



## Genetic basis and inbreeding in the Brazilian Guzerat (*Bos indicus*) subpopulation selected for milk production

M.G.C.D. Peixoto <sup>a,\*</sup>, C.F. Poggian <sup>b</sup>, R.S. Verneque <sup>a</sup>, A.A. Egito <sup>c</sup>, M.R.S. Carvalho <sup>d</sup>, V.M. Penna <sup>e</sup>, J.A.G. Bergmann <sup>f</sup>, L.F. Viccini <sup>b</sup>, M.A. Machado <sup>a</sup>

<sup>a</sup> Embrapa Gado de Leite, Rua Eugênio do Nascimento, 610, Juiz de Fora, MG, 36080-330, Brazil

<sup>b</sup> Instituto de Ciências Biológicas, UFJF, Juiz de Fora, MG, 36036-330, Brazil

<sup>c</sup> Embrapa Recursos Genéticos e Biotecnologia, Caixa Postal 02372, Brasília, DF, 70770-917, Brazil

<sup>d</sup> Instituto de Ciências Biológicas, Caixa Postal 486, UFMG, Belo Horizonte, MG, 31270-910, Brazil

<sup>e</sup> Centro Brasileiro de Melhoramento do Guzerá, Rua Nova Era, 180, Belo Horizonte, MG, 30315-380, Brazil

<sup>f</sup> Escola de Veterinária, Caixa Postal 567, UFMG, Belo Horizonte, MG, 30123-970, Brazil

### ARTICLE INFO

#### Article history:

Received 23 November 2009

Received in revised form 23 March 2010

Accepted 25 March 2010

#### Keywords:

Effective population size

Inbreeding coefficient

Genetic variability

Zebu cattle

### ABSTRACT

The Guzerat breed is well adapted to the tropical conditions of Brazil. After 1940, the widespread use of Guzerat cattle for crossing has reduced its population size. In 1994, a selection program for milk production traits was initiated in some purebred herds. However, its success is compromised by genetic drift and an increased inbreeding coefficient ( $F$ ). The objective of this study was to evaluate the genetic status of the Guzerat population under selection for milk production in order to monitor genetic variability. Genealogical data from 10,051 animals were used to estimate genetic parameters. The average  $F$  for all animals and for inbred animals in the pedigree was 0.009 and 0.025, respectively. Average relatedness was 0.011. The average generation interval was 7.48 years and the linear increase in  $F$  per generation was 0.0051. There was no trend of changes in the effective population size along generations, with the observation of an effective size of 98 in the last generation evaluated. The effective number of founders and ancestors was 318 and 101, respectively. Only 47 of 2106 ancestors contributed to 50% of the reference population. The bottleneck effect was 3.15. Average  $F$  and relatedness values are still low despite non-random mating. However, the reduced effective population size and effective number of ancestors indicate a risk of an increase in the inbreeding coefficient and genetic drift and consequent loss of variability.

© 2010 Elsevier B.V. All rights reserved.

### 1. Introduction

The Guzerat breed, which originated in India, has evolved in a semiarid region, a fact that explains its adaptation to adverse tropical conditions. The breed was introduced in Brazil at the end of the 19th century and was prevalent until 1939. An expressive reduction in the size of the purebred population to worrying numbers was observed due to the widespread use of this breed to produce crossbred animals (V.M. Penna, personal communication).



\* Corresponding author. Tel.: +55 32 3249 4780; fax: +55 32 3249 4701.  
E-mail address: [gaby@cnp.gl.embrapa.br](mailto:gaby@cnp.gl.embrapa.br) (M.G.C.D. Peixoto).

Furthermore, the properties of the Guzerat breed, e.g., resistance to parasites such as ticks, ability to consume gross forage and heat tolerance, was important to its inclusion in the FAO list of domestic animal genetic resources to be conserved by management (FAO, 1995). This is particularly important considering the world “tropicalization” mediated by the polemic global warming threats.

Considered to be a dual-purpose cattle breed, Guzerat animals have been selected in herds for meat or milk production or both traits in Brazil. In 1994, a nation-wide breeding program for the Guzerat breed based on progeny testing and an MOET selection nucleus scheme was implemented to improve milk production traits (Smith, 1988; Penna et al., 1998; Peixoto et al., 2009). The first sire summary was published in 2000. Today there are around 3966 Guzerat lactating cows being recorded in the 36 double proposal herds, whose average production is  $2039 \pm 1022$  kg and maximum production of 8891 kg. Age at first and last calving is respectively about 36.4 and a little over 216 months.

In addition to genetic improvement, the genetic diversity of a population is an important aspect to be considered in any breeding program since it allows species to face future challenges and permits a long-term response to selection (Frankham et al., 2002). According to Vieira et al. (2005) concerns about the effects of reduction of effective population size and inbreeding coefficient on cattle genetic diversity have increased mainly after the utilization of new reproductive technologies. In addition to the loss of genetic variability, inbreeding depression can reduce yield and reproductive trait performance (Falconer and Mackay, 1996). Bottlenecks can also occur, increasing the risk of the loss of genetic diversity (Nei et al., 1975).

Despite the widespread use of effective population size and inbreeding rate as parameters to assess genetic diversity, new approaches such as effective number of founders, ancestors or non-founders, genome equivalent, based on probabilities of gene origin, and data types (molecular markers) have recently been proposed (Lacy, 1989; Boichard et al., 1997; Caballero and Toro, 2000, 2002; Cañón et al., 2001; Goyache et al., 2003). Estimates of these parameters are available for many breeds (Sorensen et al., 2005; Verneque et al., 2006; Vozzi et al., 2006).

In a study using pedigree data from all registered Brazilian Guzerat animals, a small effective population size (117) and reduced effective number of founders (246) and ancestors (166) were observed among registered animals born between 1979 and 1998 (Faria et al., 2002). Faria et al. (2009) found an effective size of 104, a generation interval around 8 years and a bottleneck effect of 1.49 for the whole registered Guzerat population. At present, the number of registered animals is 164,228, with the Guzerat breed corresponding to one of the three growing and largest Zebu populations in Brazil (ABCZ, 2005). These results indicate a narrow genetic basis of the current Guzerat population, which is close to the limit at which expressive loss of adaptive value may occur (FAO, 1992).

Reduced population structure parameters can increase inbreeding and genetic drift, leading to the loss of genetic variability and reducing genetic gain in populations under selection (Falconer and Mackay, 1996). A simulation study based on Zebu MOET nucleus population parameters reported a trend of increasing inbreeding coefficients along selection generations due to the high frequency of mating among related

animals (Peixoto et al., 2005). Weigel and Lin (2000) and Colleau et al. (2004) stated that mating plans are an important tool to manage genetic variability. Furthermore, the effects of inbreeding depression may decrease animal fertility and survival, as well as the rate of genetic progress (Falconer and Mackay, 1996; Hill, 2000). In this respect, the generation interval (GI) is an important parameter since it permits a faster rate of genetic gain and the measurement of genetic progress and inbreeding over time.

The objective of the present study was to calculate population structure parameters and inbreeding coefficients for the Guzerat population selected for milk production traits in order to evaluate and monitor genetic variability.

## 2. Materials and methods

Pedigree data were obtained from the National Genetic Breeding Program of Dairy Guzerat Cattle and also from 31 participating herds located in the northeast (6 states), central-west (1 state) and southeast (4 states) regions of Brazil. Prior to this study, a survey involving these herds was carried out to complete the pedigree information. A total of 2924 individuals were included. The complete data set comprised 10,051 animals, including 2379 with unknown parents, 116 with at least one known parent and 7556 with both parents known. These animals had been registered since the end of 19th century when importation of the Guzerat breed had started (Table 1).

The population parameters were calculated using the algorithms of the freely available ENDOG v 4.0 software (Gutiérrez and Goyache, 2005). This software uses the probability that an individual carries two alleles identical by descent to calculate inbreeding coefficients ( $F$ ). The inbreeding rate ( $\Delta F$ ) per generation is calculated by the formula  $\Delta F = (F_t - F_{t-1}) / (1 - F_{t-1})$ . Using  $\Delta F$ , the ENDOG program computes the effective population size ( $N_e$ ) as  $N_e = 1/2\Delta F$ , defined as the number of breeding animals that would lead to an actual increase in inbreeding if they equally contributed to the next generation. The program also calculates the average relatedness (AR) coefficient of each animal, defined as the probability that an allele randomly chosen from the whole population in the pedigree belongs to a given animal, using the vector  $\mathbf{c}' = (1/n)1'A$ , where  $A$  is the numerator relationship matrix (NRM) of size  $n \times n$ . The NRM included 10,051 individuals (1955 males and 8096 females). When calculating  $F$  and AR, ENDOG calculates three additional values of  $N_e$  by computing the regression coefficient of the individual inbreeding coefficient over: (i) the number of fully traced generations, (ii) the maximum number of generations traced,

**Table 1**

Number of known parents, number of unknown parents (U), sire/dam ratio (S/D), average number of offspring per sire (AO), and maximum and minimum number of offspring per sire for each period.

Period	Sires	Dams	USires	UDam	S/D	AO	Min–Max
<1950	152	254	1741	1739	1/2	1.42	1–11
≥1950–1960	8	17	113	111	1/2	1.80	1–8
≥1960–1970	60	169	242	241	1/3	2.35	1–11
≥1970–1980	173	541	104	101	1/3	2.88	1–28
≥1980–1990	204	821	66	60	1/4	4.17	1–61
≥1990	221	1315	85	69	1/6	6.42	1–142

and (iii) the equivalent complete generations – the upper, lower and true limits of  $N_e$ , respectively.

ENDOG assesses further the probability of a gene to derive from founder  $K$  of both animals and genes computing the effective number of founders ( $f_e$ ),

$$f_e = 1 / \left( \sum_{k=1}^f q_k^2 \right)$$

where  $q_k^2$  is the AR coefficient of the founder  $k$ , and the effective number of ancestors ( $f_a$ ),

$$f_a = 1 / \left( \sum_{j=1}^a q_j^2 \right)$$

where  $q_j^2$  is the marginal contribution of an ancestor  $j$  (Boichard et al., 1997). The former is defined as the number of equally contributing founders that would be expected to produce the same genetic diversity as the population under study. The latter corresponds to the minimum number of ancestors, not necessarily founders, explaining the complete genetic diversity of a population. These parameters permit to account for losses of genetic variability produced by bottlenecks ( $f_e/f_a$ ). Base population was formed by individuals with unknown parents or with only one known parent.

Finally, the ENDOG program was also used to calculate the GI for both the mean age of parents at birth of their progeny kept for reproduction and the mean age of parents at birth of their offspring (used for reproduction or not). These parameters were computed for the population as a whole and for the four pathways (father–son, father–daughter, mother–son, and mother–daughter).

The complete data set was used for all the above analyses. Individuals with unknown parents or at least one unknown parent (2495) were included in the base population and the remaining animals constituted the reference population (7556).

The inbreeding trend was obtained from the regression coefficient of the inbreeding coefficients over generations. In the former analysis, for individuals with unknown birth date belonging to the first generation, the birth date was assumed to be equal to 1/1/1940. For individuals belonging to the second generation, the birth date was assumed to be 1/1/1950. Individuals of the subsequent generations without a birth date were excluded from the data set. The younger individuals were born in 2007. A total of 8990 individuals were used in this analysis.

Variance analysis was carried out using the GLM procedure of the SAS<sup>®</sup> package (SAS, 2003).

### 3. Results

The overall inbreeding coefficient ( $F$ ) of the population was 0.009 and AR was 0.011.  $F$  was the same for male and female individuals.  $F$  was 0.025 among 3471 inbred individuals. Estimates of  $F$  according to known birth year period are shown in Table 2. There were 5593 individuals with  $F=0$ . The second most frequent class of  $F$  was  $0 < F \leq 0.01$  observed for 1631 individuals (Table 3). Both classes corresponded to almost 80% of the population. The least frequent classes of inbreeding were in the  $0.10 < F \leq 0.12$  range. Only 213 individuals presented  $F > 0.12$ . The maximum individual  $F$

**Table 2**

Average inbreeding coefficient ( $F$ ) and respective standard deviation (SD) and minimum (Min) and maximum (Max)  $F$  values according to birth year period of the individuals ( $N$ ).

Period	$N$	$F \pm SD$	Min	Max
$\leq 1949$	49	$0.005 \pm 0.036$	0	0.250
1950–1959	335	$0.000 \pm 0.000$	0	0.001
1960–1969	461	$0.002 \pm 0.019$	0	0.250
1970–1979	758	$0.004 \pm 0.021$	0	0.250
1980–1989	1383	$0.012 \pm 0.035$	0	0.266
1990–1999	2649	$0.015 \pm 0.034$	0	0.313
$\geq 2000$	3355	$0.012 \pm 0.027$	0	0.317

value found was 0.317. The percentage of inbred individuals in the pedigree was 2.4%.

The effective population size ( $N_e$ ), mean inbreeding coefficient ( $F$ ) and mean AR in each generation are shown in Table 4. The results indicate an evident increasing trend in  $F$  and AR and fluctuating  $N_e$  in succeeding generations.

Fig. 1 shows the positive trend in  $F$  per complete generation. An increase in  $F$  was observed until the sixth generation, followed by a decrease in the last generation. The maximum value was observed in the 5th generation, followed by a slight decrease. The estimated inbreeding rate per complete generation, which considers only known parents and is therefore more precise, was 0.0065 (Table 5).

Table 5 shows the additional  $N_e$  calculated by regression of the individual inbreeding coefficient over the three different types of traced generations. In this population, the average  $N_e$  for complete generations was about 77.

The mean GI, calculated as the mean age of parents at birth of their progeny kept for reproduction, was 7.48 years (Table 4). The paternal pathways showed the longest GI despite small differences between GI in each pathway and the mean age of parents at birth of their progeny (Table 6).

The effective number of founders ( $f_e$ ) was 318.56. The expected increase in inbreeding due to unbalanced contribution of founders was 0.16%. The number of ancestors contributing to the reference population was 2106 (corresponding to 21.5% of the population of 10,051 individuals and to 84.4% of the base population). Only 47 of these ancestors explained 50% of the genetic background of this population. The 10 ancestor bulls

**Table 3**

Number ( $N$ ) and percentage (%) of individuals, average inbreeding coefficient ( $F$ ) and respective standard deviation (SD), and minimum and maximum  $F$  values according to  $F$  class.

$F$ class	$N$	%	$F \pm SD$	Min	Max
0 ( $F=0$ )	5593	62.21	$0 \pm 0$	0	0
1 ( $0 < F \leq 0.01$ )	1631	18.14	$0.0040 \pm 0.0028$	0.001	0.010
2 ( $0.01 < F \leq 0.02$ )	493	5.48	$0.0155 \pm 0.0029$	0.011	0.020
3 ( $0.02 < F \leq 0.03$ )	208	2.31	$0.0246 \pm 0.0025$	0.021	0.030
4 ( $0.03 < F \leq 0.04$ )	295	3.28	$0.0344 \pm 0.0029$	0.031	0.040
5 ( $0.04 < F \leq 0.05$ )	118	1.31	$0.0452 \pm 0.0027$	0.041	0.050
6 ( $0.05 < F \leq 0.06$ )	80	0.89	$0.0552 \pm 0.0026$	0.051	0.060
7 ( $0.06 < F \leq 0.07$ )	179	1.99	$0.0648 \pm 0.0028$	0.061	0.070
8 ( $0.07 < F \leq 0.08$ )	64	0.71	$0.0759 \pm 0.0029$	0.071	0.080
9 ( $0.08 < F \leq 0.09$ )	61	0.68	$0.0832 \pm 0.0022$	0.081	0.090
10 ( $0.09 < F \leq 0.10$ )	24	0.27	$0.0951 \pm 0.0021$	0.091	0.100
11 ( $0.10 < F \leq 0.11$ )	19	0.21	$0.1053 \pm 0.0025$	0.101	0.109
12 ( $0.11 < F \leq 0.12$ )	12	0.13	$0.1157 \pm 0.0013$	0.113	0.117
13 ( $F > 0.12$ )	213	2.37	$0.1573 \pm 0.0504$	0.121	0.317

**Table 4**

Average inbreeding coefficient ( $F$ ), average relatedness (AR) and effective population size ( $N_e$ ) per complete generation.

Generation	$N$	$F$ (%)	Inbred individuals (%)	$F^a$ (%)	AR (%)	$N_e$
0	2495	0.00	–	–	0.07	–
1	2803	0.13	8.03	1.62	0.64	384.1
2	1830	1.16	50.93	2.27	1.44	48.6
3	1597	1.96	72.39	2.71	1.89	61.2
4	1138	2.34	85.41	2.74	2.26	131.2
5	183	2.83	100.00	2.83	2.63	98.0
6	5	2.54	100.00	2.54	2.78	–

<sup>a</sup> For inbred individuals.

with the largest marginal genetic contribution, accounting for almost 25.4% of Guzerat dairy cattle, are presented in Table 7. The evolution of the population rate accounted by founders is shown in Fig. 2. It was found a trend of 0.16%. There is a small number of ancestors contributing intensely to reference population. The effective number of ancestors ( $f_a$ ) was 101 and the bottleneck effect ( $f_e/f_a$ ) was 3.15.

#### 4. Discussion

Investigations regarding genetic parameters and selection-based breeding programs aimed at the improvement of Zebu cattle have been carried out in Brazil, but there is a lack of studies evaluating the genetic diversity of some Zebu breeds. Genetic diversity is essential for natural and artificial selection (Falconer and Mackay, 1996; Hill, 2000; Weigel, 2001). To our knowledge, this is the first study evaluating the genetic diversity of Guzerat cattle selected for milk production – a subpopulation of the Brazilian Guzerat population.

The generation interval found in this study was similar but lower than that around 8 years observed by Faria et al. (2009) for Zebu cattle. However is too long and it can reduce genetic progress rate.

Although the dairy Guzerat breed corresponds to a subpopulation of the Guzerat population, the level of inbreeding ( $F$ ) and the inbreeding rate ( $\Delta F$ ) calculated were similar or lower than those reported for other dairy breeds worldwide (Weigel, 2001; Sorensen et al., 2005; Sewalem et al., 2006; MacParland et al., 2007). The average  $F$  has been calculated for some Zebu breeds in Brazil (Faria et al., 2002, 2009; Verneque et al., 2006; Vozzi et al., 2006). An  $F$  value of 0.03 was reported for the Gyr population selected for milk production (Verneque et al., 2006). For the Guzerat population, higher  $F$  values of 0.04 (Peixoto et al., 2006) and 0.03 (Vieira et al., 2005) have been

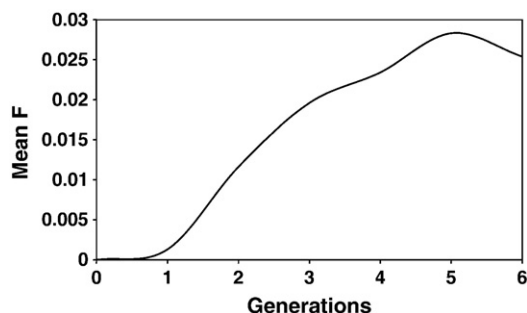


Fig. 1. Regression of generations on the average inbreeding coefficient ( $F$ ).

**Table 5**

Mean generation number, inbreeding rate ( $\Delta F$ ) and effective population size ( $N_e$ ) obtained for the different types of generation traced.

Generation type	Mean	$\Delta F$ (%)	$N_e$
Complete <sup>a</sup>	1.67	0.65	77.36
Maximum <sup>b</sup>	6.88	0.08	600.41
Equivalent <sup>c</sup>	2.80	0.38	132.82

<sup>a</sup> Furthest generation in which all ancestors are known.

<sup>b</sup> Number of generations separating individuals from its furthest ancestor.

<sup>c</sup> Sum of  $(1/2)^n$ , where  $n$  is the number of generations separating the individual from each known ancestor.

reported for inbred animals; however, different data sets were used for calculation of these values. The average  $F$  values obtained in the present study might be underestimated considering the number of unknown parents and that highly inbred individuals are discarded early in the herd (Cassel et al., 2003). Nevertheless,  $F$  represents an important tool to monitor inbreeding rates.

Many aspects may also be related to these findings. Among them, the use of founders of different origins to start each herd of the milk breeding program, the geographic distances between the regions where they are bred in Brazil, in addition to the increasing concern of breeders with inbreeding depression should be highlighted. Another contributing factor is the emphasis on dual-purpose animals in most of these herds, including the use of beef Guzerat sires, in addition to the increase in the number of participating herds (12 herds in 1994 and 31 at present) and, consequently, in the number of females in the program. The  $F$  and  $\Delta F$  values found can be considered to be low when compared to the level of inbreeding reported by Verneque et al. (2006) and Vozzi et al. (2006) for other dairy Zebu breeds and, specifically, for the Guzerat breed (Faria et al., 2002), and are probably related to the low frequency of inbred individuals in this pedigree (2.4%).

The decrease in  $F$  values after the 6th generation (Fig. 1), which corresponds to approximately the period from 1990 to 1999 (Fig. 2), coincided with the publication of the first sire summary for milk production traits. Although the Dairy Guzerat Breeding Program has been started recently (1994) and the sex ratio is increasing (Table 1), these results might

**Table 6**

Average generation interval (GI) and mean age of parents at birth of their progeny (AB) in each pathway.

Pathway	$N$	GI (years)	SD <sup>a</sup>	SE <sup>b</sup>
Sire-son	340	7.49	5.78	0.31
Sire-daughter	1864	7.65	5.57	0.30
Dam-son	310	7.22	6.38	0.35
Dam-daughter	1641	7.34	5.42	0.29
Total	4155	7.48	5.60	0.87
AB (years)				
Sire-son	1114	8.27	5.78	0.17
Sire-daughter	3764	8.10	5.64	0.17
Dam-son	1231	7.39	4.81	0.14
Dam-daughter	3681	7.28	4.96	0.15
Total	9790	7.72	5.33	0.05

<sup>a</sup> SD = standard deviation.

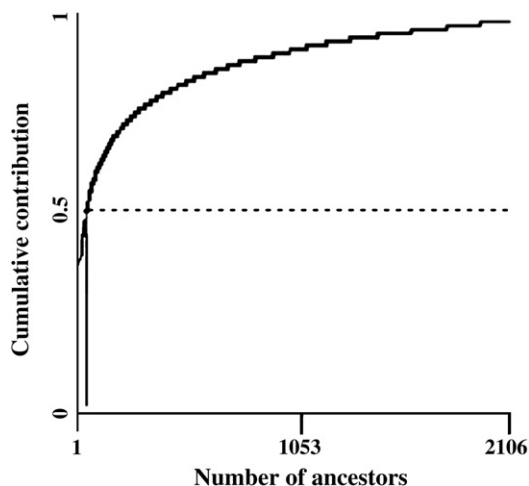
<sup>b</sup> SE = standard error.

**Table 7**  
Top marginal genetic contributions of founders for Guzerat dairy cattle.

Individual	Generation	<i>F</i>	AR	Contribution %
Seridó JA	3	0.0625	0.0386	4.15
Uai JF	2	0.0000	0.0325	3.83
Édipo A	3	0.0625	0.0456	3.72
Demais S	1	0.0000	0.0308	2.61
Gentil JA	2	0.0625	0.0289	2.44
Nambu JP	2	0.0000	0.0192	2.00
Profeta 140	1	0.0000	0.0179	1.75
Faraó Xarq.	1	0.0000	0.0135	1.71
Ghalor Imp.	0	0.0000	0.0126	1.65
Milanês S	1	0.0000	0.0227	1.55

be due to the introduction of sires of other origins and proposals, e.g. from the beef herds, into the herds by artificial insemination rather than the use of sires from the herd itself, in addition to the planned mating practice carried out in most herds (Weigel and Lin, 2000; Caballero and Toro, 2002; Colleau et al., 2004). Mating plans that minimize coancestry among pairs represents a robust tool to maximize  $N_e$  (Caballero and Toro, 2002). The impact of assessing a more complete pedigree on the estimates was demonstrated by comparing the present *F* values for inbred individuals (0.025) with those obtained in a previous study using the same population (0.04) but less pedigree information (Weigel, 2001). In addition to underestimating inbreeding levels and their consequences, the completeness of the pedigree data is relevant for the accuracy of animal genetic evaluations and the rate of genetic progress (Weigel, 2001; Cassel et al., 2003).

AR (1.06%) evaluated in relation to *F* provided an idea of how much an individual was represented in the pedigree data of this population. The AR was considered to be low, especially when compared to the 2.10% reported for dairy Gyr cattle (Verneque et al., 2006), another Zebu breed under selection for milk production. This difference reflects the effort of farmers to avoid inbreeding and the adoption of AR as a criterion for the selection of animals to be used in the progeny test and to constitute MOET families in the breeding



**Fig. 2.** Evolution of the population rate explained by ancestors.

program. In addition to planning the matings, MOET nucleus scheme is open, which contributes to minimize inbreeding.

As shown in Tables 2 and 3, in contrast to the trends of *F* and AR,  $N_e$  oscillated over generations, a finding indicating the occurrence of bottlenecks in this population during some periods (Nei et al., 1975). Several factors have contributed to this scenario, but the results can be mainly attributed to the founder effect and to the increasingly more frequent use of related sires since the beginning of the Guzerat dairy cattle breeding program.

The  $N_e$  value obtained for fully traced generations, the maximum number of generations traced and the equivalent complete generations corresponds to the lower, upper and true limits of  $N_e$ , respectively. According to Gutiérrez and Goyache (2005), these values are useful to approximate estimates in populations with scarce pedigree information. The reduced effective size ( $N_e$ ) in the fifth complete generation (98) might be a consequence of the intense use of fewer top sires. These values comprised the average  $N_e$  of 117 estimated for all registered Guzerat cattle by Faria et al. (2006) and are close to the threshold at which the loss of genetic variability by genetic drift and inbreeding depression is observed (FAO, 1992; Frankham et al., 2002). Therefore, although the levels of *F* and AR are considered to be low, continuous monitoring of effective size and inbreeding coefficients is recommended, as well as the adoption of mating plans, because of the importance of this breed in tropical regions (FAO, 1992, 2006; Colleau et al., 2004).

The average GI was a few months shorter than that reported for the whole registered Guzerat population (7.93 and 8 years) (Faria et al., 2006, 2009). The little fast replacement of parents in the dairy Guzerat cattle population under selection might explain this small difference, although the two GIs were considered to be extremely long. Long GIs are relevant in breeding programs since they limit the rate of genetic progress and the economic efficiency of the milk production system (Falconer and Mackay, 1996). The small difference in the GI between paternal and maternal pathways indicates a slightly faster replacement of parents in the maternal pathway due to the use of sires for a long period of time despite the increasing commercialization of dairy Guzerat sire semen (ASBIA, 2009). A reduction in the time necessary for commercialization of the semen of proven sires, i.e., at a younger age, is expected over the next years, as well as an increase in the reproductive efficiency of Guzerat herds, a fact that should result in an even shorter GI.

The value of  $f_e/f_a$  (3.15) found indicates the occurrence of bottleneck. This value is higher than the 1.11 and 1.49 observed for Guzerat cattle as a whole in the two subsequent periods investigated (Faria et al., 2004, 2009). Although bottlenecks have occurred since the foundation of the population, the value of 3.15 indicates the narrow genetic basis of the dairy Guzerat population. Therefore, at least two bottlenecks occurred after the arrival of Guzerat cattle in Brazil: one around 1939 because of the widespread use of this breed in crosses, and another, probably severe, during the recent foundation of the dairy Guzerat population (Faria et al., 2004).

The moderate unbalanced contribution of founders to the reference subpopulation of dairy Guzerat cattle under selection was demonstrated by the small number of founders ( $n=47$ )

contributing to 50% of the current subpopulation. However, it should be emphasized, e.g., that the bull Édipo A, among the top ten for milk, is descendant from three bulls among the top ten contributors (Profeta 140 – paternal grand–grand sire; Demais S – paternal grand dam; Gentil JA – maternal grand sire); being Demais S a half brother of Milanês S, other top ten contributor (Table 7). This is an important parameter, but the genetic variability of the population can be more precisely explained by the number of ancestors ( $f_a$ ) (Boichard et al., 1997). This parameter demonstrated the broad genetic basis of the dairy Guzerat cattle population. The number of founders contributing to genetic variability is close to but higher than that found for the whole Guzerat population, with 50 animals contributing to 41% of genetic variability (Faria et al., 2004).

Bias in the estimation of the effective number of founders ( $f_e$ ) is particularly severe in intensive selection programs, in which genomes from a limited number of individuals are widely disseminated. However, this is not the case for the Guzerat population selected for milk production, in which selection is still of low intensity. Although the  $N_e$  values found are a matter of concern, the average inbreeding coefficients of this population are low. Mating plans would probably prevent inbreeding in this population (Penna et al., 1998; Weigel and Lin (2000); Colleau et al., 2004). Open schemes, an alternative chosen by animal breeders for the MOET nucleus selection scheme of dairy Guzerat cattle, allows evaluations of new strains and are another important strategy to minimize inbreeding (Smith, 1988). In the MOET nucleus also, the Guzerat bulls can be evaluated in advance, irrespective of whether they come from the beef population, and, if positives for milk production, they will be available to breeders. Therefore, gene flow allows inbreeding minimization not only in nucleus but in the dairy herds as well.

All modern breeding programs, especially those based on the use of advanced reproductive technologies, should continuously monitor the level of inbreeding to guarantee the accuracy of selection and a high rate of genetic progress (Weigel and Lin, 2000).

## 5. Conclusions

The National Breeding Program for milk production of Guzerat cattle has encouraged the broad use of semen from proven sires of different origins and of high genetic merit in the herds, an approach that resulted in low inbreeding coefficients of younger individuals in the population. Despite the low average  $F$  and  $AR$  values and the low frequency of high inbred individuals, the  $N_e$  values are only slightly below the threshold indicating a risk of loss of genetic variability and should therefore be considered. Furthermore, the extensive use of a few sires, mainly after the introduction of modern reproductive technologies, may result in a reduction of the effective population and consequently increase average inbreeding coefficients and allow genetic drift.

Continuous monitoring of genetic diversity using population structure parameters is essential to prevent losses in genetic variability and to permit high genetic progress in this subpopulation, especially when the bottleneck effect is regarded. The present results thus indicate the need for further studies evaluating population parameters in the MOET nucleus sub subpopulation and the effects of inbreed-

ing on productive and reproductive traits. To our knowledge, there are no studies evaluating inbreeding depression in dairy Guzerat cattle, although the Dairy Guzerat Cattle Breeding Program is aimed at maintaining inbreeding at a low rate.

The results of this study indicate the need for the establishment of conservation policies for dairy Guzerat cattle in order to preserve the existing strains. For this purpose, studies evaluating the genetic population structure are necessary.

## Acknowledgements

The authors thank Fapemig and CNPq for the financial support, CBMG (Brazilian Center for the Guzerat Improvement) and Professors Gutierrez and Goyache for the free access to the software ENDOG.

## References

- ABCZ, 2005. Estatística total Brasil RGN + RGD: período 1939–2008. ABCZ, Uberaba, Brazil. Retrieved November 20, 2009 from <http://www.abcz.org.br>.
- ASBIA, 2009. Relatório Estatístico de Produção, Importação e Comercialização de Sêmen 2008. Retrieved September 30, 2009 from <http://www.asbia.org.br/download/mercado/relatorio2008.pdf>.
- Boichard, D., Maignel, L., Verrier, E., 1997. The value of using probabilities of gene origin to measure genetic variability in a population. *Genet. Sel. Evol.* 29, 5–23.
- Caballero, A., Toro, M.A., 2000. Interrelations between effective population size and other pedigree tools for management of conserved populations. *Genet. Res.* 75, 331–343.
- Caballero, A., Toro, M.A., 2002. Analysis of genetic diversity for the management of conserved subdivided populations. *Conserv. Genet.* 3, 289–299.
- Cañón, J., Alexandrino, P., Bessa, I., Carleos, C., Carretero, Y., Dunner, S., Ferran, N., Garcia, D., Jordana, J., Lalão, D., Pereira, A., Sanchez, A., Moazami-Goudarzi, K., 2001. Genetic diversity measures of local European beef cattle breeds for conservation purposes. *Genet. Sel. Evol.* 33, 311–332.
- Cassel, B.G., Adamec, V., Pearson, R.E., 2003. Effect of incomplete pedigrees on estimates of inbreeding and inbreeding depression for days to first service and summit milk yield in Holsteins and Jerseys. *J. Dairy Sci.* 86, 2967–2976.
- Colleau, J.J., Moureaux, S., Briend, M., Bechu, J., 2004. A method for the dynamic management of genetic variability in dairy cattle. *Genet. Sel. Evol.* 36, 373–394.
- Falconer, D.S., Mackay, T.F.C., 1996. *Introduction to Quantitative Genetics*, Fourth Ed. Longman Scientific and Technical, Harlow, UK.
- FAO, 1992. *The Management of Global Animal Genetic Resources*. FAO Anim. Prod. Health Paper. United Nations, Rome.
- FAO, 1995. *World Watch List for Domestic Animal Diversity*. FAO, Rome.
- FAO, 2006. *Livestock Report*. FAO, Rome. 83 pages.
- Faria, F.J.C., Vercesi Filho, A.E., Madalena, F.E., Josahkian, L.A., 2002. Pedigree Analysis in the Brazilian Zebu Breeds. Proceedings of the 6th World Congress on Genetic Applied to Livestock Production, Montpellier. CD-ROM.
- Faria, F.J.C., Vercesi Filho, A.E., Madalena, F.E., 2004. Variabilidade genética da raça Guzerá. Proceedings of the V Simpósio da Sociedade Brasileira de Melhoramento Animal. Universidade de São Paulo, São Paulo. CD-ROM.
- Faria, F.J.C., Vercesi Filho, A.E., Madalena, F.E., Josahkian, L.A., 2009. Pedigree analysis in the Brazilian Zebu Breeds. *J. Anim. Breed. Genet.* 126, 148–153.
- Frankham, R., Ballou, J.D., Briscoe, D.A., 2002. *Introduction to Conservation Genetics*. Cambridge University Press, Cambridge, UK.
- Goyache, F., Gutiérrez, J.P., Fernández, I., Gomez, E., Alvarez, I., Diez, J., Royo, L.J., 2003. Using pedigree information to monitor genetic variability of endangered populations: the Xalda sheep breed of Asturias as an example. *J. Anim. Breed. Genet.* 120, 95–105.
- Gutiérrez, J.P., Goyache, F., 2005. A note on ENDOG: a computer program for analyzing pedigree information. *J. Anim. Breed. Genet.* 122, 172–176.
- Hill, W.G., 2000. Maintenance of quantitative genetic variation in animal breeding programmes. *Liv. Prod. Sci.* 63, 99–109.
- Lacy, R.C., 1989. Analysis of founder representation in pedigrees: founder equivalents and founder genome equivalents. *Zoo Biol.* 8, 111–123.
- MacParland, S., Kearney, J.F., Rath, M., Berry, D.P., 2007. Inbreeding trends and pedigree analysis of Irish dairy and beef cattle populations. *J. Anim. Sci.* 85, 322–331.
- Nei, M., Maruyama, T., Chakraborty, R., 1975. The bottleneck effect and genetic variability in populations. *Evolution* 29, 1–10.

- Peixoto, M.G.C.D., Pereira, C.S., Fonseca, C.G., Madalena, F.E., 2005. Seleção para produção de leite em núcleos MOET das raças zebuínas: um estudo de simulação. *Arq. Bras. Med. Vet. Zoot.* 57, 673–683.
- Peixoto, M.G.C.D., Verneque, R.S., Teodoro, R.L., Penna, V.M., Martinez, M.L., 2006. Genetic trend for milk yield in Guzerat herds participating in progeny testing and MOET nucleus schemes. *Genet. Mol. Res.* 5, 454–465.
- Peixoto, M.G.C.D., Verneque, R.S., Pereira, M.C., Machado, M.A., Carvalho, M.R.S., 2009. Impact of milk production milk breeding program on the Guzerat population structure in Brazil. The 2009 Interbull Meeting, Barcelona, Spain. Retrieved November 26, 2009 from [http://www-interbull.slu.se/bulletins/bulletin40/Pre/Scientific\\_program2009rev\\_chairs.htm](http://www-interbull.slu.se/bulletins/bulletin40/Pre/Scientific_program2009rev_chairs.htm).
- Penna, V.M., Madalena, F.E., Alvim, M.T.T., 1998. Open MOET Nucleus of Selection in Guzerá. Proceedings of the 6th World Congress on Genetics Applied to Livestock Production, Armidale, Australia. CD-ROM.
- Statistical Analysis Systems Institute (SAS), 2003;. SAS/STAT. SAS Systems for Windows. Release 9.1. SAS Institute Inc., Cary, N.C., USA.
- Sewalem, A., Kistemaker, G.J., Miglior, F., Van Doormaal, B.J., 2006. Analysis of inbreeding and its relationship with functional longevity in Canadian dairy cattle. *J. Dairy. Sci.* 89, 2210–2216.
- Sorensen, A.C., Sorensen, M.K., Berg, P., 2005. Inbreeding in Danish dairy cattle breeds. *J. Dairy Sci.* 88, 1865–1872.
- Smith, C., 1988. Genetic improvement of livestock using nucleus-breeding units. *World Anim. Rev.* 65, 2–10.
- Verneque, R.S., Torres Filho, J.C., Reis Filho, J.C., Martinez, M.L., Lopes, P.S., Teodoro, R.L., Machado, M.A., Peixoto, M.G.C.D., 2006. Population Genetic Structure of Brazilian Gyr Dairy Cattle. Proceedings of the 8th World Congress on Genetic Applied to Livestock Production, Belo Horizonte, Brazil. CD-ROM.
- Vieira, H.C.M., Vozzi, P.A., Zambianchi, A.R., Bezerra, L.A.F., Lobo, R.B., Freitas, M.A.R., Oliveira, J.A., 2005. Estudo da endogamia em bovinos da raça Guzerá participantes do programa de melhoramento genético. Proceedings of the 42th Reunião Anual da Sociedade Brasileira de Zootecnia, Goiânia, Goiás, Brazil. CD-ROM.
- Vozzi, P.A., Marcondes, C.R., Magnabosco, C.U., Bezerra, L.A.F., Lôbo, R.B., 2006. Structure and genetic variability in Nellore (*Bos indicus*) cattle by pedigree analysis. *Genet. Mol. Biol.* 29, 482–485.
- Weigel, K.A., 2001. Controlling inbreeding in modern breeding programs. *J. Dairy Sci.* 84, E177–E184.
- Weigel, K.A., Lin, S.W., 2000. Use of computerized mate selection programs to control inbreeding of Holstein and Jersey cattle in the next generation. *J. Dairy Sci.* 83, 822–828.