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Genetic variability of Guzerat cattle raised in northern Brazil, based on pedigree analysis

[*Variabilidade genética do gado Guzerat criado no norte do Brasil,
com base na análise do pedigree*]

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ABSTRACT

Genealogical data comprised 45,711 animals born between 1901 and 2016, with 48,127 animals in the pedigree file. Population structure was analyzed in terms of pedigree completeness, individual inbreeding coefficient (F), generation interval (L), rate of inbreeding (ΔF), effective population size (N_e), effective number of founders (f_f), and effective number of ancestors (f_a). The herd initially consisted of 13 bulls and 14 cows, and there were variations in the number of selected bulls and cows throughout the analyzed period, with 2,575 bulls, 13,691 cows, and 45,711 births recorded at the end of 2016. In total, 48.81% of the cows had only one progeny. Most dams (47.59%) were between three and seven years old, with a mean L in the population of 7.9 years. According to the results, 52.75% of the cows, 44.92% of the bulls, and 63.71% of the calves of the Guzerat breed in the northern region of Brazil showed some degree of inbreeding, with small-magnitude coefficients (0.56, 0.83, and 0.71% for cows, bulls, and calves, respectively). This fluctuation did not hinder the genetic evolution of the herd in the region. The effective population size does not seem to compromise the maintenance of genetic variability in the breed.

Keywords: ancestor, effective size, founder, generation interval, inbreeding

RESUMO

Os dados genealógicos compreenderam 45.711 animais nascidos entre 1901 e 2016, com 48.127 animais no arquivo de pedigree. *A estrutura populacional foi analisada em termos de completude de* pedigree, *coeficiente de endogamia individual (F), intervalo de geração (L), taxa de endogamia (ΔF), tamanho efetivo da população (Ne), número efetivo de fundadores (ff) e número efetivo de ancestrais (fa). O rebanho consistia inicialmente de 13 touros e 14 vacas, e houve variações no número de touros e vacas selecionados ao longo do período analisado, com 2.575 touros, 13.691 vacas e 45.711 nascimentos registrados no final de 2016. No total, 48,81% das vacas tiveram apenas uma progênie. A maioria das barragens (47,59%) tinha entre três e sete anos, com média de L na população de 7,9 anos. De acordo com os resultados, 52,75% das vacas, 44,92% dos touros e 63,71% dos bezerros da raça Guzerá na região Norte do Brasil apresentaram algum grau de endogamia, com coeficientes de pequena magnitude (0,56, 0,83 e 0,71% para vacas, touros e bezerros, respectivamente). Essa flutuação não impediu a evolução genética do rebanho na região. O tamanho efetivo da população não parece comprometer a manutenção da variabilidade genética na raça.*

Palavras-chave: ancestral, tamanho efetivo, fundador, intervalo de gerações, endogamia

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INTRODUCTION

The beef cattle industry in northern Brazil is of great importance for the local and national economy. For the beef production system to be efficient and profitable, knowledge of population and genetic-phenotypic parameters as well as of trends of production and reproduction traits in the herd is paramount. This is especially due to the low number of herds assessed, which hinders the process of selecting genetically superior animals for breeding (Lopes *et al*., 2017; Ferreira *et al*., 2017).

The Guzerat breed is highly adaptable and exhibits good meat and milk production performance. Thus, there is a growing interest in raising or using it in different production systems, particularly in crosses with European breeds. Guzerat was the first zebu breed to be introduced in Brazil, and its history dates to the mid-1870s, when it was widespread in Rio de Janeiro (Santiago 1970, 1984). Today, it is present in all regions of the country, where it is well-adapted to the climate and the different existing production systems (Pacheco *et al*., 2008).

Studies on the genetic trends, genetic parameters, and population structure of the Guzerat breed in some regions of Brazil are scarce, especially in the northeast. According to census data (Produção Pecuária Municipal (IBGE) 2020), the Brazilian northeast had the highest growth in cattle herd size (22%, versus the national average growth of 4%). Nevertheless, most of the Brazilian cattle herd is still concentrated in the *cerrado* biome region (Rivero *et al*., 2009; Assad, 2016).

As stated by Gomes *et al.* (2017), Brazilian livestock underwent a process of modernization supported by advances in production systems and the organization of the production chain, which had an impact on the quality of beef. According to McMannus *et al.* (2016), this rapid growth and modernization occurred mainly in the north and center-west regions of Brazil, especially from the beginning of this century.

Considering the evolution of the Brazilian herd from 1994 to 2014 by region and states of the federation, over the last 30 years, cattle farming (beef, mainly) has migrated to the Legal Amazon. While the herds in the south, southeast, and northeast regions grew 34.9, 3.77, 2.41, and 28.59%, respectively, the Legal Amazon cattle herd grew 136.67% (Neiva *et al*., 2016).

Zebu breeds (*Bos primigenius indicus*) play an important role in meat production and livestock development in several regions of the country, particularly in the northeast. As mentioned by Santana Júnior *et al.* (2016), about 80% of the national herd consists of zebu breeds or their crosses, due to their undeniable adaptability and good reproductive capacity in hot weather and rainy conditions, besides their ability to resist parasites.

However, this herd has been subjected to an intense process of selection and mating, which may involve some degree of subdivision that may increase inbreeding and consequently reduce genetic diversity in the herd (Cervantes *et al*., 2008, 2011).

This strong growth further warrants the need for information about the genetic evolution and genealogical architecture of breeds. The structure of a population is assessed through estimates of herd size, inbreeding, average co-ancestry coefficient, and effective number of founders and ancestors, which are used to reduce problems that may affect genetic progress or selection.

The evaluation of genetic diversity, structure, and gene flow based on pedigree data has been widely used across different herds/species for conservation and breeding purposes (Santana Júnior *et al*., 2016). Studies based on pedigree analysis have been carried out for different breeds in Brazil, the majority of which revealed problems in effective population size, increases in mean inbreeding (Faria *et al*., 2009; Malhado *et al*., 2009; Peixoto *et al*., 2010), and bottlenecks in the pedigree.

Therefore, the present study was undertaken to analyze the population structure of Guzerat cattle raised in the northern region of Brazil, focusing on the parameters of effective size, generation interval, degree of inbreeding, and contribution of ancestors.

MATERIAL AND METHODS

Genealogical records of 45,711 animals (born between 1901 and 2016) were considered. All data were provided by the Brazilian Association of Zebu Breeders (ABCZ). The generation interval (L) was considered as the mean age of parents at the birth of their selected offspring (with progeny records) (Falconer and Mackay, 1996). The L was calculated along the four possible selection pathways, namely, sire to male offspring; sire to female offspring; dam to male offspring; and dam to female offspring. Accordingly, the average L was considered as the arithmetic mean of these four selection lines.

The generation interval (L) was determined using the equation below, considering the four selection pathways, sire to male offspring (L_{mm}), sire to female offspring (L_{mf}), dam to male offspring (L_{fm}), and dam to female offspring (L_{ff}):

$$\boldsymbol{L} = \frac{\mathbf{Lmm+Lmf+Lfm+Lff}}{\mathbf{4}}$$

The effective population size (N_e) was calculated considering all pedigree information. The calculation was made each year based on the rate of inbreeding (ΔF) and on census information (i.e., the number of males and females), using the following formula: $N_e = 1/2\Delta F$ (Falconer and Mackay, 1996).

The N_e is the number of individuals that would originate the observed or calculated rate of inbreeding, if mating were random and equally likely. The rate of inbreeding per generation was calculated by the formula below (Falconer and Mackay, 1996):

$$\boldsymbol{\Delta F} = \frac{\boldsymbol{F_t - F_{t-1}}}{\boldsymbol{1 - F_{t-1}}}$$

where F_t and F_{t-1} are the average inbreeding coefficients of the offspring and their parents.

Pedigree completeness was calculated by the algorithms developed by MacCluer *et al.* (1983). This procedure summarized the proportion of known ancestors in each ascending generation. This parameter quantifies the change in detection of inbreeding in the pedigree (Sørensen *et al.*, 2005). The following equations were used:

$$\boldsymbol{I_d = \frac{4I_{dpat}I_{dmat}}{I_{dpat}+I_{dmat}}} \qquad \boldsymbol{I_{dk} = \frac{1}{d}\sum_{i=1}^{d} a_i}$$

k = pat, mat, where K represents the paternal or maternal line of an individual; a_i is the proportion of known ancestors in generation i; and d is the number of generations considered in the calculation of the complete pedigree.

Values can range from 0 to 1. If all ancestors are known, then Id = 1; if one parent is unknown, then Id = 0. Founders were assumed to be ancestors with unknown parents. The effective number of founders (f_e) was calculated by the following formula (Lacy, 1989): $\boldsymbol{f_{e=\{1|\sum p^2\}}}$,where p_i is the proportion of the genes of the descendant population contributed by founder i.

The effective number of ancestors (f_a) was proposed by Boichard *et al.* (1997), as the minimum number of ancestors that explain the same level of genetic diversity as the reference population. This variable was calculated by the following formula: $\boldsymbol{f_a = \frac{1}{\sum(q_i^2)}}$, where q_i is the marginal genetic contribution of ancestor i. The population bottleneck was calculated as the ratio of f_e to f_a (f_e/f_a) (Boichard *et al.*, 1997).

All population parameters and inbreeding rates were estimated using the CFC (Sargolzaei *et al.*, 2006) and POPREP (Groeneveld *et al.*, 2009) software packages.

After the genetic contribution of the founders was calculated, results were transformed into a percentage by dividing each contribution by the sum of all contributions. Founders whose contribution to the reference population was greater than 1% were selected to investigate the formation of founder lines in the reference population (Bussiman *et al.*, 2022).

For this analysis step, the most influential founders ($p \geq 1\%$) were treated as variables and their coefficient of kinship with each animal in the reference population was treated as observations. This new database was subjected to principal component analysis (PCA), as proposed by Costa *et al.* (2005) and adapted by Bussiman *et al.* (2022).

Initially, the adequacy of PCA to the data was checked by the Bartlett test ($P = 0.001$) and the number of principal components (PC) was determined by the Kaiser criterion. The first two PCs were used to graphically visualize the clustering between founders in a biplot. In this way, founders that remained clustered in the resulting biplot were assumed to form a line in the reference population.

Principal component analysis was conducted using the "*principal*" function of the "psych" package (Revelle, 2017), available in R software/language (Core Team, 2016), and adopting varimax rotation.

RESULTS AND DISCUSSION

The Guzerat herd of the northern region was initially constituted, in 1901, by 13 bulls and 14 cows. Throughout the analyzed period, there were variations in the number of selected bulls and cows, with 2,575 bulls, 13,691 cows, and 45,711 births registered at the end of 2016. Figure 1 shows the evolution of breeding bulls and cows and calves over the analyzed years. A significant evolution in the number of animals only occurred from the 80s. However, the number of bulls selected as parents remained practically stable. The mean age of bulls (sires) was 8.7 years, whereas the cows (dams) were on average 5.9 years old.

These numbers are possibly associated with the period of animal registration, since registration and control by the Brazilian Association of Zebu Breeders (ABCZ) only began in the mid-60s.

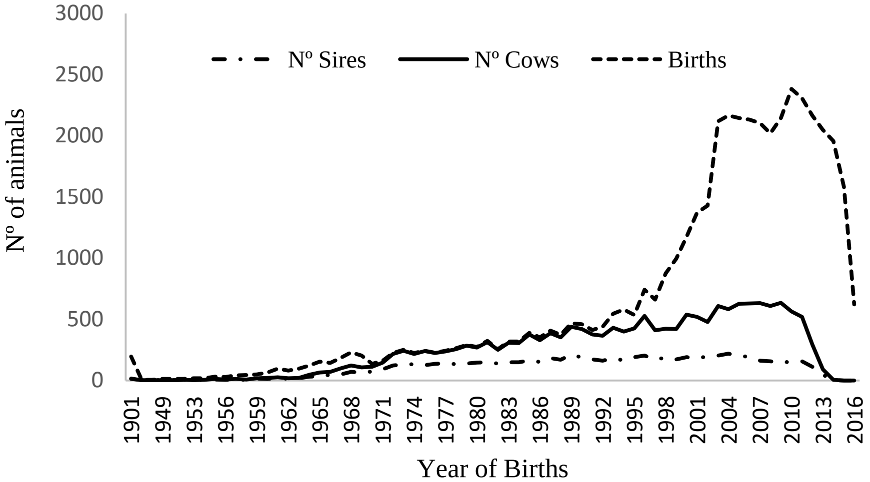

Figure 1. Number of bulls, cows, and births in the Guzerat cattle population raised in the northern region of Brazil from 1900 to 2016.

Figure 2A shows the mean age of the parents (bulls and cows) relative to the proportion of offspring. In the period from 1960 to 1980, the age of the parents (bulls and cows) used in the herd was high, indicating an increase in inbreeding and a low replacement rate. Furthermore, in the Guzerat herd of the northern region, 48.81% of the cows had only one offspring, 20.89% two, and 11.49% three (Fig. 2B). Additionally, the highest proportion of dams was between three and seven years old, corresponding to 47.59% of the total, and the average generation interval in the population was 7.9 years.

The generation interval (L) between sire-son, sire-daughter, and dam-daughter was practically equal to that of the general population, which shows that the replacement of males and females was practically similar. These values (sire-son, sire-daughter) are lower than those calculated by Faria *et al*. (2009) for the Nellore (10.7 and 10.5 years), Gir (9.9 and 9.5 years), and Guzerat (10.9 and 10.8 years) breeds. This reduction in the average generation interval was possibly essential for the evolution and genetic gain of the population under study, as well as to keep inbreeding relatively low in the population and favor genetic gain using genetically superior young bulls.

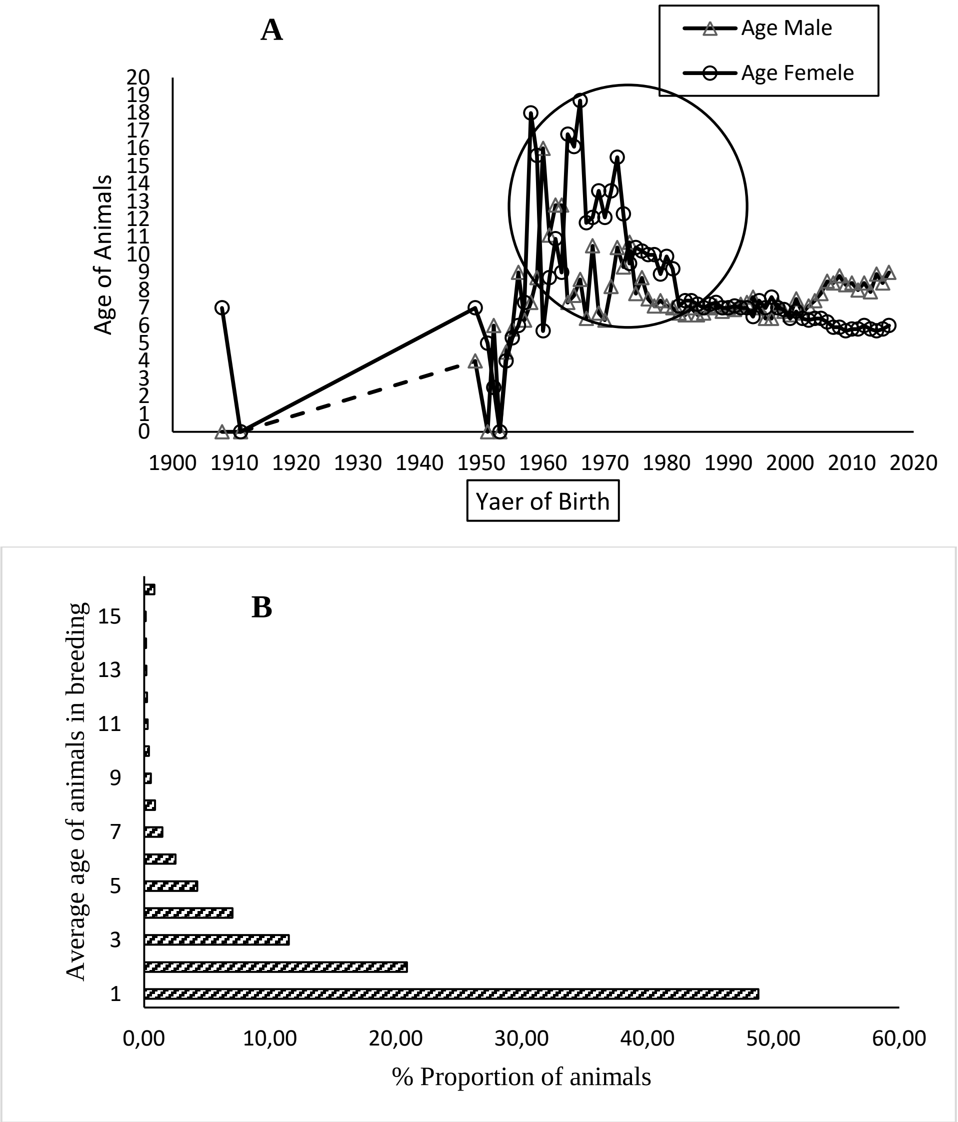

Figure 2**.** Mean age of parents (cows and bulls) (Fig. 2A) and proportion of offspring per cow (Fig.2B) of the generations of the population of Guzerat animals raised in the northern region of Brazil.

The mean age of the cows (dams) was lower (5.9 years) than that of the bulls (8.7 years). This could mean that some bulls were used repeatedly, without a quicker replacement with their offspring. This continuous use of bulls for long periods is a common practice in Brazilian livestock, especially in the case of herds in formation, and/or in the introduction of herds for colonization, as is the case in the Amazon region. This practice can result in longer generation intervals, low genetic gain, overlapping generations, and greater variations in population size. The consequence of increased variation in family size is an increase in the rate of inbreeding and a reduction in the effective size of the population (Vercesi Filho *et al*., 2002; Carneiro *et al*., 2009; Peixoto *et al*., 2010; Amaral *et al*., 2019).

However, a high proportion of older cows was found to bear offspring in the population. The cow/bull ratio varied widely between years, but this ratio remained low until the mid-1990s, when there was a change. This was likely a consequence of the organization of producers; differences in reproductive management, with the use of reproductive biotechnologies; and the selection intensity imposed (Vozzi *et al.*, 2006; Santana Júnior *et al.*, 2016; Pezzini *et al.*, 2018; Amaral *et al.*, 2019).

The proportion of known parents in each pedigree generation, for animals born in the last 10 years, was 95.8% for one complete generation, 92.9% for two, 90.3% for three, 87.7% for four, 84.6% for five, and 80% for six complete generations. Figure 3 illustrates the average proportion of complete pedigrees in the generations established in the population.

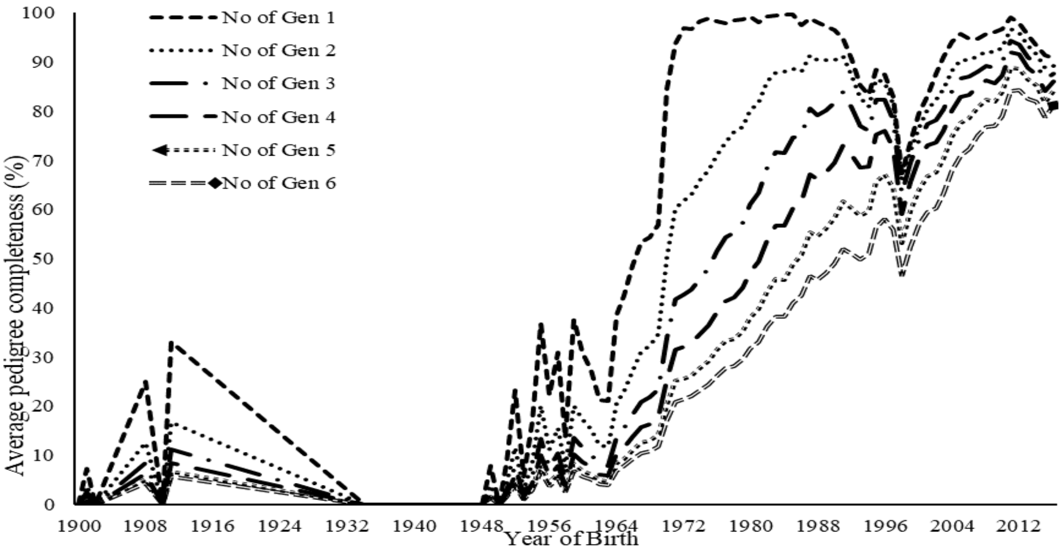

Figure 3**.** Proportion of complete pedigrees per generation of the Guzerat population raised in the northern region of Brazil.

Over the years, as occurred in the percentage of pedigree completeness, there was an increase in the average inbreeding coefficient (F). This can be explained by the fact that the more complete generations of an individual are known, the greater the possibility of an important ancestor appearing several times in the pedigree (Peixoto *et al.*, 2010; Santana Júnior *et al.*, 2016; Amaral *et al.*, 2019).

According to Queiroz *et al.* (2000), the increase in F over the generations, as observed in the present study, can be explained by the structure of the herd itself, where the founder animals are little related or of unknown ancestry. Over time, the occurrence of mating within the herd increases the degree of kinship between individuals, thereby increasing inbreeding.

In terms of conservation of genetic diversity, long generation intervals favor the process of inbreeding and genetic drift in the herd, possibly due to the use of sires for excessively long periods. Santana Júnior *et al.* (2016) commented that this was a common practice in Brazilian livestock, mainly due to the use of elite/famous bulls as parents of future generations for long periods.

The generation intervals in the sire-son and sire-daughter pathway were similar (7.9±2.94 and 7.9±1.18, respectively) (Table 1), and can be considered high and similar to the others found for zebu breeds raised in Brazil (Reis Filho, 2010; Oliveira *et al.*, 2011).

These high estimates are attributed in part to the hardiness and high age of the cows at calving (seven years, on average) and their low replacement rate. The reduction in genetic gain per unit of time, with lower economic returns, is the main consequence of long generation intervals. This is especially true for the 1960-1980 period, when the age of the parents (bulls and cows) used in the herd was high, which led to increased inbreeding due to the low replacement rate.

Table 1. Mean and standard deviation (SD) of the generation interval (L) and number of observations (N) in Guzerat animals raised in the northern region of Brazil

Pathway	N	L (years)	SD
Sire-son	2060	7.9	2.94
Sire-daughter	14978	7.9	1.18
Dam-son	2154	8.2	5.03
Dam-daughter	14900	7.7	3.27
Males	17038	7.9	1.49
Females	17054	7.8	3.30
Population	18154	7.9	1.99

N = number of individuals; L = generation interval; SD = standard deviation.

Overall, the average generation interval was 7.9 years. This result is possibly due to the introduction of bulls of other origins through insemination, as opposed to using bulls from their own herd, in addition to the practice of planned mating, carried out in most herds (Weigel and Lin, 2000; Caballero and Toro, 2002; Colleau *et al*., 2004).

Mating plans that minimize co-ancestry between pairs constitute a robust tool to maximize N_e (Caballero and Toro, 2002), in addition to reducing inbreeding and its consequences. Completeness of pedigree data is relevant to the accuracy of assessments of animal genetics and the rate of genetic progress (Weigel, 2001; Cassel *et al*., 2003).

Eleven inbreeding classes were defined in the analysis of the variability of the individual inbreeding parameters of the Guzerat cattle population in the northern region of Brazil. Of the total individuals, 90.47% showed an F between 0 and 5%; 6.52% between 6 and 10%; and 1.95% between 11 and 15%.

According to the results, 52.75% of the Guzerat cows, 44.92% of the bulls, and 63.71% of the calves raised in the northern region of Brazil showed some degree of inbreeding and estimates of the mean inbreeding coefficients were of small magnitude (0.56, 0.83, and 0.71% for cows, bulls, and calves, respectively). The average inbreeding coefficient in the herd has a minimum value of zero (0.0), a maximum value of 13.99, a mean of 0.79 with a standard deviation of 1.73, and a rate of inbreeding per generation of 0.0121. Among the inbred animals, the average coefficient had a minimum value of 0.62, a maximum value of 13.99, and a mean of 3.12 with a standard deviation of 2.70.

In a study on inbreeding in Gir herds, Queiroz *et al.* (2000) also obtained low average inbreeding coefficients: 1.04, 0.96, and 1.66% for cows, bulls, and calves, respectively. In Nellore herds registered with ABCZ, Faria *et al.* (2002) described average inbreeding coefficients of 0.90, 1.03, 1.60, and 2.13 over four different evaluation periods. Gutierrez *et al.* (2003) stated that the average inbreeding coefficient can vary over generations, having a direct dependence on pedigree completeness.

In a study with an isolated herd of the Guzerat breed, Oliveira *et al.* (2011) obtained average F values of 1.08 and 1.36% for males and females, respectively. Similarly, in an evaluation with data from the Brazilian Association of Zebu Breeders (ABCZ) Faria *et al.* (2009) reported an increase in the average inbreeding coefficient over the years (1979-1998), which reached 2.13, 2.28, and 1.75% for the Nellore, Gir, and Guzerat breeds, respectively.

The low degree of inbreeding observed in the Guzerat herd from farms in the northern region of Brazil was expected, since many generations (approximately 11) were detected (Table 2). Thus, it is understood that those responsible for the formation of the herds sought to avoid inbred mating, since the degree of kinship between individuals is not high, on average.

However, in analyzing the number of founders in the population, we found that 10 ancestors contributed more than 1% to the formation of the population, which ranged from 3.19 to 1.09%, as shown in Table 3.

Table 2. Number of animals by class of inbreeding coefficients (F) and respective percentages for Guzerat cattle raised in the northern region of Brazil

F class *(%)*	N of animals per class	Percentage
0.00 to 5.00	41,357	90.47
6.00 to 10.00	2,982	6.52
11.00 to 15.00	892	1.95
16.00 to 20.00	231	0.51
21.00 to 25.00	92	0.20
26.00 to 30.00	148	0.32
31.00 to 35.00	06	0.01
36.00 to 40.00	03	0.01

Table 3. Contribution percentage of the 10 most influential founders in the population of Guzerat cattle raised in the northern region of Brazil

Founders	% Contribution
A	1.17
B	1.44
C	1.10
D	1.09
E	1.81
F	2.28
G	1.40
H	3.19
I	1.12
J	2.75

Ten founders contributed more than 1% to the gene pool, and when added to the contributions, these accounted for 31.96% of the gene pool of the reference population. The total number of founders was certainly greater than that shown in the table, and the reduction in this number to the number of founders whose contribution was more than 1% shows a possible asymmetrical use of certain individuals, which might have contributed to the formation of lines in the population (Figure 3).

Figure 3 shows a pattern of dispersion of observations relative to the eigenvectors. There was a high correlation between seven founders, indicating that their descendants are mating with each other and thereby favoring the formation of a line, which explains the greater genetic diversity of the population.

Based on the scree-plot (Figures 3A and 3B), five PCs should be sufficient to explain the data, and these first five PCs explained 75.00% of the total variance. Using the first two PCs (explaining 47.57% of the total variance), six founder lines were found, whose result is shown graphically (Figure 3C).

Data analysis revealed an unequal contribution of the founders, which is based mainly on the reduction in their number (Melka and Schenkel, 2010; Tang *et al.*, 2013). According to Tang *et al.* (2013), the unequal contribution of founders directly increases inbreeding in the reference population, which might explain the inbreeding averages found in this study. Another consequence is the reduction of genetic variability (Duru, 2017).

In the study population, the proportion of inbred animals was higher in the cow population than among bulls (+56%, on average). However, this higher proportion of related cows resulted in an increase in the average inbreeding coefficient of the study population (0.06). The average rate of change of additive genetic relationships between 1952 and 2016 for the Guzerat breed was 0.00021 per year, based on the slope of the fitted regression. This results in a Δf per generation of 0.00148. The rate of change of the mean inbreeding occurrences based on the slope of the regression over the same period was 0.00041, which represents a ΔF per generation of 0.00297.

The estimated effective size (N_e) calculated based on Δf (average rate of change of additive genetic relationships) and ΔF (average inbreeding coefficient) was 338 and 168, respectively. This value represents the size of the genetically active population, i.e., that which could generate the same inbreeding rate or variance in allele frequencies, as observed in the population under study, if these animals were raised under the conditions of an ideal population (Falconer and Mackay, 1996). Faria *et al.* (2009) also estimated low values for populations of the Nellore, Gir, and Guzerat breeds, which ranged from 45 to 117. Meuwissen and Woollians (1994), suggested an effective size between 31 and 250 to prevent a decline in the adaptive values of animals because of inbreeding depression, an interval that encompasses the result observed in the present study.

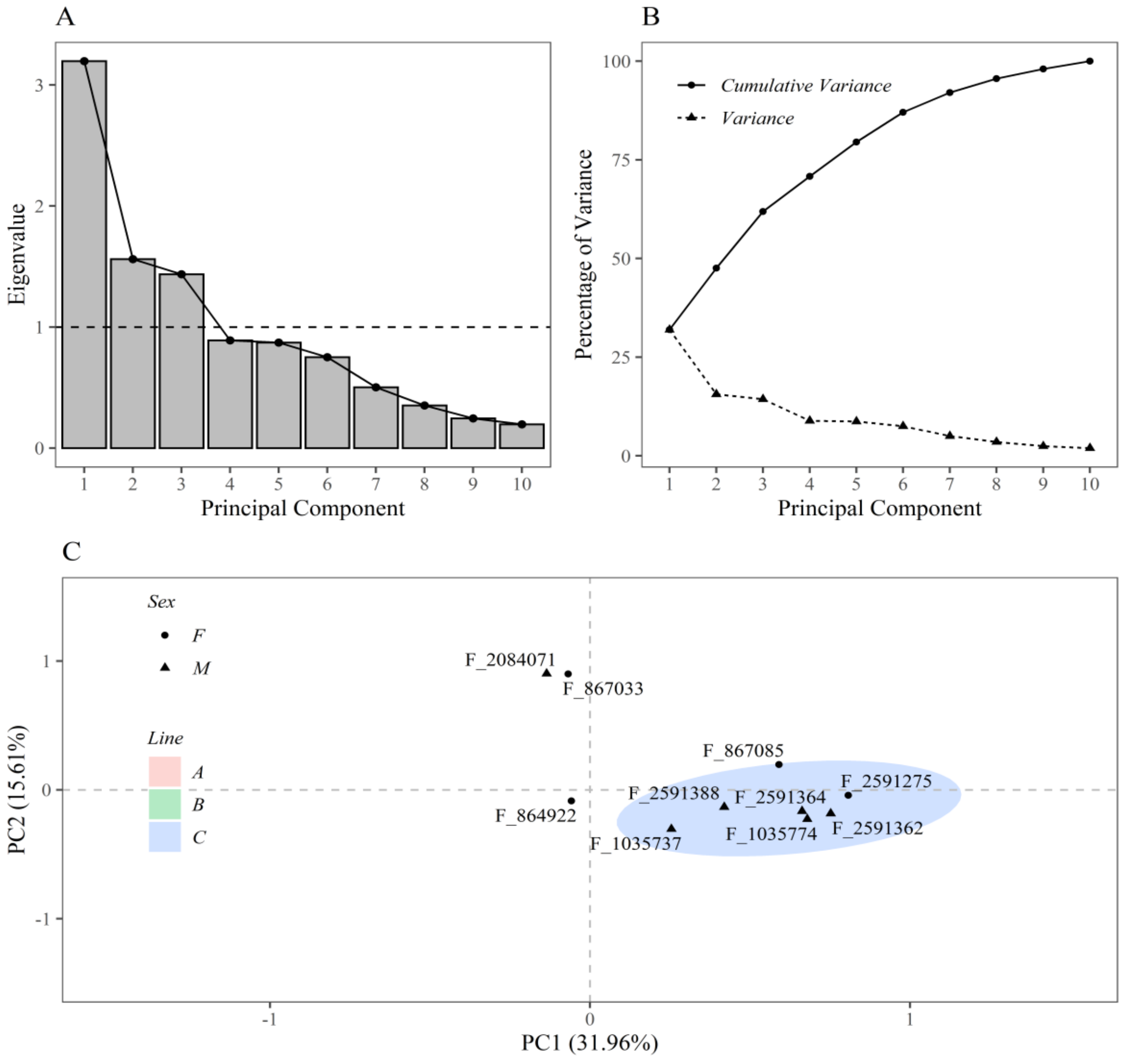

Figure 3. Principal component analysis of the contribution of the most influential founders applied to the current population of Guzerat cattle raised in the northern region of Brazil. A: Principal components; B: Percentage of variance explained by each principal component and cumulative variance; and C: Line identification.

Figure 4 illustrates the comparison between the number of inbred animals and the mean *F* of the animals in the study population. In the evolution (Figure 4) of the herd, from 1996 to 2012 (18 years), the average F remained almost constant, with a reduction in the number of inbred animals in the population that allowed a variability that provided genetic gain within the population.

However, this period was also marked by a strong reduction in the herd (bulls, dams, and births), which may explain the reduction in N_e and in the genetic variability of the herd. Furthermore, the formation of lines in the population can also explain the results presented, since the monitoring of genetic gain should be a concern for any breed (Euclides Filho *et al*., 2000), and knowledge of the variability and genetic evolution of a population is important not only for making the necessary changes, but also for evaluating selection programs that are being adopted.

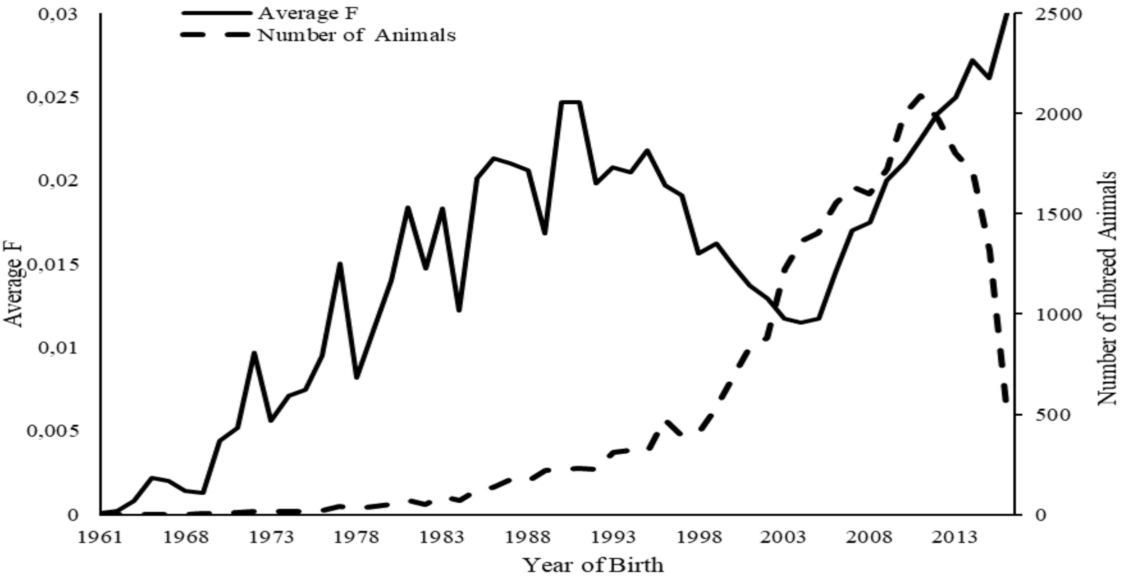

Figure 4. Comparison between the average inbreeding coefficient (F) and the number of inbred animals per year.

Exploiting the genetic diversity of farm animals is necessary to meet current production requirements in various environments, thereby favoring sustainable genetic improvement and facilitating rapid adaptation to changes in selection objectives.

CONCLUSIONS

Inbreeding levels in Guzerat herds raised in northern Brazil have remained moderate over the years. However, this fluctuation did not hinder the genetic evolution of the herd in the region. The effective size of the population does not seem to compromise the maintenance of genetic variability in the breed.

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