

## Female fertility in a Guzerat dairy subpopulation: Heterogeneity of variance components for calving intervals

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### ABSTRACT

The objectives of the present study were to determine if variance components of calving intervals varied with age at calving and if considering calving intervals as a longitudinal trait would be a useful approach for fertility analysis of Zebu dairy herds. With these purposes, calving records from females born from 1940 to 2006 in a Guzerat dairy subpopulation in Brazil were analyzed. The fixed effects of contemporary groups, formed by year and farm at birth or at calving, and the regressions of age at calving, equivalent inbreeding coefficient and day of the year on the studied traits were considered in the statistical models. In one approach, calving intervals (CI) were analyzed as a single trait, by fitting a statistical model on which both animal and permanent environment effects were adjusted for the effect of age at calving by random regression. In a second approach, a four-trait analysis was conducted, including age at first calving (AFC) and three different female categories for the calving intervals: first calving females; young females (less than 80 months old, but not first calving); or mature females (80 months old or more). Finally, a two-trait analysis was performed, also including AFC and CI, but calving intervals were regarded as a single trait in a repeatability model. Additionally, the ranking of sires was compared among approaches. Calving intervals decreased with age until females were about 80 months old, remaining nearly constant after that age. A quasi-linear increase of 11.5 days on the calving intervals was observed for each 10% increase in the female's equivalent inbreeding coefficient. The heritability of AFC was 0.37. For CI, the genetic-phenotypic variance ratios ranged from 0.064 to 0.141, depending on the approach and on ages at calving. Differences among genetic variance components for calving intervals were observed along the animal's lifetime. Those differences confirmed the longitudinal aspect of that trait, indicating the importance of such consideration when accessing fertility of Zebu dairy females, especially in situations where the available information relies on their calving intervals. Spearman rank correlations among approaches ranged from 0.90 to 0.95, and changes observed in the ranking of sires suggested that the genetic progress of the population could be affected by the approach chosen for the analysis of calving intervals.

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## 1. Introduction

Originally imported from South Asia beginning in the nineteenth century, the ability of the Zebu breeds (*Bos indicus*) to breed under harsh tropical and subtropical environmental conditions has been the main reason for their continuous use in beef and dairy industries in many American tropical countries (Santiago, 1972). Milk production in tropical regions has relied mostly on Zebu breeds or their crossbreds (Lacorte et al., 2006; Ruas et al., 2007).

In the year 2005 there were 14,703 Guzerat animals registered by the Brazilian Zebu Breeders Association (ABCZ), including both beef and dairy herds (Faria et al., 2009). Some genetic improvement was achieved with the use of estimated breeding values to select for milk yield in the Guzerat breed, but the evaluation of reproductive efficiency for the dairy Zebu breeds in general has needed development (Paneto et al., 2008; Peixoto et al., 2006). Some studies with *Bos taurus* dairy breeds have shown that selection for high milk yield has led to a decline in fertility (Hare et al., 2006; Lucy, 2001; Weigel, 2006).

There has been a lack of systematic recording of reproduction traits in the Zebu herds, limiting the development of the genetic evaluation and selection process. Pedigree information and milk yields have been commonly available for most elite herds of Zebu breeds in Brazil. The dates of exposure to natural services or number of artificial insemination attempts could be useful information, but such records have not been available for most herds. Thus, female reproduction efficiency usually has been evaluated only from pedigree information and calving dates observed for each cow. Ages at calving, calving intervals and days open frequently have been feasible options for the reproductive evaluation of Zebu cattle herds.

Heritability estimates have been low for calving intervals, and it is not clear if the genes involved in the fertility are the same for young and mature cows (Peña et al., 2008). Also, (co)variance components may diverge among observations at different ages, and procedures for estimating the genetic merit of animals for these traits are not straightforward (Urioste et al., 2007). The objectives of the present study were to determine if variance components of calving intervals varied with age at calving and if considering calving intervals as a longitudinal trait would be a useful approach for fertility analysis of Zebu dairy herds.

## 2. Materials and methods

Data from a dairy subpopulation of the Guzerat breed in Brazil were considered in this study. Mating system has been mostly natural service or artificial insemination, but embryo transfer or *in vitro* fertilization techniques were also applied for approximately 2% of the females. Reproduction records from females used in embryo transfer or *in vitro* fertilization have been excluded because they would not be within the scope of the present study. After those exclusions, the data set included 4420 calving records from 1114 females born in the period from 1940 to 2006. Calving distribution corresponded to 23, 21, 31 and 25% for the first, second, third or fourth trimesters of each year, on average.

As it has been common practice for many elite stock Zebu herds in Brazil, it was true also for the studied subpopulation,

that some animals left their herds at different moments of their lives for reasons not necessarily related to their reproductive performances. This happened for several reasons including animals were sent to shows at distant locations, or they were temporarily exchanged or sold to other breeders. Thus, they were not always exposed to breeding as soon as they reached puberty, or their reproductive events were not properly recorded.

Taking into account the scenario cited above, the upper limits for ages at first calving and calving intervals were defined in order to eliminate extreme data contributing to increased residual variances, but minimally to the genetic variances. Various limits were tested by the authors in an initial analysis within this Guzerat subpopulation (results not shown) and the appropriate ones were chosen according to those variances changes. A similar approach, of editing data and defining upper limits to interval traits have been used by Oseni et al. (2004) when analyzing days open and pregnancy rates in US Holsteins. For the present study, any animal with the first calving recorded later than 45 months were considered as lacking such information.

Calving intervals (CI) were calculated as the difference, in months, between any two subsequent calves. For some of the analyses conducted in the present study, calving intervals observed in different moments of the cow's lifetime were considered as different traits, as described ahead.

The First Calving Interval (CI1) was calculated as the interval between the first and the second calving records of each animal. The subsequent observations of calving intervals were designated as calving intervals for young females (CIY) or calving intervals for mature females (CIM). If the age of the animal at its calving record, defining the beginning of an interval observation, was smaller than 80 months, the observation was designated as CIY. If the age of the animal was 80 months or more, at its calving record, it was designated as CIM. The observations were divided this way because in a preliminary analysis the additive genetic correlations within these categories were sufficiently close to unity. Consequently, repeated records from animals older than 80 months were considered as the same trait.

Any animal with calving intervals larger than definite limits (30 months for CI1 or 28 months for CIY or CIM) was considered to have been incompletely recorded and assigned as missing a CIY or CIM observation.

Contemporary groups for ages at first calving (AFC) were formed from year and farm at birth. Contemporary groups for calving intervals included year and farm at the calving starting the interval. Records from contemporary groups with less than 3 observations, or including daughters from just one sire have been eliminated from the analysis. After all restrictions applied the data file was summarized as shown in the Table 1.

Animal models were applied in three different approaches, named analysis A, B and C. In analysis A, a single trait random regression model was used to analyze calving intervals. In analysis B, a 4-trait analysis was conducted, including age at first calving and calving intervals regarded as three different traits for different moments of the cow's lifetime, CI1, CIY and CIM, as previously defined. In analysis C, a 2-trait analysis was performed, also including age at first calving and calving intervals, but with calving intervals regarded as a single trait in a repeatability model.

**Table 1**

Descriptive analysis of the phenotypic data for age at first calving (AFC), first calving interval (CI1), and subsequent calving intervals for young (CIY) or mature (CIM) females.

trait	N	Mean (months)	SD (months)	Min (months)	Max (months)
AFC	743	39.8	3.5	22.2	45.0
CI1	589	18.7	4.9	10.0	30.1
CIY	1712	16.6	4.6	8.9	27.9
CIM	2108	15.4	4.1	9.2	27.9

Ninety levels of calving contemporary groups entered into the random regression analysis of calving interval (analysis A). The calving interval solutions had minimum and maximum averages of 11.44 months and 21.03 months, respectively, and a standard deviation of 1.12 months.

In the case of the 4-trait analysis (analysis B), calving contemporary group averages by category are summarized in Table 2.

For the 2-trait analysis (analysis C), birth contemporary groups used for the analysis of AFC composed 88 categories, with minimum and maximum age averages of 29.52 months and 43.50 months, respectively, and a standard deviation of 1.38 months among groups. For the analysis of CI in the repeatability model, 111 contemporary groups were formed, with minimum and maximum averages of 12.64 months and 22.55 months, respectively, and a standard deviation of 1.03 months among groups.

The purpose of the random regression model was to provide knowledge about the longitudinal aspect of calving interval, to determine if there was heterogeneity of variance components. The purpose of the 4-trait analysis was to perform a multi-trait genetic evaluation including age at first calving and calving interval, while considering the problem of heterogeneous variances by segregating the interval trait according to age ranges. The purpose of the repeatability model was to determine if not accounting for the heterogeneity of variance would have a substantial impact of the ranking of sires.

In analysis A, calving interval was analyzed by fitting a random regression model with Legendre polynomials of order 3 fitted for the fixed effect of age at calving for both random animal and permanent environment effects. The model in matrix notation was:

$$y = Xb + Qu + Zpe + e,$$

where  $y$  was the vector containing the observed calving intervals;  $b$  was the vector of solutions for contemporary

**Table 2**

Statistics for the contemporary groups used for First Calving Interval (CI1), and subsequent Calving Intervals for Young (CIY) and Mature (CIM) females in the 4-trait analysis.

Trait	No. of levels	Minimum average (m)	Maximum average (m)	Standard deviation (m)
AFC	67	29.93	43.84	1.30
CI1	57	13.08	22.76	1.17
CIY	85	13.09	22.22	1.28
CIM	83	11.44	21.54	0.84

groups and fixed regressions, including equivalent inbreeding coefficients – fitted with linear and quadratic effects, age at calving and day of the year – both fitted by their Legendre polynomials of order 3;  $u$  was the vector of random regressions for the animal additive genetic effect;  $pe$  was the vector of random regressions for the permanent environment effect;  $X$  was the incidence matrix relating records to the systematic effects;  $Q$  and  $Z$  were covariable matrices containing the orthogonal polynomials relating the animal genetic and permanent environment effects to age at calving.

Average breeding values were calculated for the age range considered in the study in order to provide a unique solution for each animal and allow a comparison among approaches. The average estimated breeding value for calving intervals from 26 to 150 months of age for animal  $k$  ( $EBV_{k26-150}$ ) was calculated as:

$$EBV_{k26-150} = \mathbf{t} \mathbf{u}_k,$$

where  $\mathbf{t}$  is a row vector containing averages of orthogonal polynomials calculated for 26 to 150 months of age, and  $\mathbf{u}_k$  is a vector for the regression coefficient of animal  $k$ .

In analysis B, (co)variance component estimation was performed in a 4-trait analysis, based on the general model described by the following equation:

$$y = Xb + Za + Wpe + e,$$

where  $y$  was the vector containing phenotypic values for AFC, CI1, CIY and CIM;  $b$  was the vector of systematic effects, including contemporary groups, season, inbreeding and age, the last specifically for the calving interval traits;  $a$  was the vector of random animal additive genetic effects;  $pe$  was the vector of random permanent environmental effects, the last particularly for CIY and CIM;  $e$  was the vector of random residual effects; and  $X$ ,  $Z$  and  $W$  represented incidence matrices relating records to systematic, animal and permanent environmental effects, respectively. Contemporary groups were formed by year and farm at birth, in the analysis of age at first calving (AFC), or formed by year and farm at the calving starting the period, in the analyses of calving intervals (CI1, CIY and CIM). Linear and quadratic effects of equivalent inbreeding and the seasonal effect, using Legendre Polynomials of order 3, fitted to the day of the year, were included as covariates for all the four studied traits. The effect of age at the calving starting the intervals, using its Legendre Polynomials of the order up to 3 was included as a covariate for CI1, CIY and CIM.

In order to provide a unique solution for calving intervals, and allow a comparison among models, weighted means were calculated for the sires using each breeding value estimated for CI1, CIY and CIM with the multi-trait model. Each value was weighted proportionally to the number of months included in the age range covered by the respective trait. Thus, estimated breeding values for calving intervals from 26 to 150 months of age for animal  $k$  ( $EBV_{k26-150}$ ) were calculated as:

$$EBV_{k26-150} = (20 * EBV_{kCI1} + 35 * EBV_{kCIY} + 70 * EBV_{kCIM}) / 125,$$

where  $EBV_{kCI1}$ ,  $EBV_{kCIY}$  and  $EBV_{kCIM}$  were estimated breeding values of the animal  $k$  for CI1, CIY and CIM. Each weight in

the equation (20, 35 or 70) was proportional to the number of months included in the age range covered by the trait it represents, 26 to 45 months, 46 to 80 months or 81 to 150 months, respectively.

In analysis C, a 2-trait analysis was conducted including age at first calving and calving intervals. With this model, calving intervals were considered as repeated measures of the same trait along with each female's lifetime. The statistical model and effects used were the same for the 4-trait analysis.

All mixed model analyses were conducted by restricted maximum likelihood using the software Wombat – version 1.0 (Meyer, 2007). At convergence, the lower bound sampling covariances among parameters estimated were used to approximate sampling errors of covariance components and genetic parameters. Also, the curves for the fixed covariates fitted in the model were obtained from the generalized least-squares solutions. Differences between these solutions and each trait average were calculated as estimated effects according to the levels of the covariates. Raw means of the observations on each trait were also obtained according to the levels of the covariates. Differences between these raw means and each trait average have been calculated as the average observed differences according to the levels of covariates.

The effects of inbreeding in all models were fitted using increase in inbreeding coefficients, as described by González-Recio et al. (2007), modified by Gutiérrez et al. (2009), and applied to this same Guzerat subpopulation from this study by Panetto et al. (2010). The increase in inbreeding coefficient is a measure of inbreeding trend that is not biased with time because the number of known generations on the pedigree of each animal is taken into account. Traditional inbreeding coefficients tend to increase with time because recent animals usually have bigger numbers of known ancestors in their pedigrees, when compared to animals from previous generations. The increase in inbreeding coefficients was multiplied by the average number of equivalent complete generations to obtain equivalent inbreeding coefficients. Individual inbreeding coefficients, number of equivalent complete generations and individual increase in inbreeding coefficients were computed using the ENDOG program (Gutiérrez and Goyache, 2005).

Breeding values estimated with the three different approaches were used to build rankings of sires. A Spearman rank correlation analysis was performed using the software Statistica 7.1 (Statsoft Inc., 2003) for the comparison among results.

### 3. Results

#### 3.1. Fixed effects

The distribution of female's ages at calving is shown in Fig. 1, including reproductive records until 150 months of age.

With regard to the random regression approach (analysis A), solutions (standard errors in parenthesis) showing the effect of age at calving on CI, for the Legendre polynomials of order 3 were  $-1.3878 (\pm 0.4590)$ ,  $1.2186 (\pm 0.1912)$  and  $-0.4185 (\pm 0.1118)$ , respectively for the linear, quadratic

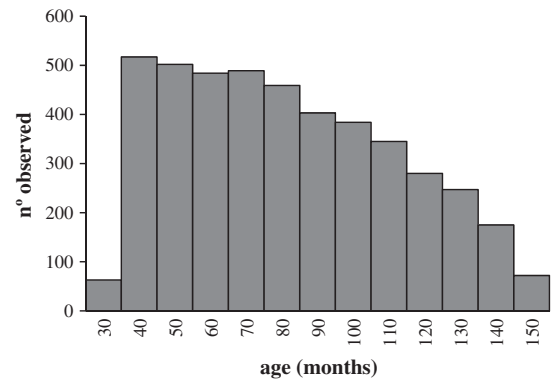


Fig. 1. Number of observations according to ages at calving.

and cubic effects. The observed deviations from average on calving intervals according to ages at calving and the predicted effect of age, obtained from the generalized least-square solutions, on calving intervals are presented in Fig. 2.

In analysis C, with the repeatability model, the effect of age on CI followed the same form as obtained for the random regression model (analysis A). Regarding the 4-trait analysis (analysis B): first calving intervals (CI1) were not significantly affected by age at calving, which could be due to the small age range used in the definition of that trait; calving intervals for young females (CIY) have been significantly affected by ages at calving, decreasing with the advance on age; calving intervals for mature females (CIM) were not significantly affected by age at calving.

Resulting from analysis A, the random regression approach solution (standard errors in parenthesis) shows the effect of inbreeding on CI, for the linear and quadratic effects were 0.0378 months ( $\pm 0.0225$ ) and 0.0006 months ( $\pm 0.0018$ ), respectively. Since the quadratic effect was not significantly different from zero, the observed effect observed for inbreeding was approximately linear. The observed deviations from average calving intervals according to equivalent inbreeding coefficients and predicted effects of inbreeding on calving intervals, obtained with the generalized least-square solutions from the random regression analysis are presented in Fig. 3.

From analysis B or analysis C, 4-trait or 2-trait approaches, the predicted effects of inbreeding on calving intervals

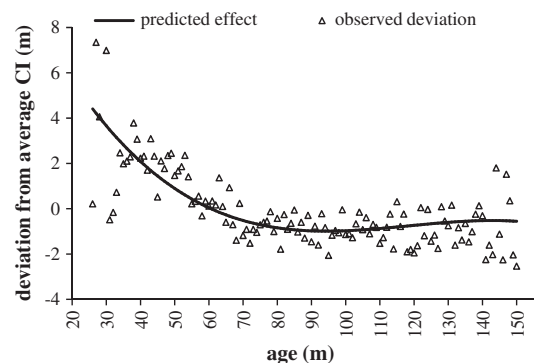
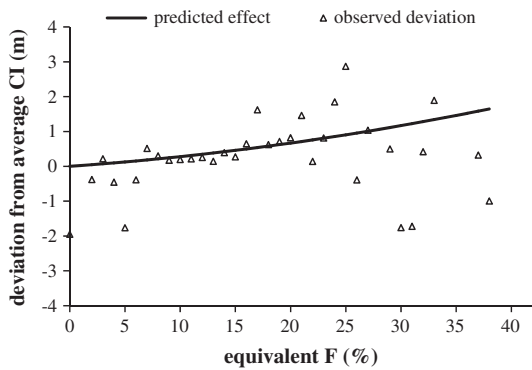


Fig. 2. Predicted effect of age on calving intervals (CI) and observed deviations from average CI, according to ages at calving.



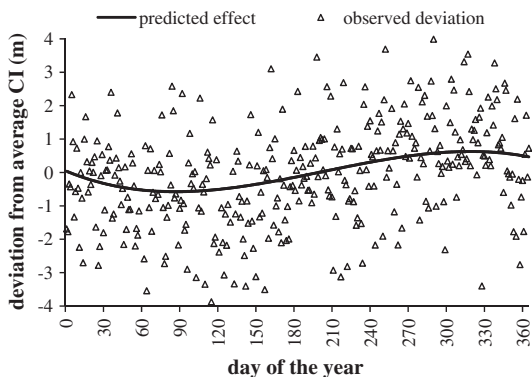
**Fig. 3.** Predicted effect of inbreeding on calving intervals (CI) and observed deviations from average CI, according to equivalent inbreeding coefficients.

followed the same pattern obtained with the random regression model, with a quasi-linear increase of the calving intervals resulting from increased equivalent inbreeding coefficients. Solutions for the effect of inbreeding on ages at first calving resulted in linear increases of about 0.03 months for each 1% increase in the equivalent inbreeding coefficients. However, those results were not statistically significant within this study.

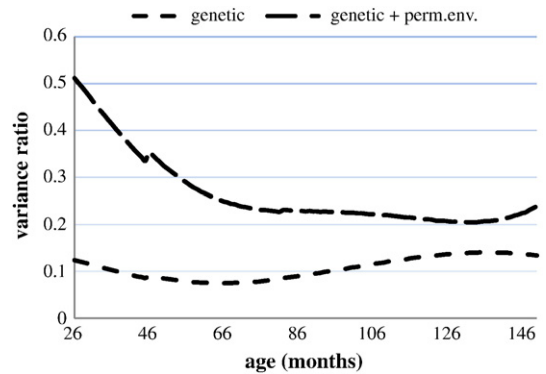
The solutions (standard errors in parenthesis) showing the seasonal effect on AFC, for the Legendre polynomials of the order 3 were  $-0.6476 (\pm 0.1835)$ ,  $0.2387 (\pm 0.1796)$  and  $0.4309 (\pm 0.1795)$ , respectively for the linear, quadratic and cubic effects. These results obtained with the 4-trait analysis (analysis B) showed that animals born in the first five months of the year tended to have their first calving at a later age than animals born in the second half of the year.

From the random regression analysis, the solutions (standard errors in parenthesis) show that the seasonal effect on CI, for the Legendre polynomials of the order 3 were  $0.5544 (\pm 0.0915)$ ,  $0.1591 (\pm 0.0900)$  and  $-0.2479 (\pm 0.0897)$ , respectively for the linear, quadratic and cubic effects. The observed deviations from average on calving intervals according to the day of the year and the predicted effect of the day of the year, obtained from the generalized least-square solutions, on calving intervals are presented in Fig. 4.

The seasonal effect on CIY and CIM followed the same pattern obtained with the random regression analysis on



**Fig. 4.** Predicted effect of the day of the year on calving intervals (CI) and observed deviations from average CI, according to the day of the year.



**Fig. 5.** Genetic and permanent environment variance ratios.

which the shortest calving intervals were obtained for animals calving between the months of March and May, and the longest ones for animals calving between the months of October and December.

### 3.2. (Co)variance components estimates

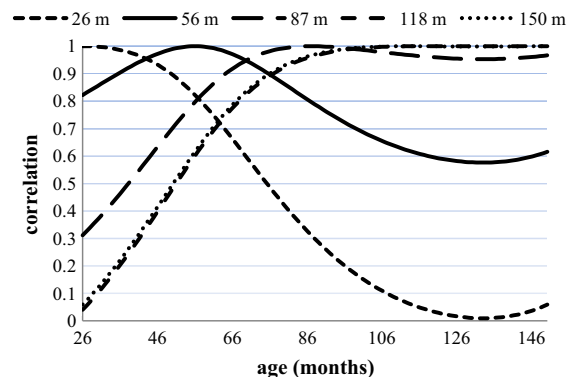
From analysis A, estimated animal additive genetic and permanent environment variance ratios obtained for calving intervals according to ages of cows at calving are represented in Fig. 5.

Correlations among estimates at different ages are shown in Fig. 6, for the genetic effects, and in Fig. 7, for the permanent environmental effects.

Estimates resulting from analysis B, including animal additive genetic, permanent environment and residual (co)variance ratios with sampling errors on the parenthesis, are summarized on Table 3.

Estimates resulting from analysis C, including animal additive genetic, permanent environment and residual (co)variance ratios with sampling errors on the parenthesis, are summarized on Table 4.

Heritability coefficients for calving intervals obtained from the random regression analysis had the same trend as the multi-trait analysis, of increased values for observations at younger ages, but seemed to be more similar among observations at different ages. At the same age range than CI1, CIY and



**Fig. 6.** Correlations among parameters estimated at various different age points for genetic effects: 26, 56, 87, 118, and 150 months.



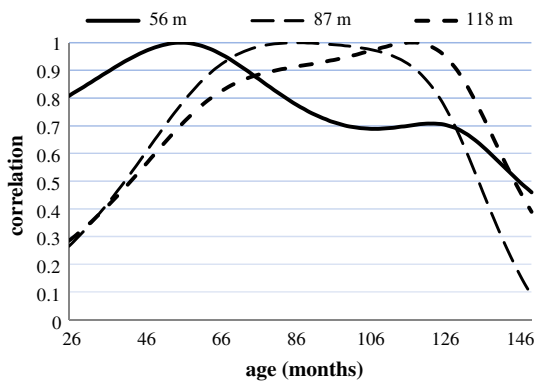


Fig. 7. Correlations among parameters estimated at various different age points for the permanent environmental effects: 56, 87 and 118 months.

CIM, the average heritability coefficients from the random regression analysis were 0.13, 0.10 and 0.10 respectively.

Variance ratios for the permanent environmental effects on CIY and CIM were 0.18 and 0.09, respectively. From the random regression analysis, the average values were 0.18 and 0.11 for the same average age ranges. In the case of the 2-trait analysis, the random permanent effect ratio for CI was 0.13.

Comparing residual variances for the age ranges of CIY and CIM, they have been similar for the random regression or multi-trait models, ranging from 13.21 to 13.36 months<sup>2</sup> within both approaches. Regarding CI1, residual variance has been higher ( $p < 0.01$ ) for the multi-trait model (21.48 months<sup>2</sup>) when compared with the random regression model (14.97 months<sup>2</sup>). For the repeatability model, the estimated residual variance and sampling error in the parenthesis for calving interval was 14.44 (0.36).

Genetic correlations between age at first calving and calving intervals were not significantly different from zero in any approach. Genetic correlations among the 3 calving interval traits analyzed in the multi-trait model were not different to what was obtained with the random regression model

Table 3

Variance component ratios and correlations estimated within the 4-trait approach, followed by their sampling errors in the parenthesis, for age at first calving (AFC), first calving interval (CI1), and calving intervals observed for young (CIY) and mature (CIM) females.

Trait	(Co)variance component ratios			
	AFC	CI1	CIY	CIM
<i>Animal additive genetic effects</i>				
AFC	0.373 (0.099)	-0.169 (0.348)	0.030 (0.329)	-0.011 (0.254)
CI1		0.119 (0.082)	0.932 (0.329)	0.299 (0.365)
CIY			0.064 (0.039)	0.582 (0.286)
CIM				0.109 (0.040)
<i>Permanent environmental effects</i>				
CIY			0.182 (0.043)	0.714 (0.166)
CIM				0.090 (0.034)
<i>Residual effects</i>				
AFC	0.627 (0.099)	0.099 (0.089)	0.152 (0.074)	0.043 (0.063)
CI1		0.881 (0.082)	0.196 (0.062)	0.182 (0.053)
CIY			0.671 (0.033)	0.039 (0.038)
CIM				0.801 (0.028)

Table 4

Variance component ratios and correlations estimated within the 2-trait approach, followed by their sampling errors in the parenthesis, for age at first calving (AFC) and calving interval (CI).

Trait	(Co)variance component ratios	
	AFC	CI
<i>Animal additive genetic effects</i>		
AFC	0.366 (0.099)	0.089 (0.240)
CI		0.086 (0.029)
<i>Permanent environmental effects</i>		
CI		0.130 (0.025)
<i>Residual effects</i>		
AFC	0.634 (0.099)	0.091 (0.050)
CI		0.784 (0.019)

(Fig. 6), but were not in agreement with the assumption of the repeatability model, in which the genetic correlation between calving intervals measured at different ages should be equal to one. The permanent environment correlation between CIY and CIM was also in agreement with those observed for the random regression model.

### 3.3. Ranking of sires

Comparison among estimated calving interval breeding values of 57 sires, all of them with minimum accuracy of 0.5 for the three approaches, resulted in rank correlations ( $p < 0.01$ ) of 0.90 between the results from the multiple trait analysis and the random regression analysis, 0.93 between the repeatability analysis and the random regression analysis, and 0.95 between the multiple trait analysis and the repeatability analysis.

## 4. Discussion

Calving intervals tended to decrease with age until animals were nearly 80 months old. After this point, age did not cause any influence on the length of calving intervals, as can be observed in Fig. 2. Peña et al. (2008) have found a decrease in the calving intervals from the first to the fifth calving when studying Zebu beef females in Cuba. The results of the present study are in agreement with their findings. Yagüe et al. (2009) found a constant increase in the calving intervals of Rubia Gallega females in Spain, beginning at early ages. One possible explanation for this difference among studies could be that Zebu females take longer to reach their complete maturity, and would reduce their calving intervals until their late maturity.

To illustrate the effect of inbreeding on calving intervals, using results from analysis A, a cow whose parents were half sibs with no previous inbreeding on common ancestors (12.5% inbreeding) would be expected to present an average delay on its calving intervals of approximately 11 days. In the case of daughters of full sibs, also with no previous inbreeding on common ancestors (25% inbreeding), the expected average delay would be around 27 days.

The fact that animals born in the first five months of the year tended to have their first calving at later ages than animals born later in the year may be related to the fact that the

dry season where this population was raised usually occurs from May to November, and the average daily milk yield usually decreased significantly around the fifth month of lactation. Thus, one possible explanation for this results would be that animals weaning during the dry season were exposed to low quality pasture, and had slower growth and consequently also a later sexual development.

The trend of animals calving in the first part of the year to have shorter calving intervals was valid for all the different statistical approaches applied to the present study. One explanation would be that animals with good pasture conditions during the period of high nutritional demands, corresponding to the beginning of their lactations, would be more likely to get pregnant earlier after calving. Those animals with low quality pasture conditions during this period would enter a state of negative nutritional balance and thus increase their time to re-conceive.

When comparing the seasonal effects among CI1, CIY and CIM in analysis B, they became more evident for calving intervals observed at older ages. One speculation would be that younger animals would still be growing and, for this reason, would be more affected by the previous calving and by the high nutritional demand period of the beginning of their lactations, resulting in a shrinking of the seasonal effect. On the other hand, seasonal effects became more evident for mature animals.

The heterogeneous aspect of variance components and variance ratios of calving intervals can be noticed through the observation of the curves on Fig. 5, where the genetic and permanent environment variance ratios are reduced with increased ages of the animals up to a certain point of their lifetimes.

Genetic correlations between calving intervals in very young females and calving intervals in older females decreased as the age on the second group increased (26-month curve in Fig. 6). Such trend gives good reason for first calving interval (CI1) to be measured as a separated trait in the multi-trait approach of the study, and also for the repeatability model to fail in considering the variance structure of calving intervals observed at different ages.

Genetic effects estimated for calving intervals of young females (56-month curve in Fig. 6) kept reasonably high correlations, more than 0.8, with estimates for younger ages, but smaller correlations with estimates for intervals of older females. Genetic effects related to older females (87, 118, and 150-month lines in Fig. 6) were highly correlated among each other (values above 0.9), but correlations were decreased with estimates for intervals of young and very young females. These results indicate the existence of heterogeneous variances of calving intervals observed at different ages. The last three curves in Fig. 6 indicate that from the age of 80 months and above, the correlations among estimates from intervals at different ages were constantly high, and thus the maturity of animals would have been reached. The segregation between young and mature females for the multi-trait approach of the study can be justified with this indication.

Permanent environmental effects could not be properly accessed for estimates for the youngest or the oldest animals because of lack of repeated records at these age ranges. Regarding intermediate age ranges, estimates for young animals

(56-month curve in Fig. 7) held intermediate correlations (around 0.7) with estimates for mature animals. Correlations between estimates for mature animals (87 and 118-month curves in Fig. 7) were very high (above 0.9) for the range between 87 and 118 months of age.

These findings indicated that an approach regarding first calving interval, young calving intervals, and mature calving intervals as separate traits, in a multi-trait analysis, would be suitable to accomplish a proper female's lifetime fertility evaluation in a situation where calving intervals are the only available information.

Balieiro et al. (2003) has estimated the value of 0.18 for the heritability coefficient of age at first calving, observing Zebu dairy cows of the Gyr breed. Panetto et al. (2008), in a previous study using a subset of the data from the same sub-population analyzed in the present study, between the years 1941 and 2005, estimated a heritability coefficient of 0.20 for age at first calving. The higher value found in the present study (0.37) can be explained by the data editing criteria, with a restriction applied for the maximum age allowed to consider a record as first calving. After many attempts with different upper limits to AFC, it has been realized that when observations from animals calving for the first time after 45 months of age were included, residual variances increased but genetic variances did not increase (results not shown). Such data have been excluded from the analysis conducted in the present study, but were kept in the studies of Balieiro et al. (2003) and Panetto et al. (2008), where average ages at first calving were 45.52 and 45.34 months, respectively.

Most calving intervals evaluations in the literature have been conducted using repeatability models (De Haas et al., 2007; Facó et al., 2008; Yagüe et al., 2009), with heritability coefficients that ranged from 0.05 to 0.10.

Some authors have studied fertility with consideration to the heterogeneous nature of its variance components. Balieiro et al. (2003) has studied the first, second and third calving intervals as separated traits, founding heritability coefficients of 0.07, 0.05 and 0.05 respectively. The age range for second and third calving intervals in the study of Balieiro et al. (2003) would fit the definition of CIY in the present study. Peña et al. (2008) have studied days open for the first five calves of each cow as five separated traits in Cuban Zebu beef females. They have estimated values that ranged from 0.06 to 0.08 for the heritability coefficients. In the same study, Peña et al. (2008) have estimated a heritability coefficient of 0.10 for calving intervals, treated as a single repeated trait, and have concluded that number of days open and calving intervals could be considered as the same trait, because of the genetic correlation close to the unit between them. Heritability coefficients estimated for calving intervals in the present study (ranging from 0.064 to 0.141) were in the same range or higher than what have been found in the literature.

Urioste et al. (2007) have analyzed calving day as a fertility trait, defined as the number of days from the beginning of a herd's calving season to the cow's calving date. They considered the first three opportunities of calving as three separated traits. Although it's a different trait than calving interval, the evaluation has also been about intervals depending upon the animal's fertility, observed at a fixed age. In the present study the separation of calving interval traits were independent from previous records of each cow, but dependent only on

the age of the cow at calving. Urioste et al. (2007) have estimated heritability coefficients ranging from 0.19 to 0.23 for calving day, which have been higher than the values for the observations at similar age ranges in the present study, which have been 0.119 for CI1 and 0.064 for CIY.

Urioste et al. (2007) have estimated correlations above 0.82 among calving days at the first three opportunities, in agreement to the present study. Similar results have been found by Peña et al. (2008), that have estimated correlations close to the unit among the three first calving intervals, but the correlations of the first two with the fourth or fifth calving intervals have been always below 0.7, also in agreement with what was found in the present study.

Despite of all high rank correlation results observed among the different approaches, significant differences between ranks of some sires were observed. When compared against the rank obtained with the random regression analysis, the average deviation of the multiple trait analysis rank was 4.9 and the maximum was 31 positions. In the case of the repeatability analysis, the average deviation from the random regression analysis rank was 4.3 and the maximum was 25 positions. These results indicate that differences among approaches could cause important differences in sires chosen by breeders and consequently in the genetic progress of the herd, depending on the chosen sires.

## 5. Conclusion

Differences among genetic variance components for calving intervals observed along the animal's lifetime suggested that segregation among observations at different age ranges and use of multi-trait models, or the use of random regression models, would be useful approaches to be applied when accessing the fertility of Zebu dairy females when the available information relies on their calving intervals. Changes observed for the ranking of sires suggested that the genetic progress of the herd can possibly be affected by the approach chosen for the analysis of calving intervals.

## Conflict of interest statement

The authors confirm that there was no conflict of interest involved in the present study, which could possibly influence their work.

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