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Population structure of Nellore cattle in northeastern Brazil

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ABSTRACT - The objective of this study was to evaluate the population genetic structure of Nellore cattle in northeastern Brazil. Pedigree information was collected from 175,231 animals born from 1967 to 2007. Probability of gene origin, inbreeding, average relatedness coefficient (AR), completeness pedigree, effective population size and generation interval were calculated. Generation interval was high due to the long period of time animals were used as reproducers. The bottleneck effect was evidenced as a result of intensive use of limited breeders over the last years. Low values were observed in the effective number of founder animals (434) and ancestors (427) comparing with the number on the base (175,231) and reference populations (130,038). Generally, the variability explained by the founders and ancestors is considered low. The average coefficient of inbreeding (0.11%) and AR (0.14%) estimated for this population is considered low and can be partly explained by the increased population effective number in recent periods; however, it may be underestimated by shallow pedigree.

Key Words: effective size, generation intervals, inbreeding, pedigree

Introduction

In northeastern Brazil, cattle livestock farming basically consists of pure and crossbred pasture-raised zebu animals. This is primarily the result of a great adaptation of these animals to the edaphoclimatic region conditions but, still, the production indexes are considered low. As a beef producer, the Nellore breed has demonstrated remarkable economic performance over the last years. It may be safely assumed that even in those market niches where crossbreeding showed economic growth, Nellore has a fundamental role and represents a wide and valuable genetic resource for the livestock industry (ABCZ, 2010).

Some population parameters largely dependent upon management, and breeding systems have a key impact on genetic variability. According to Malhado et al. (2008a), in order for breeding programs to become feasible, it is essential to know the different factors that potentially interfere with the selection and genetic progress, such as effective population size, generation interval and inbreeding.

The inbreeding coefficient (F) is as function of the effective population size; therefore, the smaller the population size in previous generations, the greater the number of common ancestors and likewise the inbreeding coefficient (Breda et al., 2004). According to Faria et al. (2001), there is a tendency towards the increase of inbreeding coefficient over new generations, especially taking into account the low effective population size. In addition, wrong or incomplete information may result in inaccurate estimates of inbreeding, average relatedness coefficient (AR) and effective population size.

The AR of a founder animal indicates its genetic contribution to the population. Hence, AR can be used as an alternative or complement to the inbreeding coefficient to predict the inbreeding of a population in the long term, since it takes into account the percentage of full pedigree originated from a founder (Gutiérrez & Goyache, 2005). Another important population parameter is the effective population size (Ne), which summarizes the magnitude of genetic drift and the likelihood of increased inbreeding. This parameter affects the behavior of genes under selection, influencing the variance of response to selection, the limits of selection and the survival of populations in conservation programs in the short and long term (Wang & Caballero, 1999).

Population structure studies based on pedigree information and population parameters are important tools for understanding the history of the genetic improvement of Nellore in northeastern Brazil. Furthermore, these studies will form the basis for future actions that will certainly allow the achievement of greater genetic progress. Thus, the objective of this study was to evaluate the Nellore

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population structure in northeastern Brazil in order to contribute with complementary information to breeding programs.

Material and Methods

Pedigree information was obtained for 175,231 Nellore beef cattle born from 1967 to 2007 and raised in northeastern Brazil. The used data originated from the monitoring of weight development of Nellore of Associação Brasileira dos Criadores de Zebu - ABCZ (Brazilian Association of Zebu Breeders).

The ENDOG software (Gutiérrez & Goyache, 2005) was used for pedigree analysis and parameters estimation based on the probability of gene origin, average coefficient of inbreeding, average relatedness coefficient, effective population size and generation interval. The average generation interval of the four gametic pathways was estimated in the following order: sire-son, sire-daughter, dam-son and dam-daughter.

The effective number of founders denotes the number of animals that should produce the same genetic variability observed in the studied population. The effective number of ancestors represents the minimum number of animals (founders or not) needed to explain the entire genetic diversity of the studied population (Gutiérrez & Goyache, 2005).

The algorithm proposed by Meuwissen & Luo (1992) was used to calculate the inbreeding coefficient. The changes in inbreeding (ΔF) were calculated as described by Falconer and Mackay and modified by Gutiérrez et al. (2009), using the formula:

$$\Delta F_i = 1 - \sqrt[t-1]{1 - f_i}$$

where F_i is the individual inbreeding coefficient and t is the equivalent generation for this individual (Boichard et al., 1997). The expression relating inbreeding in generation t with inbreeding rate proposed by Gutiérrez et al. (2009) is

$$F = 1 - (1 - \Delta F)^{t-1}$$

The average relatedness coefficient of each individual is defined as the probability that an allele randomly chosen from the whole population in the pedigree belongs to a given animal (Gutiérrez & Goyache, 2005).The AR of each individual is defined as the probability that an allele chosen at random in the family tree of the entire population belongs to a particular animal. The AR can therefore be interpreted as the representation of the animal in the entire pedigree, regardless of the knowledge of its own pedigree.

The completeness pedigree was computed following the method of MacCluer et al. (1983), and includes the description of the completeness of each ancestor in the pedigree to the 4th parental generation. The following parameters were calculated for each individual: 1) complete generation - defined as the number of generations separating the offspring of the furthest generation where both generation ancestors of the individual are known. Ancestors with no known parents are considered as founders (generation 0); 2) the maximum number of generations traced - defined as the number of generations separating the individual from its furthest ancestor; and 3) equivalent complete generations - computed as the sum over all known ancestors of the terms computed as the sum of $½^n$, where n is the number of generations separating the individual from each known ancestor (Maignel et al., 1996).

The effective population size (Ne) was calculated from the variances of family sizes as

$$\frac{1}{N_e} = \frac{1}{16ML}\left[2 + \sigma^2_{mm} + 2\left(\frac{M}{F}\right)\mathrm{cov}(mm, mf) + \left(\frac{M}{F}\right)^2 \sigma^2_{mf}\right] + \frac{1}{16FL}\left[2 + \left(\frac{F}{m}\right)^2 \sigma^2_{fm} + 2\left(\frac{F}{M}\right)\mathrm{cov}(fm, ff) + \sigma^2_{ff}\right],$$

where M and F are the number of male and female individuals born or sampled for breeding each time period (five years); L is the average generation interval σ^2_{mm}; σ^2_{mf} are the variances of the male and female offspring of a male; σ^2_{fm} and σ^2_{ff} are the variances of the male and female offspring of a female; and *cov (mm,mf)* and *cov (fm,ff)* are the respective variances.

Results and Discussion

During the first decade (1970-1980) there was a small increase in the number of Nellore animals (Figure 1). From 1982 to 2001, there were alternate periods of rise and decline in the number of animals. Starting on 2001 there was a significant increase until 2004, which was the year with the highest number of births, totaling 7823 registered animals. After that year, the number of births decreased, reaching 5804 births in 2006. The annual birth rate for a particular breed indicates the numerical progress of herds,

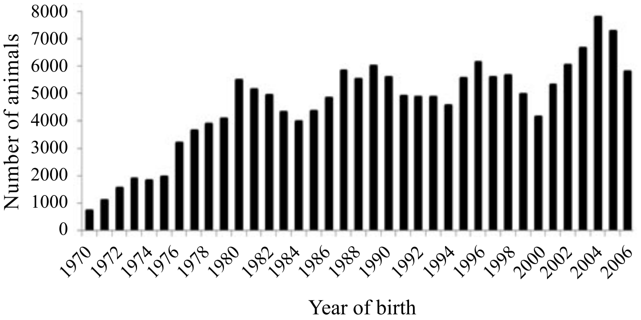

Figure 1 - Nellore animals born in northeastern Brazil.

demonstrating the interest or disinterest of the producer for the respective breed (Santos, 2009).

Generation interval estimates were equal to 9.7±5.3 (sire-son), 9.5±5.0 (sire-daughter), 7.1±3.2 (dam-son) and 7.4±3.5 years (dam-daughter), the average generation interval being 8.5±4.5 years (Table 1). According to Malhado et al. (2010), the long interval between sire-son and sire-daughter can be diminished by the rapid replacement of male breeders by their descendants. Besides, the reduction of age at first calving is important to reduce the average generation interval and increase the annual genetic gain.

Similar results were found in studies with Nellore cattle in Bahia State conducted by Malhado et al. (2008b), who observed intervals of 9.1±4.6 (sire-son), 9.0±4.5 (sire-daughter), 7.6± 3.6 (dam-son) and 7.5±3.5 years (dam-daughter) with an average generation interval of 8.3±4.2 years. Faria et al. (2002) and Vercesi Filho et al. (2002a) estimated average values of 7.2 and 7.1 (sire-son), 7.2 and 7.2 (sire-daughter), 7.0 and 7.2 (dam-son) and 6.9 and 7.1 (dam-daughter) for registered Polled Nellore and Tabapuã animals, respectively.

The average interval reported in this study can be considered high and may result in reduced genetic gain per unit of time. Moreover, a long permanence of a herd may increase the chances of mating between relatives and thereby lead to an increased inbreeding coefficient. The effective population size (Ne) was low until the 1980s (Figure 2). Since 1988, there was an increase in Ne, reaching 358.24 individuals between 1989 and 1996. After this period, a significant increase was observed, reaching the highest Ne value (484.54 animals) during the 1991-1998 period, contrasting with the shrinkage observed until 2002. Malhado et al. (2010), studying the effective size of Nellore breed in Northern Brazil, observed the same trend, with low effective size until the end of the 80s, with increase from the 90s. Gutierrez et al. (2008) reported that Ne computed from variances of family sizes was not useful to characterize the ‘real’ effective size. However, the authors described that calculating Ne in this way does reflect a temporary mating policy and can be useful when the pedigree knowledge is limited and/or subdivision has not yet occurred.

Table 1 - Generation intervals parameters for the Brazilian northeastern Nellore

Gametic pathways	Number of observations	Interval (years)	Standard deviation (years)
Sire-son	986	9.7	5.3
Sire-daughter	15,936	9.5	5.0
Dam-son	985	7.1	3.2
Dam-daughter	15,919	7.4	3.5
Average generation interval	-	8.5	4.5

Frankham (1995) suggests the adoption of an effective population size of 500 animals for the maintenance of evolutionary potential. However, the author points out that an effective size of 50 animals is sufficient to prevent inbreeding depression. Similarly but with a wider range, Meuwissen & Woolliams (1994), recommended values between 30 and 250 to prevent a decrease in the adaptive value.

The mean coefficient of inbreeding for the whole population and the mean inbreeding value for only inbred animals (2371) were 0.11% and 8.32%, respectively. There was a greater increase in inbreeding coefficient from 0.15% in the second generation to 0.95% in the fifth generation (Table 2). Similarly, the percentage of inbred animals had a considerable growth in all generations. Contrarily, the mean F value for inbred animals decreased from 18.56% to 3.88% from the second to the sixth generation, revealing that mating between close relatives was controlled, contributing to maintain the genetic variability in the population.

In a study on the genetic population structure of Nellore cattle in Bahia State, Malhado et al. (2008b) reported an increment in the mean inbreeding coefficient, from 0.8% on the second generation to 1.57% on the seventh generation; however, the mean F value for inbred animals decreased from 16.76% on the second generation to 3.85% on the seventh generation. In another research project addressing the Nellore herd from northern Brazil, the same authors found a mean inbreeding coefficient of 0.2% and a mean F value for inbred animals of 6.24% for inbred animals. Furthermore, the average inbreeding coefficient and the percentage of inbred animals in the population have accumulated over generations, whereas the average F value for inbred animals diminished along the same time frame.

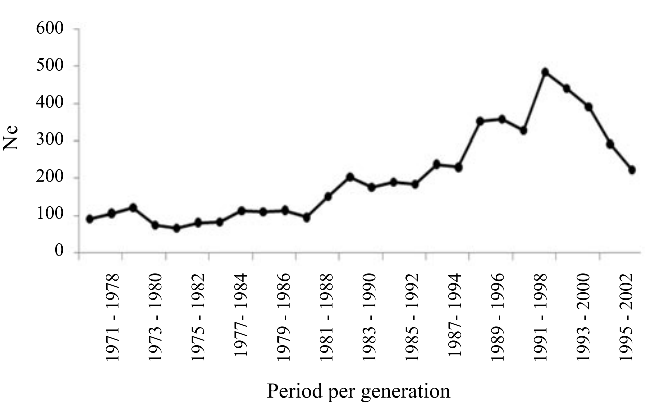

Figure 2 - Effective size of Nellore (Ne) bovines in northeastern Brazil from 1971 to 2002.

Table 2 - Inbreeding for Nellore in northeastern Brazil

Generation	Number of animals	Average coefficient of inbreeding (%)	Inbred animals (%)	Mean F value for inbred animals (%)
1	70,182	0.00	-	-
2	31,405	0.15	0.83	18.56
3	16,578	0.33	3.50	9.51
4	8,248	0.60	8.45	7.11
5	3,433	0.95	17.71	5.36
6	1003	0.87	22.43	3.88
7	122	1.28	30.33	4.23
8	1	0.00	-	-

Inbreeding depression causes reduction in individual genetic merit - regarding productive traits - possibly due to the fixation of unfavorable alleles. However, at low inbreeding levels, the depressive effect is relatively minor. Therefore, monitoring kinship level among the animals selected for breeding is important for the maintenance or even reduction of inbreeding in the population (Breda et al., 2004).

In the whole population, 172,841 animals showed no inbreeding; 1630 demonstrated inbreeding within a range of 0.04% to 0.12%; 493 animals exhibited 0.12% to 0.20%; and only 267 animals showed higher values of inbreeding (Table 3).

Of the 175,231 animals studied, 74.47, 21.48 and 5.76% had known pedigree in the first, second and third generations, respectively (Figure 3). The result for Nellore is in agreement with another study with zebu cattle from Brazil (Malhado et al., 2010) which reported knowledge of less than 10% after the third generation. By contrast, Marquéz et al. (2010), studying 2,141,506 registered Red Angus animals born between 1927 and 2006 from Red Angus Association of America (RAAA), reported 94, 92 and 88 percent of all animals in the pedigree having parents known at first, second and third generations. The lack of precise ascendant information stems from the fact that ABCZ has recently initiated the bookkeeping (3-4 generations).

Table 3 - Frequency of inbreeding coefficient (F) for the Nellore population in northeastern Brazil

Inbreeding coefficient (F)	Inbreeding class	Number of animals
0	1	172,841
0.01 - 0.04	2	960
0.04 - 0.08	3	648
0.08 - 0.12	4	22
0.12 - 0.16	5	481
0.16 - 0.20	6	12
>0.20	7	267
Total	-	175,231

The pedigree completeness is important because the inbreeding coefficient of an individual depends on how much of its ancestry is known; therefore, more accurate information gives more reliable estimation of F value for a given population (Faria et al., 2010). Queiroz et al. (2000) emphasize that a better knowledge of genealogy would enable more accurate calculation of the coefficient of inbreeding, with an almost always consequent increase in values.

The AR was estimated at 0.14% for the present study. Malhado et al. (2010) estimated AR and F values of 0.13% and 0.2%, respectively, for Nellore animals raised in northern Brazil. The mean coefficient of inbreeding and the AR value for the whole population were zero from 1970 to 1974 (Figure 4a). This result coincides with the small number of complete gen through this period (Figure 4b). Since the mid-80s, there was an increase in AR, while inbreeding had a large increase during the 90s. This AR accrual without increased inbreeding indicates intensive use of bulls, with inbreeding control.

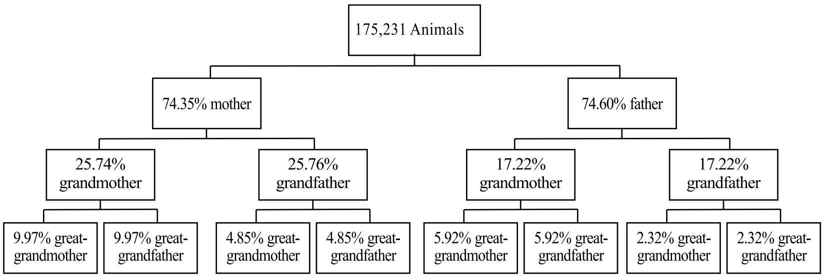

Figure 3 - Pedigree completeness and level of identification of ancestors until the third generation of Nellore cattle reared in northeastern Brazil.

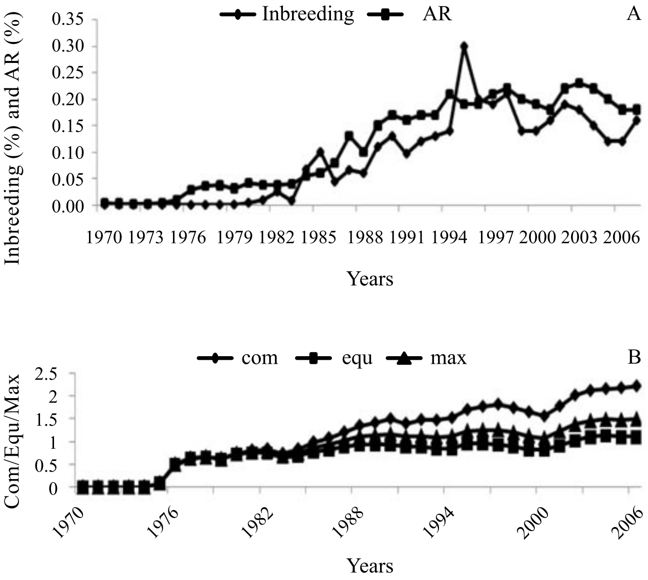

Figure 4 - A) Inbreeding (F), average coefficient of relationship of population (AR) on the basis of year of birth. B) Means of maximum (max), complete (com) and equivalent (equ) generations traced by year.

Malhado et al. (2010) emphasized that the knowledge of an accurate genealogy increases the possibility of an important ancestor appearing several times downstream in the pedigree, therefore justifying the increased inbreeding and AR (Figure 4b). According to theses authors, it is important to assess whether low inbreeding values are due to mating control between related animals or if these are underestimated due to lack of complete pedigree information. Furthermore, the fact that the number of known ascendant generations gradually increases will enable more accurate parameters for estimation in the future.

The number of founder animals with one or more unknown parents was 45,193. Considering animals with only one known parent (half-founder), it was 44,726, accounting for about 25.52% of the tested animals (Table 4). The effective number of founders (f_e) was 774.5 (0.44% of the total population). The effective number of ancestors (f_a) was equivalent to 427. Malhado et al. (2010) observed effective number of founders equal to 370 in Nellore from the Northern region. During a genetic historic evaluation of pure Nellore animals from the northeastern hinterlands, Malhado et al. (2008b) estimated 309 as the effective number of founders (f_e).

The f_e/f_a ratio observed in the present project was 1.81 (expression of the "bottleneck effect"), which is higher than the 1.52 reported by Faria et al. (2004). According to Vercesi Filho et al. (2002a), the calculated value for the Tabapuã breed ranged between 1.02 and 1.44 in the first and last periods. The f_e/f_a ratio results from a decrease in the number of breeders over the years. This effect can lead to accrued inbreeding and loss of alleles in the population, reducing the genetic diversity of the original gene pool.

The number of ancestors that contributed to the reference population was 45,573. Only 521 were responsible for half of the population genes (Table 4). These results reveal that a small number of breeders have been used intensively on breeding programs. A Nellore cattle study conducted in Bahia State, Brazil (Malhado et al., 2008b) reported that 50% of the genetic variability was explained by 414 ancestors.

Compared with the base number (175,231) and reference population (130,038), low values were observed for the effective numbers of founder animals and ancestors (Table 4). This caused the herd to develop from a narrow genetic basis, demonstrating the founder effect. These low values may be explained by the greater use of few individuals, or the fact that some individuals had a higher number of descendants than others.

The top 10 founders are the 10 individuals from the founder group that show more representation in the herd. The most relevant male - ancestor and founder of 1,353,767 - had AR of 1.51% and explained 2.02% of the population genetic variability (Table 5). Generally, the variability explained by the listed genetic founders and ancestors can be considered low, because only the first ancestor explained over 2% of genetic variability.

Table 4 - Parameters characterizing gene origin in the Nellore breed from northeastern Brazil

	Number of animals
Total population	175,231
Effective number of founders	774.5
Number of founder animals with one or more unknown parents	45,193
Equivalent number of founder animals (one parent is unknown = half-founder)	44,726
Number of animals in the reference population	130,038
Number of founder animals in the reference population	44,189
Effective number of founder animals in the reference population	434
Number of ancestral animals in the reference population	45,573
Effective number of ancestral animals in the reference population	427
Number of ancestors explaining 50% of the variability	521

Table 5 - Description of 10 major ancestors (founders or not) in the Nellore cattle raised in northeastern Brazil

Ancestors	Sex	AR	Contribution (%)	Offspring
1353767	Male	1.51%	2.02	3021
1355385	Male	1.14%	1.53	1589
1843896	Male	1.06%	1.42	2811
1491270	Male	1.05%	1.40	2249
554008	Male	0.77%	1.19	953
2860551	Male	0.74%	1.03	2290
1144401	Male	0.67%	0.99	1748
560557	Male	0.67%	0.91	220
142884	Male	0.67%	0.89	1256
123496	Male	0.60%	0.81	936

AR - average relatedness coefficient.

Conclusions

The average coefficient of inbreeding estimated for this population is considered low and can be explained by the increased effective number in recent periods. However, it may be underestimated by shallow pedigree. The generation interval is high due to the long period of use of animals for reproduction. Intensive use of small number of breeders may cause a bottleneck effect.

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