeil et al., 1994; Melton, 1995; Bergmann et al., 1996; Phocas et al., 1998; Evans et al., 1999; Eler et al., 2002; Formigoni et al., 2005).

Age at subsequent rebreeding (ASR) is a reproductive trait that is feasible to measure but is rarely studied, even though it is a very important trait in *Bos indicus* in tropical environments. The particular type of management used can substantially interfere with the expression of this trait, especially the use of a restricted breeding season. Analysis of ASR using linear models would be suitable if all females had an equal and continuous opportunity to become pregnant; otherwise, the females that do not become pregnant within a given breeding season could not be evaluated. This is more severe in zebu breeds, where females are often exposed to sires too young and a majority cannot become pregnant (Pereira et al., 2006). Moreover, among the females that do conceive, conception generally occurs toward the end of the breeding season, thus reducing the time available for subsequent reproduction in the following season. Nutritional demands of heifers during pregnancy exceed that of mature cows, because the heifer is sharing nutrients for its own growth with demands for fetal growth and development. This increased demand for nutrients continues throughout early lactation, when nutritional requirements are highest. Deficiency in energy or proteins for extended periods during any production phase will have a negative impact on reproduction for the subsequent pregnancy.

The only heritability estimate of ARS in beef cattle reported to date is 0.19 ± 0.14 (Doyle et al., 2000) in Angus cattle, which can be considered as low to moderate. A threshold model was used for this analysis, which considers the categorical nature of the phenotype by modeling an underlying normal distribution. When studying dairy cattle, Boettcher et al. (1999) suggested adopting survival time analysis as an alternative to evaluating the stayability of cows in the herd, which is a binary trait. This type of analysis models the trait with a hazard rate or probability of survival over time (t), given survival up to t. According to Boettcher et al. (1999), analysis of survival time could increase the precision of such evaluations, as the differences in days are taken into account, i.e., the values "zero" and "one" are displayed in observed values. Survival models are already widely defined concerning longevity breeding in dairy cattle (Yazdi et al., 2002); however, in beef cattle, its use has not yet been fully explored.

Survival analysis is a class of statistical methods that are ideal for studying the occur-

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rence of events over time. It provides adequate statistical treatment for censored records, i.e., animals that did not express the event of interest until the end of the study (right censoring), and takes into account data from nonlinear traits (Ducrocq and Casella, 1996). Therefore, this type of analysis could be effectively applied for studying ARS, while considering restricted breeding seasons, as is the case for beef cattle.

In the present study, the survival analysis methodology was used for studying ARS in Nellore breed females with the objective of verifying the possibility of modifying this trait by selection.

MATERIAL AND METHODS

Data

A dataset for Nellore females born between 1992 and 2002, with first calving occurring between 1993 and 2003, was used. These data were obtained from nine herds owned by Agro-Pecuaria CFM Ltd., located in the states of São Paulo, Mato Grosso do Sul, and Goiás, in Brazil. Agro-Pecuaria CFM owns close to 17,000 Nellore cows and sells approximately 2000 young bulls annually out of 7000 weaned bull calves.

The trait evaluated was ASR (in days). Females were exposed to sires for the first time at approximately 14 months of age (between 11 and 16 months) and those that calved were exposed again in the subsequent breeding season.

Data from females that did not show any record of a calving date for the subsequent year following exposure to a sire were censored. For these females, the ASR value was calculated as age at the beginning of the breeding season (in days) + 100 days (duration of the breeding season). This clarified the fact that these females were not pregnant up to this age. For females with an available calving record (uncensored), the ASR was calculated as age at calving (in days) - 290 days (average pregnancy period in these herds) (Pereira et al., 2002). It should be stated that if the female reconceived within the 100 days of the breeding season, its record was not censored since the failure, i.e., conception, occurred within the study period, otherwise it was considered as censored (censoring to the right). In order to adjust the data to fit the Weibull distribution, the minimum observed value of ASR was subtracted (768 days) from the values obtained for ASR, since one of the frequent causes of deficiency of adjustment of data to this distribution is the lack of observations between the origin and a given point, t₀ (Ducrocq, personal communication, 2002, cited by Pereira et al., 2006).

The initial file was edited, providing data of 2885 females of known parents and belonging to contemporary groups with variability; groups presenting only censored records or with less than four observations were eliminated. Contemporary groups were defined as farm of birth + year of birth + weaning management group + 18-month management groups + breeding farm (14 months) + breeding farm (24 months). A summary of the dataset is shown in Table 1.

Cattle management

A detailed description of herd management can be found in Eler et al. (2004, 2006). The cows were maintained on pasture, with salt and mineral supplementation (11% Ca, 6% P, 1% Mg, 4% S, 16% Na, 0.15% Cu, 0.15% Mn, 0.45% Zn, 0.015% I, 0.007% Co, and 0.002%

Se). In each year, the mating season began in November and ended in January, for the duration of 60 days for cows and 100 days for heifers and 2 year-old cows. Artificial insemination and natural service mating were used in lots with single or multiple sires (uncertain paternity). The ratio of cows per bull was approximately 35:1. All cows were evaluated for pregnancy (rectal palpation) approximately 60 days after the end of the breeding season, and non-pregnant cows were culled. Some culling may have also been performed on the basis of poor progeny performance and health. Bulls were selected based on an index including expected progeny differences (EPD) for weaning weight, post-weaning gain, scrotal circumference, and muscle score, in proportions of 20, 40, 20, and 20%, respectively.

ctor	Summary
mber of records	2,885
mber of animals in pedigree	10,093
mber of right censored records	1,393
nimum censoring time (days)	33 + 768
ximum censoring time (days)	181 + 768
an censoring time (days)	104.8 + 768
nimum time to rebreeding (days)	1 + 768
ximum time to rebreeding (days)	171 + 768
an time to rebreeding (days)	79.8 + 768
nsored records (%)	48.3
mber of contemporary groups	200
nber of bulls	496
nber of years in analysis	11

Model

The following mixed survival model was used:

$$\lambda(t; z) = \lambda_0(t) \exp\{z(t)'\beta\},\$$

where $\lambda(t; z)$ is the hazard function of an individual depending on time t (ASR14 in days); λ_0 (*t*) is the baseline hazard function, assuming that the trait followed a Weibull hazard distribution $[\lambda_0(t) = \lambda \rho(\lambda t)^{\rho - t}]$ with shape and scale parameters ρ and λ , respectively; β is a vector that contains fixed and random effects (possibly time dependent) that affects the hazard with z(t)' being the corresponding vector of incidence.

The effects included in the model were:

(i) sire and maternal grandsire (mgs): time-independent random effects. It was assumed that the effects followed a multivariate normal distribution with mean zero and variance $A\sigma_s^2$, where σ_s^2 is the variance between sires. The numerator relationship matrix **A** for the sire-mgs model contained 496 animals;

(ii) contemporary group (CG): as defined previously, time-independent fixed effect;

(iii) period: time-dependent fixed effect, with two classes (the definition of these classes is explained below).

The sire-mgs model was initially used to obtain the variance component of sire together with ρ , the shape parameter of the Weibull distribution. The variance component obtained was multiplied by four and fixed to estimate the breeding values with an animal model and the effects of sire and mgs substituted by the time-independent random effect of animal. It was assumed

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that this effect followed a multivariate normal distribution with mean zero and variance $A\sigma_{a}^{2}$, where σ_{a}^{2} is the additive genetic variance and A is the numerator relationship matrix between all animals, up to the tenth generation at most. The pedigree file contained 10,093 animals.

To determine the adequacy of the Weibull model in describing the ASR14 (age of reproduction subsequent to 14 month pregnancy) the data was verified graphically (Cantor, 1997) by plotting $\ln[-\ln S(t)] \propto \ln(t)$, where \ln is the natural logarithm, S(t) is the estimate of the Kaplan-Meier function of survival $[S(t) = \exp(-(\lambda t)^{\rho}]$, and t is the ASR14 in days. Adequacy would be revealed if this graph were roughly linear. For the estimate of S(t) in the dataset, the LIFETEST procedure of SAS was used. Graphical inspection of Figure 1 showed no linearity of $\ln[-\ln S(t)] \times \ln(t)$ over the whole period of cow age, leading to the conclusion that one Weibull distribution was not adequate to describe the data over the whole period. However, it did permit the distinction of two periods in which linearity was observed. Within each of these periods, the assumption of a Weibull model was plausible. The limit of this period represents the age at which abrupt changes occur in the chances of females becoming pregnant again. In the first period, up to 26 months, there is a slight increase in the chance that a female will become pregnant. In the second period, over 26 months, the increase is greater than in the first period. This increase in the rate of pregnancy of subsequent reproduction during the second period coincides with the age mode of females at the beginning of the breeding season. Perhaps the females that are ready for subsequent reproduction prior to the beginning of the breeding season readily became pregnant after being exposed, resulting in a peak of pregnancy during this period. In this case, censoring also occurs to the left in these data. As previously suggested (V. Ducrocq, personal communication, 2003, cited by Pereira et al., 2006), a time-dependent fixed effect (period) was defined to account for these features, leading to the assumption of one-shape parameter (ρ), but different scale parameters (λ) for the different periods. The limits of these periods were initially established by graphical inspection and were then defined by comparing the probability values obtained by performing small changes in these limits (Ducrocq, 2002).

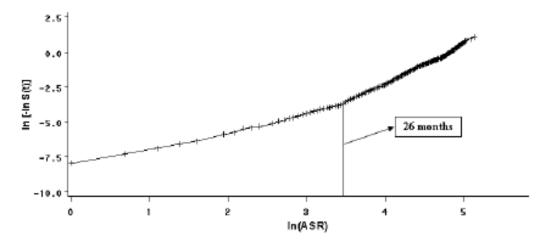


Figure 1. Graphical verification of the adequacy of age at subsequent reproduction (ASR14) data to the Weibull distribution. Vertical line delimits the two distinct periods considered. S(t) = Kaplan-Meier estimate of survival function; ln = natural logarithm.

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The 'Survival Kit' V3.12 software (Ducrocq and Sölkner, 1998) was used to perform the survival analysis. This software uses Bayesian empirical approximation to estimate the parameters. The heritability for the sire-mgs model was calculated in logarithmic scale as:

$$h_{\log}^2 = \frac{4\sigma_s^2}{\left(\frac{5}{4}\right)\sigma_s^2 + \frac{\pi^2}{6}}$$

and in original scale as:

$$h_o^2 = \frac{4\sigma_s^2}{\left(\frac{5}{4}\right)\sigma_s^2 + 1}$$

(V. Ducrocq, personal communication, 2002, cited by Pereira et al., 2006).

RESULTS AND DISCUSSION

Descriptive analyses

Figure 2 presents the average ages at which all females that calved when exposed at approximately 14 months of age (all records and only uncensored records) entered the next breeding season, according to year of birth.

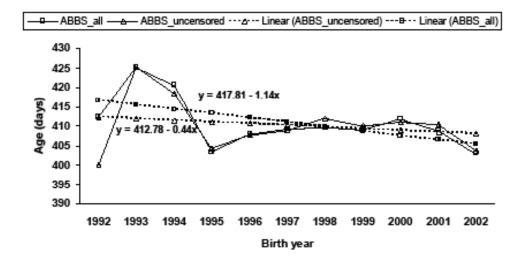


Figure 2. Average ages at the begining of the breeding season for all records (ABBS_all) and uncesored records (ABBS_uncensored) (with respective tendency lines), per year of birth in Nellore females.

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First, a reduction in the age at which the females entered the breeding season was observed, and consequently, in the age at which they ended the breeding season. This reduction was approximately 1.14 days per year, indicating that for every 5 years there is a reduction of almost 8 days in age. As the breeding season has a relatively short duration (mean of 100 days) and the females are reaching the capability of conceiving during this phase, the fact that these females reach the end of the breeding season at an early age may indicate a considerable loss in the time available for the 2-year-old cow to become pregnant. This factor may be due to management decisions or to an increase in the calving interval of the females (dams of females) in the herd.

As presented in Figure 3, the average ASR or censoring rate increased over the years. As age at censoring has a direct relationship with age at the beginning of the breeding season, this increase was due to an increase in ASR, or a reduction in the rate of subsequent reproduction, which can be verified in Figure 4.

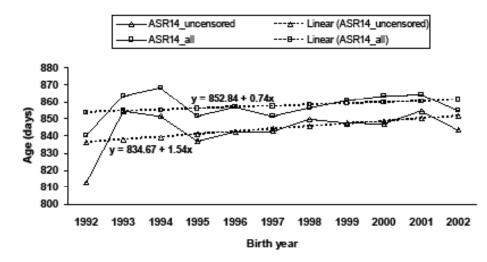


Figure 3. Average ages at subsequent rebreeding or censoring (ASR14_all) and at subsequent rebreeding (ASR14_ uncensored) (with respective tendency lines), per year of birth in Nellore females.

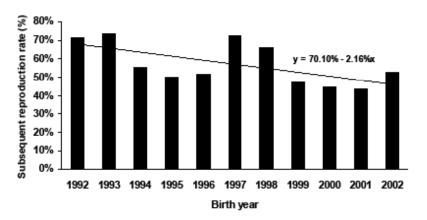


Figure 4. Subsequent reproduction rate of 2 year-old cows of Nellore cattle per year of birth.

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Observations revealed that ASR (for uncensored records) did not decrease over the years, and that although the age at which these females (those who became pregnant) entered the breeding season decreased, did so to a lesser extent than all the females as a whole. This indicates that females are becoming pregnant later in the breeding season. Considering that the period and duration of the breeding season remained unaltered each year, this is most likely explained by females conceiving later in the breeding season (subsequent reproduction) due to the shorter rest period post pregnancy.

The subsequent reproduction rate decreased by approximately 2.2% per year (Figure 4). This change in the subsequent reproduction rate could be due to variations in the environment that resulted in worse conditions for the females to become pregnant, especially when considering the change in age at the beginning of the breeding season. The results revealed that the reduction in ASR occurred especially during the first few years, and remained relatively stable thereafter (Figure 3). The reduction in age at which the females entered reproduction derives inevitably from a delay in the mean date of birth of these females, since the date of the beginning of the breeding season remained unaltered.

Environmental effects

The effect of CG on ASR was significant (P < 0.01). The proportional risk ratios, compared to an established standard group (group with the greatest number of uncensored observations, with risk ratio set to 1.00), showing a higher or lower chance of 2 year-old cows becoming pregnant, varied between 0.21 and 25.9, considering only CGs with more than five uncensored observations. This result shows that compared to a CG with a risk rate arbitrarily set to 1.0 (the base group), the females of the group with the highest risk ratio presented a 26-fold greater chance of becoming pregnant at the same age. For those in the group with the lowest risk rate, this chance was approximately five times lower. This effect is considered to be environmental and is always expressed in relation to a given age even though it is independent of the age at which females enter the breeding season. Thus, the observed variation indicates that changes in the environment may lead to very important changes in pregnancy rates.

Figure 5 presents the mean values for risk ratios (log transformed) of the CG, according to year of birth of the females. Higher values indicate a greater chance of subsequent reproduction at a given age. Observations showed that a diminishing tendency occurred in the risk ratio, especially in later years of birth, indicating that the chances of becoming pregnant (subsequent reproduction) were lower for cows born in recent years. The reduction was -0.0555, representing a risk ratio of 0.946, i.e., 5.7% less chance of subsequent reproduction per year. These results are in agreement with those observed in Figure 4, i.e., the more recent the year of birth, the lower the subsequent reproduction rate, with the exception for the year 1997. In this year, there were few CGs, and some with high risk ratios, leading to an abnormally high mean risk ratio. As the analyses were performed using the animal model, the genetic effects were removed, indicating that this result reflects a tendency of the environment. Therefore, changes in the environment can increase the chances of subsequent reproduction in 2 year-old cows. It should be emphasized that the hazard is given for a certain age, suggesting that a greater hazard does not necessarily reflect a greater pregnancy rate if, for example, the age at which heifers enter the breeding season decreases in successive years. According to

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the results obtained, modifications in the environment may be diminishing the chance of the subsequent reproduction of 2 year-old cows over time.



Figure 5. Mean values of risk ratios (log transformed) of CG according to year of birth of the 2 year-old cows.

Genetic parameters

The main parameters estimated by the survival model are presented in Table 2. A value of $\rho = 1$ indicates that the hazard is constant over time and that the Weibull distribution simplifies itself to an exponential distribution. A $\rho > 1$, as observed in this study, indicates that the hazard increases with time (Boettcher et al., 1999). The estimated value for ρ (3.18) was expected for the present data, since the older the females become, the greater the chance of becoming pregnant (subsequent rebreeding). The standard error (0.09) is acceptable, indicating a relatively small error for this estimate.

Factor	Obtained value*
Weibull shape parameter (r)	3.18
Standard error of r estimate	0.09
Sire variance	
Mean	0.02
Standard error	0.01
Mode	0.01
Heritability in logarithm scale (h_{log}^2)	0.03
Heritability in original scale (h^2)	0.04

*Convergence criterium used was 10⁻⁹.

The interpretation of heritability in the case of survival analysis has been a subject of great debate (Korsgaard et al., 1999), since it is not straightforward, as in the case of the linear model. Heritability in the logarithmic scale is not adequate for obtaining the EPD accuracies, making it preferable to use heritability in the original scale (Yazdi et al., 2002).

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The heritability estimate for ASR found in this study was lower than the result for subsequent reproduction obtained by Doyle et al. (2000) of 0.16 for Angus cattle. Although the low heritability estimate indicates that ASR should not be recommended as a trait for selection criterion in this population, consideration must be given to the fact that the quantity of records may not have been ideal for effective genetic parameter estimation and that further studies using a larger dataset should be carried out to confirm this value.

Estimated breeding values (EBVs)

Although the results of the survival analysis are best interpreted in terms of risk ratios, the presentation of the risk ratio logarithm is more adequate, as it refers to normally distributed variables and allows for EBVs to be interpreted in additive form. Figure 6 presents the distributions of the EBVs for all females exposed during the breeding season.

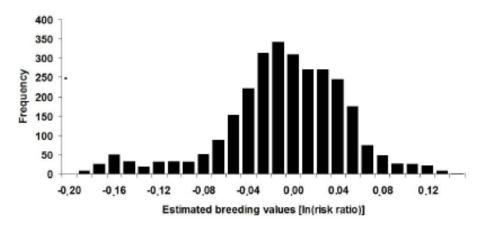


Figure 6. Distribution of estimated breeding values for all females exposed during the breeding season (2085 animals with records).

The mean EBV of these females was -0.01689, representing a risk ratio of 0.9833, i.e., a 1.7% lower chance of pregnancy than that of the genetic baseline of the population. Ninety-five percent of the EBVs of these females were between -0.1625 and 0.0806, representing risk ratios from 18% lower to 8.4% higher than the baseline population for the same age.

Regarding sires, considering that only those that produced more than five daughters among those entering the breeding season, the distribution of EBVs ranged from -0.2938 to 0.177, representing hazards from 34% lower to 19% higher than the genetic baseline of the population. Comparing the extremes, the risk ratio of the sire with the highest EBV was 60% greater than that of the sire with the lowest EBV. Considering the transmission ability of sires, it can be expected that the daughters of the sire with the highest EBV would have a 23% greater chance of becoming pregnant than the daughters of the sire with the lowest EBV at a given age and under the same conditions. Ninety-five per cent of the EBVs of sires were between -0.1283 and 0.0972, which represents risk ratios from 14% lower to 10% higher than the baseline of the population.

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Genetic trends

The genetic trend of ASR, which was measured by the regression of EBVs for females within their years of birth, was -0.0019 per year. This value represents a decrease of 0.2% per year for this risk ratio. Therefore, for each year, the females born in the herd have a 0.2% lower chance of becoming pregnant at a given age. As these effects are multiplicative, over 10 years, the accumulated decrease would be approximately 2.02%, i.e., the rate of subsequent reproduction would remain practically constant over the years. This is to be expected given the heritability of the ASR trait.

CONCLUSIONS

The results obtained from the survival analysis, particularly the low heritability estimate, indicate that the possibility of genetic improvement in fertility of 2 year-old Nellore cows through selection for ASR or at subsequent rebreeding is extremely low or even unfeasible. However, improvement of the environment could have a positive effect on fertility.

Implications

Despite our interest in increasing the rate of subsequent reproduction in 2 year-old cows, the estimated heritability levels indicate that the ASR trait cannot be effectively modified by direct or indirect selection. However, the results suggest that improvement of the environment could be fundamental for this important trait. It should be highlighted that an increase in the mean date of birth can produce an adverse effect in the future, since this cannot be compensated by genetic improvement.

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