Pedigree analysis and inbreeding depression on growth traits in Brazilian Marchigiana and Bonsmara breeds[1]

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ABSTRACT: The study of population structure by pedigree analysis is useful to identify important circumstances that affect the genetic history of populations. The intensive use of a small number of superior individuals may reduce the genetic diversity of populations. This situation is very common for the beef cattle breeds. Therefore, the objectives of the present study were to analyze the pedigree and possible inbreeding depression on traits of economic interest in the Marchigiana and Bonsmara breeds and to test the inclusion of the individual inbreeding coefficient (F_i) or individual increases in inbreeding coefficient (ΔF_i) in the genetic evaluation model for the quantification of inbreeding depression. The complete pedigree file of the Marchigiana breed included 29,411 animals born between 1950 and 2003. For the Bonsmara breed, the pedigree file included 18,695 animals born between 1988 and 2006. Only animals with at least 2 equivalent generations of known pedigree were kept in the analyses of inbreeding effect on birth weight, weaning weight measured at about 205 d, and BW at 14 mo in the Marchigiana breed, and on birth weight, weaning weight, and scrotal circumference measured at 12 mo in the Bonsmara breed. The degree of pedigree knowledge was greater for Marchigiana than for Bonsmara animals. The average generation interval was 7.02 and 3.19 for the Marchigiana and Bonsmara breed, respectively. The average inbreeding coefficient was 1.33% for Marchigiana and 0.26% for Bonsmara. The number of ancestors explaining 50% of the gene pool and effective population size computed via individual increase in coancestry were 13 and 97.79 for Marchigiana and 41 and 54.57 for Bonsmara, respectively. These estimates indicate reduction in genetic variability in both breeds. Inbreeding depression was observed for most of the growth traits. The model including ΔF_i can be considered more adequate to quantify inbreeding depression. The inclusion of F_i or ΔF_i in the genetic evaluation model may not result in better fit to the data. A genetic evaluation with simultaneous estimation of inbreeding depression can be performed in Marchigiana and Bonsmara breeds, providing additional information to producers and breeders.

Key words: beef cattle, genetic diversity, inbreeding, scrotal circumference, weaning weight

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INTRODUCTION

The study of population structure by pedigree analysis is useful to identify important circumstances that affect the genetic history of a population (Valera et al., 2005). The intensive use of a small number of superior individuals, which are often selected using procedures such as BLUP, may reduce the genetic diversity of populations. This reduction in genetic diversity and its effects have been extensively studied in different species, particularly in beef cattle (Swiger et al., 1961; Burrow, 1998; Santana et al., 2010). One of the most relevant effects resulting from reduced genetic diversity is inbreeding depression, which compromises the performance of domestic animals (Croquet et al., 2007; González-Recio et al., 2007; Panetto et al., 2010).

In Brazil, the Marchigiana and Bonsmara breeds are important for beef cattle crossbreeding systems. The Marchigiana breed that originated in Italy arrived in

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Table 1. Data structure[1]

	Marchigiana			Bonsmara		
Item	Birth weight	WW	W14	Birth weight	WW	SC
Number of records	5,535	2,147	1,998	6,808	4,070	1,158
Mean[2]	40.21	211.24	375.30	33.56	205.42	29.70
SD[2]	5.74	53.13	95.94	5.02	37.96	4.16
Mean F_i, %	0.80	0.75	0.76	0.61	0.50	0.36
Inbred animals, %	44.39	45.55	45.24	26.68	22.60	16.40
No. of sires	206	95	104	184	146	73
No. of dams	2,250	883	857	4,049	2,276	968
Range F_i						
$F_i = 0$	3,078	1,169	1,094	4,991	3,150	968
$0 < F_i \leq 6.25$	2,264	916	842	1,641	834	171
$6.25 < F_i \leq 12.5$	137	44	44	124	65	16
$12.5 < F_i \leq 25$	44	13	13	51	21	3
$F_i > 25$	12	5	5	1	0	0
Pedigree						
No. of animals	10,589	4,790	4,649	13,370	9,416	3,772
No. of sires	694	469	482	816	777	592
No. of dams	4,462	2,214	2,206	6,208	4,706	2,024

[1] WW = weaning weight; W14 = BW at 14 mo; SC = scrotal circumference; F_i = individual inbreeding coefficient.

[2] For birth weight, WW, and W14, values are expressed in kilograms. For SC, values are expressed in centimeters.

Brazil through 5 major imports (137 animals between 1969 and 1975), followed by minor imports of animals, semen, and frozen embryos from Italy, Canada, and Argentina. The Bonsmara breed originated in South African and first arrived in Brazil in 1997 through the semen imported from Argentina and the United States to be used in the composite beef cattle program of Brazil (CFM Montana Leachman). A total of 3,500 embryos imported from South Africa were born after the year 2000, giving origin to the first purebred animals of the country.

In view of the small number of animals introduced in Brazil and its consequences, the objectives of the present study were to analyze the pedigree and possible inbreeding depression on traits of economic interest in the Marchigiana and Bonsmara breeds and to test the inclusion of the individual inbreeding coefficient or individual increases in inbreeding in the genetic evaluation model for the quantification of inbreeding depression.

MATERIALS AND METHODS

Animal Care and Use Committee approval was not obtained for this study because the data were obtained from existing databases (Associação Brasileira dos Criadores de Marchigiana and Associação Brasileira dos Criadores de Bonsmara).

Data

The pedigree and production data of animals of the 2 breeds were obtained from the respective breeder associations (Associação Brasileira dos Criadores de Marchigiana, São Paulo, Brazil, and Associação Brasileira dos Criadores de Bonsmara, Presidente Prudente, Brazil). The complete pedigree file of the Marchigiana breed included 29,411 animals born between 1950 and 2003 on farms located in the states of São Paulo, Minas Gerais, Mato Grosso do Sul, and Paraná. For the Bonsmara breed, the pedigree file included 18,695 animals born between 1988 and 2006 on farms located in the states of São Paulo, Tocantins, Goiás, Mato Grosso do Sul, Bahia, and Paraná. All population parameters were computed for the animals belonging to the reference population, defined by animals born in the last generation interval. Animals with at least 2 equivalent generations of known pedigree were kept in the analyses of inbreeding effect on birth weight, weaning weight (**WW**) measured at about 205 d, and BW at 14 mo (**W14**) in the Marchigiana breed, and on birth weight, WW, and scrotal circumference (**SC**) measured at 12 mo in the Bonsmara breed (Table 1).

Population Structure and Inbreeding

Pedigree completeness level was assessed by computing the equivalent number of generations and by counting the proportion of known ancestors several generations back. The average relatedness coefficient of each individual was computed. Average relatedness is defined as the probability that an allele randomly chosen from the whole population in the pedigree belongs to a given animal. Average relatedness can then be interpreted as the representation of the animal in the whole pedigree, regardless of the knowledge of its own pedigree. The effective number of founders ($\boldsymbol{f_e}$) and effective number of ancestors ($\boldsymbol{f_a}$) were obtained to determine the concentration of the origin of both animals and genes. The parameter f_e is defined as the number of equally contributing founders that would be expected to produce the same genetic diversity as in the population under study (Lacy, 1989). When founders contribute to the reference population more equally, the effective number of founders is greater. This parameter is computed as $f_e = 1 / \left[\sum_{k=1}^{f} q_k^2\right]$, where q_k is the probability of gene origin of ancestor k. The parameter f_a is the minimum number of ancestors, not necessarily founders, explaining the complete genetic diversity of a population. This parameter complements the information offered by the effective number of founders by accounting for the losses of genetic variability produced by the unbalanced use of reproductive individuals producing bottlenecks. This parameter is computed as $f_a = 1 / \left[\sum_{j=1}^{a} q_j^2\right]$, where q_j is the marginal contribution of ancestor j, which is the genetic contribution made by an ancestor that is not explained by other ancestors chosen before. The founder genome equivalents (**f_g**) can be defined as the number of founders that would be expected to produce the same genetic diversity as in the population under study if the founders were equally represented and no loss of alleles occurred (Ballou and Lacy, 1995). According to Caballero and Toro (2000), parameter f_g was obtained by the inverse of twice the average coancestry of the individuals included in a predefined reference population.

Individual increases in inbreeding coefficients (**ΔF_i**) were calculated as described by Falconer and Mackay (1996) and modified by González-Recio et al. (2007) and Gutiérrez et al. (2009):

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

where F_i is the individual inbreeding coefficient and t is the equivalent complete generations for this individual (Maignel et al., 1996; Boichard et al., 1997). The expression relating inbreeding in generation t with inbreeding rate proposed by Gutiérrez et al. (2009) is

$$F_t = 1 - \left(1 - \Delta F\right)^{t-1}. \qquad [2]$$

The estimate of effective population size ($\overline{N_e}$; Gutiérrez et al., 2008), called realized effective size by Cervantes et al. (2008), was computed from $\overline{\Delta F}$ by averaging ΔF_i of the n individuals included in a given reference subpopulation, as $\overline{N_e} = 1/2\overline{\Delta F}$. The effective population size $\left(\overline{N_{ec}}\right)$ from an increase in coancestry (Δ_{cjk}) for all pairs of individuals j and k in a reference subpopulation was obtained according to Cervantes et al. (2011). The parameter Δ_{cjk} is computed as $\Delta_{cjk} = 1 - \sqrt[\frac{(g_j+g_k)}{2}]{1 - c_{jk}}$, where c_{jk} is the inbreeding value corresponding to an offspring from j and k, and g_j and g_k are the discrete equivalent generation of individuals j and k. Averaging the increase in coancestry for all pairs of individuals in a reference subpopulation, the effective population size based on coancestries is $\overline{N_{ec}} = \frac{1}{2}\overline{\Delta_c}$, which provides information on the effective size of a population under random mating.

The generation interval was estimated based on the average age of parents at the birth of their offspring kept for breeding. The individual inbreeding coefficient (**F_i**) was calculated as proposed by Meuwissen and Luo (1992). The ENDOG (v. 4.8; Gutiérrez and Goyache, 2005) and Poprep (Groeneveld et al., 2009) programs were used for pedigree analysis.

Inbreeding Depression

Genetic analyses to determine the effect of inbreeding on the traits studied were performed with the GIBBS1F90 software (Misztal et al., 2002) using a Bayesian approach. Each analysis consisted of a single chain with a length of 225,000 samples, discarding the first 25,000 samples. A lag period of 25 samples was used. Thus, 8,000 samples were used for final inferences. The statistical models for all traits included the fixed effect of contemporary group [herd, management group, birth year, birth season (1 = dry, 2 = rainy), and sex]; dam age at calving (linear and quadratic) and age at recording (linear) as covariates; and effect of animal, maternal, and maternal permanent environmental as random effects. Single-trait analyses were carried out for each breed including or not including F_i or ΔF_i as the covariate. Five models were used [without inbreeding, F_i (linear), ΔF_i (linear), F_i (linear and quadratic), ΔF_i (linear and quadratic)]. A total of 30 analyses were performed (2 breeds × 3 traits × 5 models). The deviance information criterion (**DIC**; Spiegelhalter et al., 2002) was used for comparison of the models. All records exceeding 3.5 SD above or below the mean and animals belonging to contemporary groups containing fewer than 5 animals with records were excluded.

RESULTS AND DISCUSSION

Population Structure and Inbreeding

The means and respective SD shown in Table 1. The percentage of inbred animals with records for some of the traits was greater in the Marchigiana breed than in the Bonsmara breed. Marchigiana animals were introduced in Brazil in 1969, whereas the Bonsmara breed was only introduced 28 yr later, a fact explaining the maximum number of known generations in the pedigree of each breed (Figure 1). The pedigree information of these 2 breeds still depends on the knowledge of the first imported animals. Pedigree knowledge will increase over time and with multiplication of the animals in Brazil.

The genetic contributions of ancestors to the 2 breeds are shown in Table 2. In both breeds, a small number of ancestors made a substantial contribution to the population. The number of ancestors explaining 50% of the gene pool was very small. For the Marchigiana breed, the number of ancestors contributing to the reference

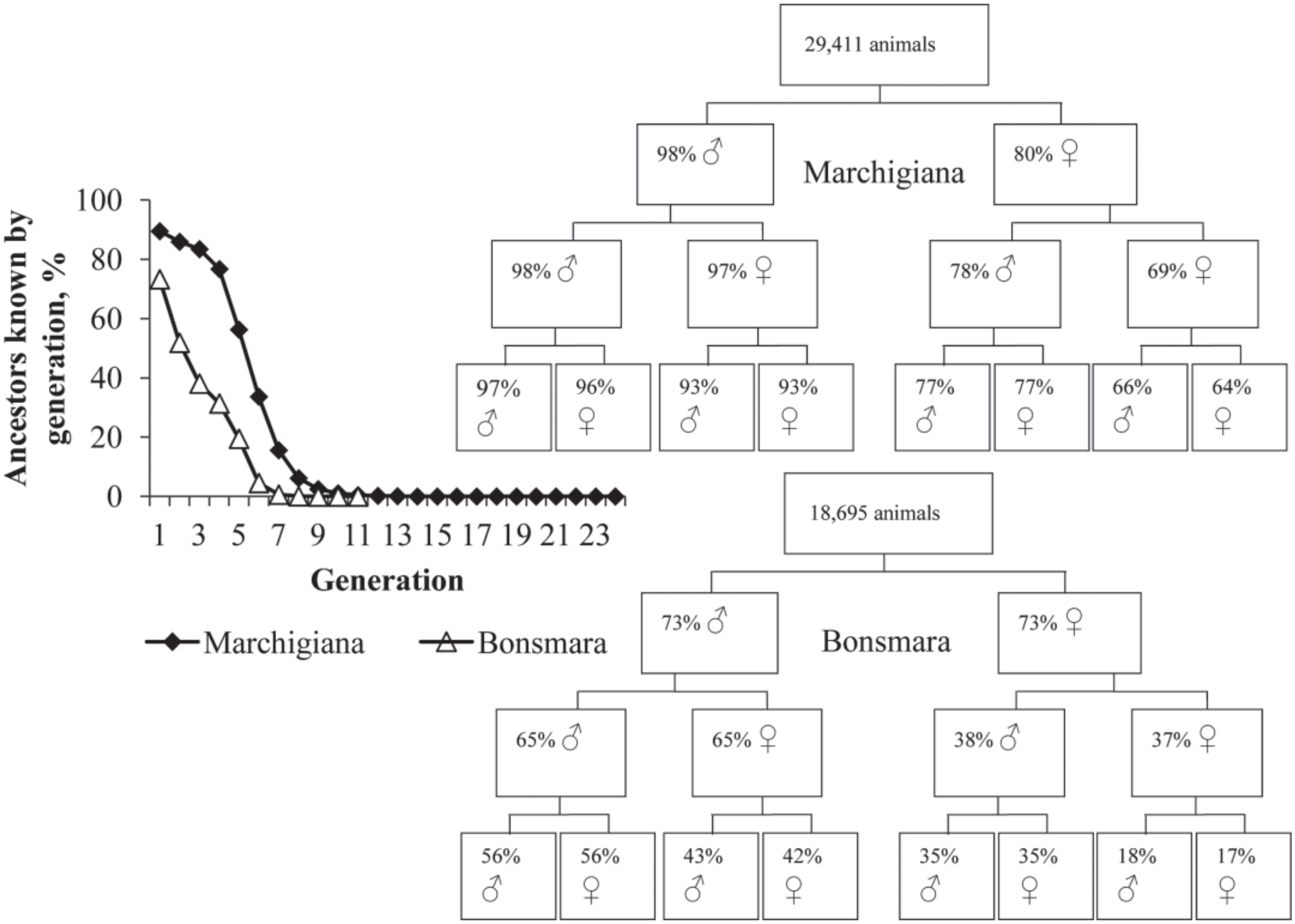

Figure 1. Aggregated for all generations known (left) and completeness of pedigree information up to 3 generations back (right) for the Marchigiana (above) and Bonsmara (below) breeds.

population was 5,626 (Table 2), corresponding to 19.1% of the population of 29,411 individuals and to 97.5% of the base population. Only 13 of these ancestors explained 50% of the genetic background of this population. In the study of Bozzi et al. (2006) on Italian Marchigiana cattle, the number of ancestors explaining 50% of the gene pool was greater than in the present work (21). Because the animals of the present study probably descended from those studied by Bozzi et al. (2006), this estimate is indeed expected to be reduced in Brazil. Similar results have been reported by Gutiérrez et al. (2003), Faria et al. (2009), and Peixoto et al. (2010) for different cattle breeds.

The Bonsmara breed is a composite breed that originated in the early 1940s from a 5/8:3/8 combination of Afrikaner (indigenous Sanga or *Bos taurus africanus*) and Shorthorn/Hereford (*Bos taurus taurus*) cattle through an initiative of the former Department of Agriculture of South Africa. In general, F_i and average relatedness tended to be less and the number of ancestors or founders tended to be greater in this population when compared with the Marchigiana breed.

The average F_i was greater in the Marchigiana breed (Table 2). This circumstance is reflected in the greater average relatedness coefficient obtained for this breed, demonstrating a greater degree of relationship among all individuals in the pedigree. Noninbred matings can be difficult in this situation.

There were a small number of ancestors contributing intensely to the reference population, especially in the Marchigiana breed (Figure 2). According to Gutiérrez et al. (2003), the differences between f_e, f_a, and f_g indicate the existence of bottlenecks in the pedigree of the 2 breeds. Furthermore, a bottleneck is logically more frequent in populations with long historical pedigree knowledge as is the case of the Marchigiana breed. The existence of a bottleneck was more important in the Marchigiana breed than in the Bonsmara breed. A slight increase of the population rate was observed for the Bonsmara breed, with several ancestors explaining a greater percentage of the population (Figure 2). The f_a/f_e and f_e/f_g ratios indicate how equally animals have contributed to the development of a population, with the ideal ratio being 1. According to Pedrosa et al. (2010), this estimate explains how an excessive use of certain individuals as breeding animals can lead to a marked reduction in the genetic stock. The expected inbreeding caused by the unbalanced contribution

Table 2. Summary statistics of the pedigree analysis of the Marchigiana and Bonsmara breeds

Variable[1]	Marchigiana	Bonsmara
Number of ancestors contributing to the reference population	5,626	4,659
Average of complete equivalent generations (entire pedigree)	4.52	2.19
Mean average relatedness, %	4.04	0.81
Animals in the reference population, birth year	1997 to 2003	2003 to 2006
Number of animals in the reference population	22,426	11,019
Base population (1 or more unknown parents)	5,765	5,110
Effective population size of founders	132.08	442.70
Expected inbreeding caused by unbalanced contribution of founders, %	0.38	0.11
Average F_i (entire pedigree), %	1.33	0.26
Average F_i for the reference population, %	2.21	0.41
Maximum inbreeding coefficient, %	28.91	26.56
Inbred animals, %	60.43	8.97
Average F_i for inbred animals, %	2.19	2.84
Effective number of founders/ancestors for the reference population	120/32	220/85
f_a/f_e ratio	0.26	0.38
Founder genome equivalents (f_g)	24.78	123.58
f_g/f_e ratio	0.20	0.56
Number of ancestors explaining 50% of the gene pool	13	41
Number of founders explaining 50% of the gene pool	39	96
Effective population size via individual increase in inbreeding $\left(\overline{N}_e\right)$	139.56	325.36
Effective population size computed via individual increase in coancestry $\left(\overline{N}_{ec}\right)$	97.79	54.57
Matings between sibs	328 (1.11%)	121 (0.64%)
Parent-offspring matings	137 (0.47%)	10 (0.05%)

[1] F_i = individual inbreeding coefficient; f_e = effective number of founders; f_a = effective number of ancestors.

of founders obtained for the 2 populations is shown in Table 2. The unbalanced contribution of founders was greater in the Marchigiana breed. An unbalanced contribution of founders and ancestors has also been reported by Voges and Distl (2009) for dog breeds, by Gutiérrez et al. (2003) for Spanish beef cattle breeds, and by Faria et al. (2009) for zebu breeds.

Table 3 shows the top founders contributing to the Marchigiana and Bonsmara breed. These animals played an important role in the formation of the Brazilian herds.

Although the level of inbreeding was considered to be low in the 2 populations, many animals in the pedigree, especially those of the Marchigiana breed, are inbred and some show an increased inbreeding level, a fact indicating that concern with inbreeding is required in the next generations. The average level of inbreeding has increased over the years in different populations and has become one of the main concerns of researchers and producers because of its unfavorable effect on the maintenance of genetic diversity and production of domestic animals. Bozzi et al. (2006) observed a significant increase in the average level of inbreeding in the Italian Chianina, Marchigiana, and Romagnola populations and concluded that the main cause of this increase was the intensive use of certain bulls. Mostert and Exley (2000) also reported significant increase in the average level of inbreeding over time in a South African Bonsmara population. There is consensus in most studies investigating population structures that good selection and mating strategies are the solution for the prevention of increases in inbreeding level and for the genetic preservation of species. Particularly in the case of the breeds studied here, attention should be paid to these issues to prevent genetic and economic losses.

Effective Population Size

In contrast to Cervantes et al. (2011) in a study using real data of 6 horse breeds and simulated data, the $\overline{N}_{ec}$ estimates were less than the $\overline{N}_e$ estimates in the 2 breeds studied (Table 2). This fact might be explained by an imbalance in the pedigree knowledge for males and females. For example, in the pedigree of Bonsmara animals, 5 generations back there are 1.4 to 72% of known ancestors, depending on sex. This fact may lead to overestimation of $\overline{N}_e$, particularly in the Bonsmara breed. The pedigree information of Bonsmara animals imported from South Africa is incomplete. In addition, many animals that are considered to be purebred Bonsmara were obtained by grading up of Nellore cows with unknown or uncontrolled pedigree. These explanations can be partially applied to the Marchigiana breed. Within this context, $\overline{N}_{ec}$ would provide an estimate

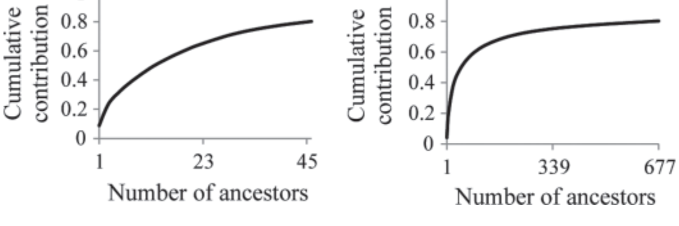

Figure 2. Evolution of the population rate explained by ancestors for Marchigiana (left) and Bonsmara (right) breeds.

Table 3. Top marginal genetic contributions of founders for Marchigiana and Bonsmara animals

Marchigiana				Bonsmara			
Individual	Sex	Contribution, %	Cumulative contribution, %	Individual	Sex	Contribution, %	Cumulative contribution, %
Savia	Female	2.54	2.54	HJLK25	Female	1.60	1.60
Ciak	Male	2.23	4.78	VVK22	Female	1.30	2.96
Spenna	Female	2.23	7.02	JRBH157	Male	1.19	4.16
Lassia	Female	1.93	8.96	AGK148	Female	1.13	5.29
Empadino	Male	1.80	10.76	AGJ8	Male	0.89	6.18
First 50	—	—	54.31	—	—	—	38.15
First 100	—	—	70.19	—	—	—	50.67

that is closer to reality than $\overline{N_e}$. In this study, Bonsmara was founded by a greater number of individuals than Marchigiana; however, the Bonsmara population census was less than the Marchigiana, leading to a smaller $\overline{N_{ec}}$ of Bonsmara. The $\overline{N_e}$ was used in Figure 3 to illustrate the behavior of effective population size over time.

As shown in Figure 3, the average level of inbreeding has increased in the 2 populations over the years, whereas $\overline{N_e}$ decreased. A drastic reduction of $\overline{N_e}$ was observed in the Bonsmara breed, a finding indicating a greater decline in the original genetic diversity of this population. Embryo transfer and AI are frequently used in this breed, with intensive use of certain bulls that are considered genetically superior. This fact might have contributed to the decline of $\overline{N_e}$ and the increase of the average inbreeding level in this population. Boichard et al. (1997) have shown that, when the pedigree information is incomplete, the computed inbreeding is biased downward and the realized effective size is overestimated. Given the low degree of pedigree knowledge for the breeds studied, the true effective size would be even less, a fact worsening the problem of maintenance of genetic variability (Gutiérrez et al., 2003).

The population parameters of the Brazilian Marchigiana and Bonsmara breeds are within acceptable levels. However, the substantial reduction in effective population size and genetic diversity, and the increase in average inbreeding level observed over the last years, support the need for interventions such as directed mating.

Generation Interval

The longest generation interval was observed for the Marchigiana breed (Table 4). Similar generation intervals have been reported by Faria et al. (2009) for Nellore, Gyr, and Guzerat animals (about 8 yr), and by Mc Parland et al. (2007) for Charolais, Limousin, Hereford, Angus, Simmental, and Holstein-Friesian cattle (6.17, 6.71, 6.03, 6.09, 6.54, and 6.66 yr, respectively). The shortest generation intervals were observed for dam-offspring pathways. This difference might be due to improved reproductive management. A reduction of genetic gain per unit of time is the main consequence of a long generation interval. Shorter generation intervals were observed for the Bonsmara breed. The Bonsmara is still being structured in Brazil, especially by grading up from crossbred cows. The shorter generation intervals, especially of females are explained by the intensive use of embryo transfer (**ET**). Many young males of South Africa (from ET) were also used extensively in Brazil. Thus, the intense use of ET in the early years of its structuring in Brazil explains the shortest genera-

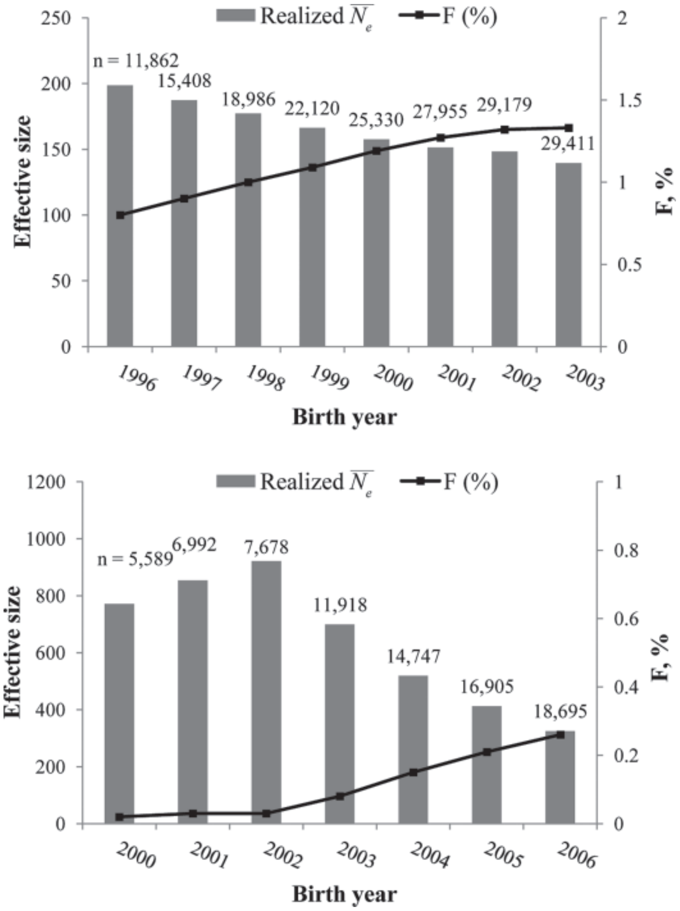

Figure 3. Inbreeding (F_i), realized effective population size $\left(\overline{N_e}\right)$, and number of animals (n) according to birth year for the Marchigiana (above) and Bonsmara (below) breeds.

Table 4. Generation interval obtained based on the average age of the parents at the birth of their selected offspring

	Marchigiana			Bonsmara		
Item	n	Interval	SD	n	Interval	SD
Sire-son	199	7.91	3.60	20	3.04	0.60
Sire-daughter	1,848	8.18	4.07	815	2.79	0.86
Dam-son	199	5.85	2.85	29	2.73	0.72
Dam-daughter	1,794	5.86	3.02	1,945	3.37	1.59
Average	4,040	7.02	3.73	2,809	3.19	1.43

tion interval in Bonsmara. The generation interval of Bonsmara may be underestimated because many of the embryos from South Africa imported by Brazil do not have complete information of pedigree. In the study of Groeneveld et al. (2009), South African Bonsmara also presented the shortest generation interval (5.6 yr) among the breeds studied. According to Gutiérrez et al. (2003) and Bozzi et al. (2006), this finding is probably due to the early replacement of sires and dams when AI and ET were used.

Model Comparison

On the basis of the DIC obtained in the present study (Table 5), the inclusion of F_i or ΔF_i (linear or quadratic effect or both) as a covariate should be seen with caution. The results regarding the goodness-of-fit of the models were inconsistent. For birth weight and W14 of Marchigiana breed, the best model was the standard model that did not include inbreeding (F_i or ΔF_i), which showed the least DIC. For WW the best models included the linear and quadratic covariates. In contrast, the model presenting the best fit for the all traits of Bonsmara breed was that including the linear covariate, mainly F_i. However, according to Panetto et al. (2010), the model with ΔF_i should be preferred; the regular inbreeding coefficients (F_i) generally grow over time and may be confused with the effects accounting for time such as contemporary group, whereas ΔF_i does not grow over time. González-Recio et al. (2007) and Gutiérrez et al. (2008) suggested the use of ΔF_i adjusted for pedigree depth of the individual as an alternative measure of inbreeding to permit the distinction between 2 animals with the same inbreeding coefficient but with differences in the number of generations in which this level of inbreeding had occurred. Gómez et al. (2008) also compared models including F_i or ΔF_i as the covariate and emphasized the good properties of ΔF_i. Therefore, because the pedigree of the breeds studied is not perfectly known, the model including ΔF_i was the best to quantify inbreeding depression.

Pearson correlations between EBV of all animals evaluated by the all models proposed were obtained for all traits studied in the 2 breeds. The correlations between expected breeding values obtained with all models were greater than 0.96. For both breeds, the percentage of animals selected in common for each trait using all proposed models was greater than 0.90% when 5, 10, or 20% of the best animals were selected. Therefore, no significant changes in the ranking of animals should occur when inbreeding (F_i or ΔF_i, linear and quadratic effects) is included in the genetic evaluation models, in agreement with the findings of González-Recio et al. (2007) for the Spanish Holstein population.

The use of a model for genetic evaluation that includes ΔF_i instead of F_i should be preferred for the correct quantification of inbreeding depression on traits of economic interest. As demonstrated in the present study, the inclusion of F_i or ΔF_i in the genetic evaluation model may not result in a model that provides the best fit depending on the breed and structure of the data set. However, the inclusion of inbreeding as

Table 5. Deviance information criterion of the proposed models as deviation from the standard model[1]

Item	Standard model	F_i,^{2} %	ΔF_i,^{2} %	F_i,^{2,3} %	ΔF_i,^{2,3} %
Marchigiana					
Birth weight, kg	0	4,263	4,629	16,312	16,754
WW, kg	0	−93	107	−4,779	−4,580
W14, kg	0	1,668	1,681	558	488
Bonsmara					
Birth weight, kg	0	−619,213	−618,124	−617,899	−616,753
WW, kg	0	−383,026	−382,777	−381,007	−380,784
SC, cm	0	−212,996	−212,696	−209,381	−206,658

[1] WW = weaning weight; W14 = BW at 14 mo; SC = scrotal circumference. F_i = individual inbreeding coefficient; ΔF_i = inbreeding rate.

[2] Linear covariate.

[3] Quadratic covariate.

a covariate should not have significant negative repercussions on the genetic evaluation of the animals. The inclusion of quadratic effect of inbreeding in the genetic evaluation model can be useful to check the maximum level of inbreeding that populations can sustain without loss in performance.

Inbreeding Depression

To illustrate and facilitate the interpretation of inbreeding depression when ΔF_i is included in the model as a covariate, this parameter can be transformed into the inbreeding coefficient for an animal with an average depth of pedigree using Eq. [2]. The mean number of equivalent generations of animals with records was 3.84 for the Marchigiana breed and 2.40 for the Bonsmara breed. Transforming the linear coefficient solutions of ΔF_i on birth weight, WW, and W14 of the Marchigiana breed and on birth weight, WW, and SC of the Bonsmara breed (Table 6) to F_i (%) corresponding to ΔF_i for the mean number of equivalent generations of each breed, these values would be 0.073 kg, 0.961 kg, and 0.439 kg and −0.154 kg, −2.062 kg, and −0.126 cm, respectively. In other words, $\Delta F_i = 1\%$ corresponds to an inbreeding coefficient of 2.81 and 1.39% in the Marchigiana and Bonsmara breeds, respectively, for the mean number of equivalent generations mentioned. Figure 4 illustrates the reduction in SC as a function of linear ΔF_i (%) converted to F_i (%) for 2.40 equivalent generations. The difference between an animal with 1% F_i and an animal with 12.5% F_i would be 1.58 cm.

For the Marchigiana breed, there was no evident inbreeding depression on birth weight (Table 6). However, calves with decreased birth weight may not have been recorded, which may have limited the detection of inbreeding depression for this trait. Burrow (1998) also been reported no significant effect of F_i on birth weight in a study involving tropical beef cattle. In contrast, an effect of F_i and ΔF_i (linear) on birth weight was observed for the Bonsmara breed, mainly when the model including ΔF_i was used (−0.154 kg/1% increase in F_i for 2.40 equivalent generations). Some studies reported unfavorable effects of F_i on birth weight in cattle. Swiger et al. (1961) found a negative effect of F_i (−0.38 kg/1% increase in F_i), whereas Pariacote et al. (1998) reported a reduction of 5.8 kg in birth weight per 1% increase in F_i. Falcão et al. (2001) also observed a significant effect of inbreeding (linear and quadratic) on birth weight in Brown Swiss cattle. These authors reported that inbreeding coefficient above 11% was detrimental for birth weight.

The inbreeding depression was observed when the models including quadratic covariate were used in WW and W14 of Marchigiana breed. The sign of the quadratic coefficients indicates that a negative impact may be occurring at greater levels of inbreeding for these traits. The maximum level of inbreeding that could be absorbed by animals before beginning to negatively affect the WW and W14 is around 20% by the F_i

Table 6. Model solutions (SD) for the effect of individual inbreeding coefficient (F_i) or inbreeding rate (ΔF_i) on the traits studied of the models proposed

Item[1]	F_i,[2] %	F_i,[2,3] %		*F*max,[4] %	ΔF_i,[2] %	ΔF_i,[2,3] %		Δ*F*max, %
		1	2			1	2	
Marchigiana								
Birth weight, kg*	0.051 (0.024)	—	—	—	0.207 (0.091)	—	—	—
WW, kg	0.820 (0.383)	1.359 (0.751)	−0.034 (0.041)	19.941	2.705 (1.468)	5.948 (2.723)	−0.700 (0.500)	4.248
W14, kg	0.420 (0.688)	1.000 (1.406)	−0.037 (0.075)	13.436	1.236 (2.630)	4.772 (5.072)	−0.762 (0.903)	3.501
Bonsmara								
Birth weight, kg*	−0.074 (0.026)	—	—	—	−0.216 (0.070)	—	—	—
WW, kg*	−0.896 (0.239)	—	—	—	−2.882 (0.752)	—	—	—
SC, cm*	−0.084 (0.066)	—	—	—	−0.177 (0.188)	—	—	—

[1] WW = weaning weight; W14 = BW at 14 mo; SC = scrotal circumference.

[2] Linear solution.

[3] Quadratic solution.

[4] *F*max, Δ*F*max = maximum level of inbreeding that could be absorbed by population before beginning to negatively affect its performance.

*No significant quadratic effect of inbreeding; thus, only the linear solution is provided ($P < 0.05$).

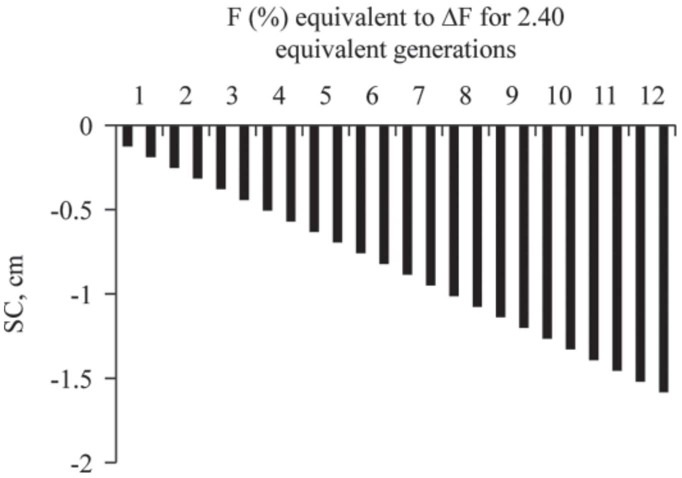

Figure 4. Trend of scrotal circumference (SC) in the Bonsmara breed as a function of the individual increase in inbreeding coefficient (ΔF_i) converted to individual inbreeding coefficient (F_i; %) for 2.40 equivalent generations.

approach and 4.248% by the ΔF_i approach (4.248% ΔF_i converted to F_i results in 1.509%). Therefore, a limited average level of inbreeding can be detrimental to animal performance. In the Bonsmara breed, only the linear effect of inbreeding (F_i or ΔF_i) was significant, probably due to decreased inbreeding in this breed. Several studies on beef cattle have shown that individual inbreeding unfavorably affects growth traits. Burrow (1998) reported a marked reduction in WW of tropical beef cattle (−0.679 to −0.720 kg/1% increase in F_i). A decrease in WW (−0.44 kg/1% increase in F_i) has also been reported by Burrow (1993) for several beef cattle breeds. Falcão et al. (2001) observed a significant decrease of WW (−0.51 kg/1% increase in F_i) in Brown Swiss cattle. Santana et al. (2010), studying Nellore animals, also found an unfavorable effect of F_i on WW. Burrow (1998) and Carolino and Gama (2008) also reported an inbreeding depression of −0.32 to −1.49 kg/1% increase in F_i on BW at 12 and 18 mo of age of beef cattle. The estimates of inbreeding depression indicate that the lack of control of inbreeding in the populations will result in economic losses for production systems.

As observed for the other traits studied, inbreeding also affected SC in Bonsmara animals. Inbreeding depression on SC has also been reported by Mc Parland (2008) for Charolais, Limousin, Simmental, Hereford, and Angus cattle (−1.2, −0.9, −1.6, −2.8, and −0.3 cm/1% increase in F_i, respectively). Santana et al. (2010) observed inbreeding depression on SC of −1.63 cm/1% increase in F_i, indicating that growth traits are unfavorably influenced by the individual inbreeding coefficient.

The effect of inbreeding is relevant to most of the studied traits. The effects of inbreeding can be detected even at limited average level of inbreeding of the population. A genetic evaluation with simultaneous estimation of inbreeding depression can be performed in Marchigiana and Bonsmara breeds, providing additional information to producers and breeders.

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