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ORIGINAL ARTICLE

Inbreeding depression in Zebu cattle traits

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Summary

The productivity of herds may be negatively affected by inbreeding depression, and it is important to know how intense is this effect on the livestock performance. We performed a comprehensive analysis involving five Zebu breeds reared in Brazil to estimate inbreeding depression in productive and reproductive traits. Inbreeding depression was estimated for 13 traits by including the individual inbreeding rate as a linear covariate in the standard genetic evaluation models. For all breeds and for almost all traits (no effect was observed on gestation length), the performance of the animals was compromised by an increase in inbreeding. The average inbreeding depression was −0.222% and −0.859% per 1% of inbreeding for linear regression coefficients scaled on the percentage of mean (β_m) and standard deviation (β_σ), respectively. The means for β_m (and β_σ) were −0.269% (−1.202%) for weight/growth traits and −0.174% (−0.546%) for reproductive traits. Hence, inbreeding depression is more pronounced in weight/growth traits than in reproductive traits. These findings highlight the need for the management of inbreeding in the respective breeding programmes of the breeds studied here.

Introduction

In view of their specific physical and physiological characteristics, Zebu cattle breeds (*Bos indicus*) are more adapted to pasture-based production systems in tropical environments (Turner 1980; Hansen 2004; Jonsson 2006), where high temperatures, high humidity and endo- and ectoparasites are frequent stressful factors. For this reason, Zebu cattle represent important genetic material and play a key role in food production in the tropics.

The Brazilian Association of Zebu Breeders (Associação Brasileira dos Criadores de Zebu – ABCZ) is responsible for the genealogical registry of Zebu breeds in Brazil and also promotes the genetic improvement of the breed through data collection, genetic evaluation and guidance regarding the use of the information resulting from this process. The Breeding Programme of Zebu Breeds (Programa de Melhoramento Genético de Zebuínos – PMGZ) comprises seven breeds (Brahman, Gir, Guzerá, Indubrasil, Nelore, Sindi, and Tabapuã). The selection process is guided by genetic evaluations which are performed using animal models and best linear unbiased prediction (BLUP). The accuracy of the predicted breeding values can be increased by including information from relatives; however, this approach increases the probability of co-selecting collateral relatives, which increases the rate of inbreeding (ΔF) and the loss of genetic variation (Woolliams *et al.* 2015). Consequently, the process of improving the productivity of herds may be negatively affected by inbreeding depression, which is defined as the decline in the phenotypic value of a trait as a direct consequence of inbreeding (Falconer & Mackay 1996).

Inbreeding depression for traits of economic interest in domestic animal populations has been estimated mainly by including the inbreeding coefficient of the individual (F_i) as a covariate in a standard genetic evaluation model. However, as suggested by González-Recio *et al.* (2007), the use of the individual inbreeding rate (ΔF_i) rather than F_i would be more adequate as ΔF_i takes into consideration the disparity in pedigree knowledge between animals and consequently permits more accurate estimation of inbreeding depression.

Few studies have been conducted in the world to estimate inbreeding depression in beef cattle traits, particularly Zebu cattle. Furthermore, only one of these studies involving Zebu cattle, that used data from a closed Guzerá herd, considered ΔF_i instead of F_i in the analyses (Panetto *et al.* 2010). Therefore, the objective with the present study was to perform a comprehensive analysis involving Zebu breeds reared in Brazil to estimate inbreeding depression in beef, milk and reproductive traits.

Material and methods

The database used in this study was provided by ABCZ and included all phenotypic and genealogical records collected by the association since the foundation of the herd book of Zebu breeds in 1919 until the end of 2012 for five breeds (Brahman, Gir, Guzerá, Nelore and Tabapuã) participating in the breeding programme. The Indubrasil and Sindi breeds were not included in this study because of the small number of phenotypic records after consistency analysis. The animals of all Zebu breeds are raised mainly on pastures, regardless of whether they are selected for milk, meat production or both. The herds are located throughout the different regions of Brazil.

The analyses were carried out in three phases. First, the pedigree files were analysed using the RELAX2 software (Strandén & Vuori 2006). The genealogical records of each breed were submitted to consistency analysis to eliminate any records with possible errors. Next, F_i, ΔF_i and the number of equivalent complete generations (ECG) of each individual were computed.

The ECG of each animal was obtained by the sum over term 0.5^n for all known ancestors, where n is the number of generations that separate the individual from each of its known ancestors (Maignel *et al.* 1996). Next, ΔF_i was estimated using the following equation (González-Recio *et al.* 2007; Gutiérrez *et al.* 2009):

$$\Delta F_i = 1 - \sqrt[\mathrm{ECG}_i - 1]{1 - F_i} \qquad (1)$$

where ECG_i is the number of equivalent complete generations of the animal.

In the second phase of the study, inbreeding depression was estimated for 13 traits: weaning weight (WW, measured at about 210 days of age); average daily weight gain from weaning to yearling (PWG); yearling weight (YW, measured at about 550 days of age); age at first calving (AFC); scrotal circumference (SC, measured at about 550 days of age); first calving interval (FCI); calving interval (CI); days open (DO); gestation length (GL); cumulative milk yield until 305 days of first lactation (MY305); cumulative fat yield until 305 days of first lactation (FY305); average milk fat percentage during first lactation (FP); and length of first lactation (LL). Phenotypic records of MY305, FY305, FP and LL were only available for Gir animals.

As suggested by Gutierrez et al. (2009), only the phenotypic records of animals whose ECG was two or higher were used for all breeds, except for Nelore, to obtain more accurate estimates of the effect of inbreeding on the different traits. In the case of Nelore animals, considering that the number of available records was sufficiently high, a greater restriction was imposed and only animals with ECG of four or higher were used. The structure of the data after appropriate consistency analysis and the descriptive statistics according to trait and breed are summarized in Table 1.

Four classes were defined for season of birth according to month of the year: (i) March to May; (ii) June to August; (iii) September to November; and (iv) December, January and February. Two calving seasons were defined according to month of the year: (i) April to September and (ii) October to December and January to March. The animals were divided into three feeding regimens: FR1 – animals grazing on pasture that received only mineral salt and eventually roughage such as hay, silage, sugarcane or green chop; FR2 – animals kept in semi-feedlot systems that received, in addition to the feed of FR1, some protein and mineral salt supplements or small portions of concentrate supplement such as cereals, industrial waste, and roots or tubers; RA3 – feedlot animals that received a diet consisting of a mixture of roughage (hay, silage, sugarcane or green chop) and concentrate, mineral and vitamin supplements.

Table 1 Descriptive statistics of the data according to breed and trait

		Descriptive statistics								F (%)							
													Frequency (%)				
Trait	Breed	ECGm	*N*	Animals	Mean	SD	Min.	Max.	NCG	Mean	Min.	Max.	0.00	0.01 to 6.25	6.26 to 12.50	12.51 to 25.00	>25.00
AFC (day)	Brahman	6.56	22 873	22 873	1150	236	655	1840	3026	1.50	0.00	31.75	29.82	66.12	3.26	0.75	0.05
	Gir	4.46	30 862	30 862	1291	243	665	1840	6166	2.32	0.00	43.52	41.37	46.60	7.08	4.23	0.71
	Guzerá	5.32	46 956	46 956	1274	238	656	1840	7112	2.07	0.00	39.60	28.64	62.12	6.30	2.56	0.39
	Nelore	5.59	831 766	831 766	1226	219	609	1840	72 480	2.96	0.00	44.23	5.72	85.28	7.30	1.32	0.37
	Tabapuã	3.88	54 401	54 401	1212	216	655	1840	6604	1.71	0.00	40.63	47.13	45.82	4.76	1.99	0.30
SC (cm)	Brahman	7.39	1530	1530	27.75	3.94	17.0	39	224	2.52	0.00	25.57	0.20	88.30	6.21	5.03	0.26
	Guzerá	6.55	3359	3359	26.09	4.10	14.5	39	364	1.87	0.00	26.22	4.26	91.10	3.22	1.28	0.15
	Nelore	6.38	58 852	58 852	25.83	3.64	13.0	39	3618	2.83	0.00	40.74	0.61	93.07	5.35	0.86	0.11
	Tabapuã	4.92	5686	5686	26.18	3.50	13.5	39	478	1.44	0.00	27.34	16.65	79.44	2.94	0.88	0.09
FCI (day)	Brahman	6.58	10 753	10 753	507	116	305	730	987	1.39	0.00	31.75	28.61	68.06	2.85	0.44	0.06
	Gir	4.66	14 982	14 982	504	109	305	730	2199	2.55	0.00	43.52	36.43	50.31	7.32	4.93	1.01
	Guzerá	5.55	24 712	24 712	512	112	305	730	2361	2.07	0.00	39.60	24.63	66.09	6.31	2.52	0.45
	Nelore	5.57	455 936	455 936	489	112	305	730	15 627	2.98	0.00	40.63	4.53	86.27	7.55	1.30	0.35
	Tabapuã	3.95	33 821	33 821	501	112	305	730	2123	1.73	0.00	37.50	45.05	47.98	4.74	1.96	0.27
CI (day)	Brahman	6.57	22 714	9655	487	114	305	730	1371	1.16	0.00	25.78	35.85	61.08	2.77	0.27	0.04
	Gir	4.43	71 732	40 460	492	109	305	730	5325	2.68	0.00	43.52	39.15	46.66	7.65	5.39	1.15
	Guzerá	5.22	101 191	60 679	487	111	305	730	4253	2.18	0.00	38.84	32.41	56.89	7.06	3.13	0.52
	Nelore	5.43	1 997 746	1 279 048	461	107	305	730	32 720	2.98	0.00	42.99	5.60	84.20	8.13	1.60	0.48
	Tabapuã	3.80	132 742	88 235	464	109	305	730	3024	1.62	0.00	37.50	55.19	38.28	4.63	1.67	0.23
DO (day)	Brahman	6.57	21 342	8694	189	114	35	460	1329	1.14	0.00	25.78	35.24	61.90	2.56	0.24	0.05
	Gir	4.43	58 228	29 740	190	105	35	458	4859	2.58	0.00	40.94	40.12	46.32	7.40	5.14	1.01
	Guzerá	5.24	84 602	46 636	183	109	35	458	3978	2.06	0.00	38.84	32.81	57.22	6.65	2.84	0.49
	Nelore	5.44	1 725 192	1 045 428	165	107	35	460	30 274	2.96	0.00	42.99	5.29	84.72	8.08	1.50	0.41
	Tabapuã	3.80	104 098	63 042	170	109	35	460	2819	1.59	0.00	37.50	54.54	39.26	4.49	1.52	0.20
GL (day)	Brahman	6.57	17 553	6505	293.1	8.2	270	315	1201	1.15	0.00	25.78	33.67	63.49	2.55	0.23	0.06
	Gir	4.42	41 268	19 237	290.9	8.5	270	315	3884	2.36	0.00	40.94	41.71	46.25	6.77	4.47	0.81
	Guzerá	5.25	57 630	27 883	294.9	8.4	270	315	3257	1.85	0.00	38.84	33.73	57.53	5.87	2.42	0.44
	Nelore	5.45	1 412 227	813 892	297	7.7	270	315	26 818	2.95	0.00	42.99	5.13	85.06	8.06	1.40	0.36
	Tabapuã	3.79	75 238	42 367	294.4	8.4	270	315	2378	1.54	0.00	31.25	55.61	38.48	4.43	1.29	0.19
WW (kg)	Brahman	7.66	18 528	18 528	193.3	39.7	50	370	2564	2.46	0.00	28.05	0.43	90.33	6.09	2.86	0.28
	Gir	5.18	6272	6272	149.1	37.1	49	320	1224	3.55	0.00	38.39	22.26	56.68	12.07	7.92	1.07
	Guzerá	6.31	52 424	52 424	182.8	38.8	47	416	6668	2.23	0.00	42.24	10.26	81.21	6.30	1.95	0.28
	Nelore	6.16	892 199	892 199	183.5	35.7	45	434	53 437	3.16	0.00	44.39	0.90	90.03	7.70	1.17	0.20
	Tabapuã	4.62	78 134	78 134	185.1	34.1	48	382	6314	1.91	0.00	37.50	22.07	71.26	4.89	1.54	0.23
PWG (g/day)	Brahman	7.50	6880	6880	454.5	176.7	51	997	1125	2.30	0.00	27.58	0.71	90.68	4.99	3.39	0.23
	Gir	5.15	1764	1764	380.1	159.1	55	992	371	3.58	0.00	34.77	23.70	53.06	15.42	7.20	0.62
	Guzerá	6.30	25 031	25 031	369.9	152.4	50	1000	3425	2.07	0.00	42.24	9.84	82.95	5.39	1.52	0.30
	Nelore	6.16	400 508	400 508	384.4	143.6	50	1000	26 280	3.11	0.00	44.39	0.94	90.46	7.35	1.09	0.16

(continued)

Table 1 (continued)

Trait	Breed	Descriptive statistics								F (%)							
													Frequency (%)				
		ECGm	*N*	Animals	Mean	SD	Min.	Max.	NCG	Mean	Min.	Max.	0.00	0.01 to 6.25	6.26 to 12.50	12.51 to 25.00	>25.00
	Tabapuã	4.58	36 189	36 189	377.5	146.2	50	1000	3547	1.80	0.00	31.25	22.46	71.72	4.43	1.24	0.15
YW (kg)	Brahman	7.50	6967	6967	349.3	77.9	134	780	1127	2.30	0.00	27.58	0.70	90.66	5.07	3.34	0.23
	Gir	5.15	1775	1775	272.1	72.4	110	555	371	3.57	0.00	34.77	23.72	53.13	15.32	7.21	0.62
	Guzerá	6.30	25 346	25 346	307.2	70.7	112	723	3426	2.07	0.00	42.24	9.85	82.91	5.41	1.53	0.30
	Nelore	6.16	403 076	403 076	314.0	62.2	82	741	26 286	3.11	0.00	44.39	0.93	90.43	7.37	1.10	0.16
	Tabapuã	4.58	36 418	36 418	315.1	61.3	112	743	3547	1.81	0.00	31.25	22.44	71.70	4.44	1.27	0.16
MY305 (kg)	Gir	4.34	6614	6614	3047	1538	260	8522	1029	0.52	0.00	17.58	51.18	47.60	1.12	0.11	0.00
FY305 (kg)	Gir	4.16	1687	1687	111.5	54.7	10	454	270	0.57	0.00	17.58	55.54	43.39	0.95	0.12	0.00
FP (%)	Gir	4.16	1687	1687	4.02	1.03	1.80	7.50	270	0.57	0.00	17.58	55.54	43.39	0.95	0.12	0.00
LL (day)	Gir	4.34	6614	6614	297	74	90	530	1029	0.52	0.00	17.58	51.18	47.60	1.12	0.11	0.00

ECGm, mean number of equivalent complete generations; NCG, number of contemporary groups; AFC, age at first calving; SC, scrotal circumference (measured at about 550 days of age); FCI, first calving interval; CI, calving interval; DO, days open; GL, gestation length; WW, weaning weight (measured at about 210 days of age); PWG, average daily weight gain from weaning to yearling; YW, yearling weight (measured at about 550 days of age); MY305, cumulative milk yield until 305 days of first lactation; FY305, cumulative fat yield until 305 days of first lactation; FP, average milk fat percentage during first lactation; LL, length of first lactation.

The traits were analysed using a single-trait animal model. The linear (systematic) effect of ΔF_i was included in all models. The remaining systematic (fixed) effects included in the specific models for each trait were for WW: contemporary group (herd–year–season of birth, feeding regimen from birth to weaning and sex), age at recording (linear effect) and age of dam at calving (linear and quadratic effects); PWG: contemporary group (contemporary group of WW, feeding regimen from weaning to yearling) and interval in days between weighing at weaning and yearling (linear effect); YW: contemporary group (contemporary group of WW, feeding regimen from weaning to yearling) and age at recording (linear effect); AFC: contemporary group (herd–year–season of birth, herd at calving); SC: contemporary group (contemporary group of WW, feeding regimen from weaning to yearling) and age at recording (linear effect); FCI: contemporary group (herd–year of first calving), month of first calving, AFC (linear effect) and sex of the second parity calf; GL: contemporary group (herd–year of previous calving), month of previous calving, age at previous calving (linear and quadratic effects) and sex of gestated calf; DO: contemporary group (herd–year of calving), month of calving and age at calving (linear and quadratic effects); MY305, FY305, FP and LL: contemporary group (herd–year–season of first calving) and AFC (linear and quadratic effects). As CI is obtained using the data of two consecutive calvings (i-1 and i), the systematic effects were contemporary group (herd–year of calving i-1), month of calving i-1, age at calving i-1 (linear and quadratic effects) and calf sex of calving i. As random effects, in addition to additive genetic effects of the animal and residual effect, the permanent environmental effect of the animal was included for CI, GL and DO and maternal additive genetic and permanent environmental effects for WW.

The general model used for analysis of the traits PWG, YW, AFC, SC, FCI, MY305, FY305, FP and LL can be described in matrix form as follows: $\mathbf{y} = \mathbf{X}\boldsymbol{\beta} + \mathbf{Za} + \mathbf{e}$, where $\mathbf{y}$ is the vector of observations; $\boldsymbol{\beta}$ is the vector of systematic effects; $\mathbf{a}$ is the vector of random additive genetic effects; $\mathbf{e}$ is the vector of the random residual effect; and $\mathbf{X}$ and $\mathbf{Z}$ are incidence matrices corresponding to the observations for these effects, respectively. For the traits CI, GL and DO, the general model was modified to include the $\mathbf{Wp}$ term, where $\mathbf{p}$ is the vector of random animal permanent environment effects and $\mathbf{W}$ is incidence matrix corresponding to the observations for these effects. For WW, the basic model was modified to include the $\mathbf{Z_m a_m}$ and $\mathbf{W_m p_m}$ terms, where $\mathbf{a_m}$ and $\mathbf{p_m}$ are the vectors of random maternal additive genetic and maternal permanent environment effects;

and $\mathbf{Z_m}$ and $\mathbf{W_m}$ are incidence matrices corresponding to the observations for these effects, respectively. The following assumptions were made for these models:

$$\mathbf{y}|\beta, \mathbf{a}, \sigma_e^2 \sim \mathbf{N}(\mathbf{X}\beta + \mathbf{Za}, \mathbf{I}\sigma_e^2),\ \mathbf{Var}\begin{bmatrix} \mathbf{a} \\ \mathbf{e} \end{bmatrix} = \begin{bmatrix} \mathbf{A}\sigma_a^2 & \mathbf{0} \\ \mathbf{0} & \mathbf{I}\sigma_e^2 \end{bmatrix},$$

$$\mathbf{y}|\beta, \mathbf{a}, \mathbf{p}, \sigma_e^2 \sim \mathbf{N}(\mathbf{X}\beta + \mathbf{Za} + \mathbf{Wp}, \mathbf{I}\sigma_e^2),\ \mathbf{Var}\begin{bmatrix} \mathbf{a} \\ \mathbf{p} \\ \mathbf{e} \end{bmatrix} = \begin{bmatrix} \mathbf{A}\sigma_a^2 & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{I}\sigma_p^2 & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{I}\sigma_e^2 \end{bmatrix},$$

$$\mathbf{y}|\beta, \mathbf{a}, \mathbf{a_m}, \mathbf{p_m}, \sigma_e^2 \sim \mathbf{N}(\mathbf{X}\beta + \mathbf{Za} + \mathbf{Z_m a_m} + \mathbf{W_m p_m}, \mathbf{I}\sigma_e^2),\ \mathbf{Var}\begin{bmatrix} \mathbf{a} \\ \mathbf{a_m} \\ \mathbf{p_m} \\ \mathbf{e} \end{bmatrix} = \begin{bmatrix} \mathbf{A}\sigma_a^2 & \mathbf{0} & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{A}\sigma_{am}^2 & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{I}\sigma_{pm}^2 & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{I}\sigma_e^2 \end{bmatrix},$$

where σ_a^2, σ_{am}^2, σ_p^2, σ_{pm}^2 and σ_e^2 are, respectively, the direct additive genetic, maternal additive genetic, permanent environmental, maternal permanent environmental and residual variances for the traits; $\mathbf{A}$ is the numerator relationship matrix, and $\mathbf{I}$ is an identity matrix.

Analysis was performed by the Bayesian method using the GIBBS2F90 program (Misztal *et al.* 2002). The prior distributions assumed for the parameters of the models were:

$$\begin{gathered} \beta \propto \text{constant}, \\ \mathbf{a}|\mathbf{A}, \sigma_a^2 \sim N(0, \mathbf{A}\sigma_a^2), \\ \mathbf{a}_m|\mathbf{A}, \sigma_{am}^2 \sim N(0, \mathbf{A}\sigma_{am}^2), \\ \mathbf{p}|\sigma_p^2 \sim N(0, \mathbf{I}\sigma_p^2), \\ \mathbf{p}_m|\sigma_{pm}^2 \sim N(0, \mathbf{I}\sigma_{pm}^2), \\ \sigma_a^2|v_a, s_a^2 \sim SIC(v_a, v_a s_a^2), \\ \sigma_{am}^2|v_{am}, s_{am}^2 \sim SIC(v_{am}, v_{am} s_{am}^2), \\ \sigma_p^2|v_p, s_p^2 \sim SIC(v_p, v_p s_p^2), \\ \sigma_{pm}^2|v_{pm}, s_{pm}^2 \sim SIC(v_{pm}, v_{pm} s_{pm}^2), \\ \sigma_e^2|v_e, s_e^2 \sim SIC(v_e, v_e s_e^2), \end{gathered}$$

where *N* and *SIC* indicate normal and scaled inverted chi-square distributions, respectively, and v_a, s_a^2, v_{am}, s_{am}^2, v_p, s_p^2, v_{pm}, s_{pm}^2, and v_e, s_e^2 correspond to the degrees of confidence and *a priori* values for additive genetic, maternal additive genetic, permanent environmental, maternal permanent environmental and residual variances for the traits, respectively. For all traits, zero was used for degrees of confidence and one for *a priori* values.

Inferences on the parameters of interest were made based on their corresponding marginal posterior distributions. For each trait-breed, a chain of 300 000 samples was generated. Using a burn-in period of 30 000 samples, inferences were made on the remaining 270 000 samples. Convergence was monitored by graphic inspection of the samples × iterations, as well as by the criteria included in the *boa* package of the R software (Smith 2007).

Once the posterior means of inbreeding depression were estimated, the third phase of the study was conducted to determine the occurrence of variations in inbreeding depression as a function of the different traits and breeds. As the interpretation of ΔF_i is not that simple, the regression coefficients obtained in the previous phase were converted to the F_i scale considering an animal with an average pedigree depth (using Equation (1) and the mean ECG of Table 1]. For each trait-breed, β_m and β_σ were obtained as the regression coefficient of inbreeding on the trait divided by the phenotypic mean or standard deviation, respectively. In the case of traits in which selection has the objective to reduce their phenotypic value, the sign of the regression coefficient was changed. The traits were divided into two groups, the first including growth-related traits (WW, PWG, YW and SC) and the second reproductive traits (AFC, FCI, CI, DO and GL). The traits MY305, FY305, FP and LL were not considered for this analysis as they were available for only one breed. The model used in this phase of the study was:

$$\mathrm{Y}_{ijk} = \mu + \mathrm{B}_i + \mathrm{G}_j + \mathrm{T}_k(\mathrm{G}_j) + \mathrm{DF}_{ik} + \varepsilon_{ijk} \tag{2}$$

where Y_{ijk} is the measure of inbreeding depression (β_m or β_σ) for a given trait *k* of breed *i*; B_i, G_j and T_k are the fixed effects of breed *i*, of the group of traits *j* and of trait *k*, respectively; DF_{ik} is the linear effect of average ΔF_i of breed *i* on trait *k*; and ε_{ijk} is the random error term. The method of least squares was used for analysis.

Results and discussion

The average F_i of animals with phenotypic records varied according to breed and trait analysed, with an overall mean of 2.36% (Table 1). The mean percentage of inbred animals was 74.44%; however, a relatively small percentage of animals (mean of 0.44%) had an inbreeding coefficient higher than 25%. The mean ECG for breeds were 6.99, 4.57, 5.78, 5.81 and 4.21, for Brahman, Gir, Guzerá, Nelore and Tabapuã, respectively. The overall mean ECG was 5.42, indicating reasonable knowledge of the pedigree of animals participating in the analyses and consequently permitting more accurate estimation of inbreeding depression as the estimate of F_i of these animals will also be more accurate (González-Recio *et al.* 2007; Panetto *et al.* 2010). A complete description of the structure of the populations studied here can be found in Santana *et al.* (2016).

The posterior mean estimates of heritability for the traits of each breed (Table 2) were generally similar to those reported in the literature for Zebu breeds (Boligon *et al.* 2010; Laureano *et al.* 2011; Verneque *et al.* 2014). As expected, reproductive traits exhibited lower heritabilities than traits related to growth or production. The mean heritabilities for AFC, FCI, CI, DO and GL were 0.07, 0.05, 0.05, 0.04 and 0.06, respectively, indicating a relatively small contribution of the additive genetic component to phenotype variability. For growth-related traits, the mean heritabilities were 0.16, 0.16, 0.28 and 0.42 for WW (direct effect), PWG, YW and SC, respectively. With respect to traits related to milk production, heritabilities of 0.28, 0.17, 0.17 and 0.16 were obtained for MY305, FY305, LL and FP, respectively.

To facilitate the interpretation and comparison with literature data, the regression coefficients obtained (on the ΔF_i scale) were converted to the F_i scale

Table 2 Posterior mean, standard deviation (SD) and highest posterior density interval (HPD) for heritability (h^2), heritability of direct (h_d^2) and maternal (h_m^2) effects and repeatability (r) according to breed and trait

	Brahman		Gir		Guzerá		Nelore		Tabapuã	
Trait	Mean (SD)	HPD$_{95\%}$	Mean (SD)	HPD$_{95\%}$	Mean (SD)	HPD$_{95\%}$	Mean (SD)	HPD$_{95\%}$	Mean (SD)	HPD$_{95\%}$
AFC										
h^2	0.08 (0.014)	0.05–0.11	0.10 (0.014)	0.07–0.13	0.08 (0.009)	0.06–0.10	0.07 (0.002)	0.07–0.08	0.04 (0.008)	0.03–0.06
SC										
h^2	0.59 (0.106)	0.39–0.79	–	–	0.28 (0.050)	0.18–0.37	0.36 (0.021)	0.32–0.40	0.45 (0.058)	0.33–0.56
FCI										
h^2	0.08 (0.019)	0.04–0.12	0.02 (0.009)	0.00–0.04	0.04 (0.008)	0.02–0.05	0.04 (0.002)	0.04–0.05	0.07 (0.009)	0.05–0.09
CI										
h^2	0.06 (0.010)	0.05–0.08	0.03 (0.005)	0.03–0.04	0.04 (0.004)	0.03–0.05	0.04 (0.001)	0.03–0.04	0.05 (0.004)	0.05–0.06
r	0.08 (0.010)	0.06–0.10	0.13 (0.005)	0.12–0.14	0.09 (0.004)	0.08–0.10	0.08 (0.001)	0.08–0.08	0.11 (0.003)	0.10–0.11
DO										
h^2	0.05 (0.008)	0.04–0.07	0.03 (0.005)	0.02–0.04	0.03 (0.004)	0.02–0.03	0.03 (0.001)	0.03–0.03	0.04 (0.004)	0.03–0.05
r	0.06 (0.009)	0.05–0.08	0.11 (0.005)	0.10–0.12	0.05 (0.004)	0.04–0.05	0.06 (0.001)	0.05–0.06	0.08 (0.003)	0.07–0.08
GL										
h^2	0.07 (0.011)	0.05–0.09	0.05 (0.008)	0.03–0.06	0.05 (0.006)	0.04–0.06	0.07 (0.002)	0.06–0.07	0.06 (0.006)	0.04–0.07
r	0.08 (0.011)	0.06–0.10	0.09 (0.007)	0.07–0.10	0.08 (0.006)	0.07–0.10	0.10 (0.001)	0.10–0.10	0.10 (0.005)	0.09–0.11
WW										
h_d^2	0.16 (0.025)	0.11–0.21	0.15 (0.030)	0.10–0.20	0.14 (0.014)	0.11–0.17	0.17 (0.005)	0.17–0.18	0.18 (0.015)	0.15–0.20
h_m^2	0.07 (0.019)	0.04–0.10	0.03 (0.012)	0.01–0.05	0.04 (0.007)	0.03–0.06	0.08 (0.003)	0.08–0.09	0.08 (0.009)	0.06–0.10
PWG										
h^2	0.17 (0.033)	0.11–0.24	0.15 (0.055)	0.06–0.26	0.15 (0.016)	0.12–0.18	0.15 (0.005)	0.14–0.16	0.17 (0.015)	0.14–0.20
YW										
h^2	0.22 (0.034)	0.16–0.29	0.19 (0.068)	0.07–0.32	0.29 (0.021)	0.25–0.33	0.33 (0.006)	0.31–0.34	0.37 (0.017)	0.33–0.40
MY305										
h^2	–	–	0.28 (0.032)	0.22–0.35	–	–	–	–	–	–
FY305										
h^2	–	–	0.17 (0.034)	0.10–0.24	–	–	–	–	–	–
FP										
h^2	–	–	0.16 (0.067)	0.06–0.29	–	–	–	–	–	–
LL										
h^2	–	–	0.17 (0.030)	0.11–0.23	–	–	–	–	–	–

AFC, age at first calving; SC, scrotal circumference (measured at about 550 days of age); FCI, first calving interval; CI, calving interval; DO, days open; GL, gestation length; WW, weaning weight (measured at about 210 days of age); PWG, average daily weight gain from weaning to yearling; YW, yearling weight (measured at about 550 days of age); MY305, cumulative milk yield until 305 days of first lactation; FY305, cumulative fat yield until 305 days of first lactation; FP, average milk fat percentage during first lactation; LL, length of first lactation.

considering an animal with an average pedigree depth [using Equation (1) and the mean ECG of Table 1], and all results reported refer to these converted regression coefficients. For all breeds and for almost all traits, the performance of the animals was compromised by an increase in inbreeding (Table 3). The reproductive traits AFC, FCI, CI and DO exhibited average increases of 1.72, 0.79, 0.66 and 0.81 day, respectively, per 1% increase in F_i. Therefore, it is expected that sexual precocity is reduced and reproductive performance is lower in inbred heifers across its productive life when compared to non-inbred heifers. Carolino & Gama (2008) observed a significant effect of F_i on AFC and CI in Alentejana cattle, with increases of 0.67 and 0.26 day, respectively, per 1% increase in F_i. Depression in the reproductive performance of Holstein–Friesian cows as a result of an increase in inbreeding has also been observed by Mc Parland *et al.* (2007), who estimated increases of 2.5 and 8.8 days in AFC and CI for animals with a F_i of 12.5%. Panetto *et al.* (2010) found a significant effect of F_i on AFC and CI in Guzerá cows. Studying a Nelore herd, Santana *et al.* (2010) observed a significant harmful effect of inbreeding on pregnancy probability at about 14 months of age (12–16 months). Miglior *et al.* (2008), studying different Canadian dairy breeds, observed an increase in DO of 0.29 day per 1% increase in F_i in Holstein cows. Similarly, Bezdíček *et al.* (2007), who used phenotypic records of Holstein and Czech Fleckvieh cows, estimated an increase in DO of 0.22 day per 1% increase in F_i.

In contrast to the other reproductive traits, an increase in F_i does not seem to have an effect on GL in the breeds studied here (Table 3). The calving interval of cows basically comprises two periods: the interval from previous calving to conception (DO) and gestation length (GL). According to the present results, the increase in CI of inbred animals is related to the increase in DO and not to changes in GL. Two studies investigating inbreeding depression in Holstein and Czech Fleckvieh cattle also found no significant effects of inbreeding on GL (Bezdíček *et al.* 2007; Rokouei *et al.* 2010).

Scrotal circumference, which is generally evaluated at yearling, has been used in breeding programmes as an indicator trait of sexual precocity. An average decrease of 0.07 cm in SC per 1% increase in F_i was observed in the present study (Table 3), indicating impairment of testicular development in inbred animals and a possible increase in the age at sexual maturity. Burrow (1998), studying cross-bred cattle in Australia, observed a decrease of 0.055 cm in SC per 1% increase in F_i. Similarly, Mc Parland *et al.* (2008) reported a reduction of 0.028 points in SC (evaluated on a scale from 1 to 10) per 1% increase in F_i in Irish Hereford cattle. Studying SC records from Bonsmara cattle in Brazil, Santana *et al.* (2012) found a reduction of 0.126 cm per 1% increase in F_i. In the only study involving Zebu cattle conducted by Santana *et al.* (2010) on 12 farms with Nelore animals in Brazil, inbreeding depression was −1.638 cm per 1% increase in F_i. It should be noted that in the last study, the model used by the authors only included environmental effects and not the additive genetic effect of the animal, a fact that might explain the high estimate of the linear regression coefficient.

With respect to the other growth-related traits, mean reductions of 0.41 kg for WW, of 1.83 g/day for PWG and of 0.96 kg for YW per 1% increase in F_i (Table 3) were observed, indicating a decrease in the growth rate of the inbred animals. For example, considering mating between half-sibs with $F = 0$, we would have a progeny with $F_i = 12.5\%$, which would be on average 12 kg lighter at 550 days of age when compared to animals with $F_i = 0$. Queiroz *et al.* (2000) estimated a reduction of 4.6 kg in WW (205 days of age) and of 6.7 kg in weight at 365 days of age for Gir animals with $F_i = 12.5\%$. Santana *et al.* (2010) reported a reduction of 17.55 kg in WW and of 22.47 g/day in PWG for Nelore animals with $F_i = 12.5\%$ when compared to non-inbred animals. Burrow (1998) observed a significant effect of the inbreeding coefficient on the weights of cross-bred cattle at 180, 365 and 550 days of age, with reductions of 0.679, 1.08 and 1.493 kg per 1% increase in F_i, respectively. Carolino & Gama (2008), studying the weight of Alentejana cattle from birth to maturity as well as average daily gain, also observed a negative effect of the inbreeding coefficient of the individual on its performance. Santana *et al.* (2012) reported a linear effect of F_i on WW (−2.062 kg per 1% increase in F_i) for Bonsmara animals. On the other hand, the authors observed a quadratic effect of F_i on WW in Marchigiana cattle, estimating performance losses only for F_i higher than 20%.

The average effect of the inbreeding coefficient of the dam on calf WW was −0.15 kg per 1% increase in F_i (Table 3), indicating that inbred cows wean lighter calves compared to non-inbred cows. The main reason for this finding could be that inbred cows produce less milk and the calf thus gains less weight when compared to the contemporary offspring of non-inbred cows. Carolino & Gama (2008) also observed a significant effect of maternal F_i on weights at different ages from birth to 210 days in Alentejana cattle. On the other hand, Santana *et al.* (2010) found no

Table 3 Posterior mean, standard deviation (SD) and highest posterior density interval (HPD) for linear regression solution[1] for effect of inbreeding (F) on traits according to breed

	Brahman		Gir		Guzerá		Nelore		Tabapuã	
Trait	Mean (SD)	$HPD_{95\%}$	Mean (SD)	$HPD_{95\%}$	Mean (SD)	$HPD_{95\%}$	Mean (SD)	$HPD_{95\%}$	Mean (SD)	$HPD_{95\%}$
AFC (days)	2.64 (0.85)	1.00 to 4.31	1.47 (0.32)	0.82 to 2.08	1.49 (0.30)	0.89 to 2.07	1.43 (0.09)	1.27 to 1.60	1.56 (0.28)	1.02 to 2.13
SC (cm)	−0.10 (0.02)	−0.15 to −0.05	–	–	−0.05 (0.02)	−0.09 to 0.00	−0.07 (0.01)	−0.08 to −0.06	−0.08 (0.02)	−0.11 to −0.04
FCI (days)	1.90 (0.71)	0.49 to 3.27	0.17 (0.23)	−0.27 to 0.62	0.81 (0.21)	0.39 to 1.21	0.47 (0.06)	0.36 to 0.58	0.57 (0.19)	0.21 to 0.95
CI (days)	1.35 (0.48)	0.42 to 2.29	0.44 (0.11)	0.24 to 0.65	0.53 (0.10)	0.33 to 0.72	0.40 (0.03)	0.35 to 0.46	0.59 (0.10)	0.39 to 0.79
DO (days)	1.91 (0.71)	0.49 to 3.28	0.18 (0.25)	−0.29 to 0.66	0.87 (0.22)	0.42 to 1.30	0.49 (0.06)	0.37 to 0.59	0.60 (0.20)	0.22 to 1.00
GL (days)	−0.03 (0.04)	−0.12 to 0.05	0.01 (0.01)	−0.01 to 0.04	0.00 (0.01)	−0.02 to 0.03	0.01 (0.00)	0.00 to 0.01	0.01 (0.01)	−0.01 to 0.03
WW – animal (kg)	−0.72 (0.07)	−0.86 to −0.57	−0.11 (0.07)	−0.24 to 0.02	−0.41 (0.04)	−0.48 to −0.33	−0.38 (0.01)	−0.40 to −0.36	−0.43 (0.03)	−0.48 to −0.37
WW – maternal (kg)	−0.32 (0.12)	−0.57 to −0.10	−0.02 (0.05)	−0.12 to 0.09	−0.13 (0.03)	−0.19 to −0.07	−0.16 (0.01)	−0.18 to −0.14	−0.13 (0.03)	−0.19 to −0.07
PWG (g/day)	−2.43 (0.44)	−3.31 to −1.57	−1.11 (0.51)	−2.12 to −0.12	−1.69 (0.20)	−2.07 to −1.30	−2.02 (0.06)	−2.14 to −1.91	−1.90 (0.18)	−2.26 to −1.55
YW (kg)	−1.51 (0.19)	−1.88 to −1.13	−0.57 (0.20)	−0.96 to −0.17	−0.85 (0.08)	−1.01 to −0.68	−1.00 (0.02)	−1.05 to −0.96	−0.87 (0.07)	−1.02 to −0.73
MY305 (kg)	–	–	−11.35 (4.58)	−20.20 to −2.26	–	–	–	–	–	–
FY305 (kg)	–	–	−0.27 (0.25)	−0.76 to 0.23	–	–	–	–	–	–
FP (%)	–	–	0.01 (0.01)	0.00 to 0.02	–	–	–	–	–	–
LL (days)	–	–	−0.46 (0.28)	−1.01 to 0.07	–	–	–	–	–	–

AFC, age at first calving; SC, scrotal circumference (measured at about 550 days of age); FCI, first calving interval; CI, calving interval; DO, days open; GL, gestation length; WW, weaning weight (measured at about 210 days of age); PWG, average daily weight gain from weaning to yearling; YW, yearling weight (measured at about 550 days of age); MY305, cumulative milk yield until 305 days of first lactation; FY305, cumulative fat yield until 305 days of first lactation; FP, milk fat percentage during first lactation; LL, length of first lactation.

[1] The regression coefficients were converted to the F_i scale considering an animal with an average pedigree depth, using equation $\Delta F_i = 1 - \sqrt[\mathrm{ECG}_{i}-1]{1 - F_i}$ and the mean ECG of Table 1.

significant effect of maternal F_i on WW in Nelore animals. A smaller effect of maternal F_i on WW was observed for Gir cattle. In a previous study on the same breed, Queiroz *et al.* (2000) observed no significant effect of maternal F_i on WW. The Gir breed has been submitted to dual purpose selection (meat and milk) or exclusively milk selection depending on the herd. It is possible that cows are milked in some herds and this fact is not reported to the association, which would explain the inconsistent maternal effect of F_i in this breed when compared to the other breeds of this study.

With respect to milk traits in Gir cattle, reductions in the performance of MY305, FY305 and LL were observed, but there was an increase in FP with increasing F_i (Table 3). This effect of an increase in FP is probably related to greater inbreeding depression in milk production than in fat production. In a study using models that only included environmental effects, but not the additive genetic effect of the animal, Reis Filho (2006) found a quadratic effect of F_i on MY305, FY305 and LL. The authors observed an increase in the performance of the animals until a F_i of about 10%, with a decline in performance thereafter. Queiroz *et al.* (1993) reported a linear effect of F_i on MY305 (−18.99 kg per 1% increase in F_i) and LL (−1.55 day per 1% increase in F_i) in Gir cattle. Panetto *et al.* (2010) studied a closed herd of Guzerá animals and observed a negative effect of F_i on the daily milk production of cows. Miglior *et al.* (2008), using data from seven Canadian dairy cattle breeds, reported a significant linear effect of F_i on MY305 (five breeds), FY305 (five breeds) and FP (two breeds). An increase of 0.003% in FP per 1% increase in F_i has been reported for Ayrshire cattle. Similarly, Rokouei *et al.* (2010) also found a significant linear effect of F_i on MY305 and FY305 in Iranian Holstein animals, with a reduction in performance with increasing F_i.

Using β_m and β_σ (Table 4), that is linear regression coefficients scaled on the percentage of mean and standard deviation, respectively, the average inbreeding depression for Zebu breeds was $\beta_\mathrm{m} = -0.222\%$ (SD = 0.19%) and $\beta_\sigma = -0.859\%$ (SD = 0.641%). In a meta-analysis using data from 57 studies, five species and 37 traits, Leroy (2014) found mean values of −0.137 and −0.56% for β_m and β_σ, respectively. The R^2 values of the model [2] were 0.81 and 0.92 for β_m and β_σ, respectively. The significant effects varied according to the mode that inbreeding depression was expressed (β_m or β_σ). For β_m, the significant effects were trait ($p < 0.0001$) and trait category ($p = 0.0018$), while breed ($p = 0.1652$) or average ΔF_i ($p = 0.074$) exerted no significant effect. On the other hand, for β_σ, all effects analysed were significant ($p < 0.05$). In their meta-analysis, Leroy (2014) also observed significant effects of trait (for β_m and β_σ) and trait category (for β_m) and a linear effect of average F_i (for β_σ). However, the author did not find significant effects of average F_i for β_m or trait category for β_σ.

The least square means for β_m (and β_σ) were −0.269% (−1.202%) for weight/growth traits and −0.174% (−0.546%) for reproductive traits. Hence, inbreeding depression is more pronounced in weight/growth traits ($p < 0.001$) than in reproductive traits. Similar results have been reported in the meta-analysis of Leroy (2014) in which the estimates of β_m (and β_σ) were −0.24% (−0.563%) for weight/growth traits and −0.222% (−0.336%) for reproductive/survival traits. On the other hand, DeRose & Roff (1999), who conducted a meta-analysis using data from non-domestic populations, estimated a greater effect of inbreeding on life-history traits (closely related to fitness) than on morphological traits (less closely related to fitness). According to Falconer & Mackay (1996), the change in means due to inbreeding can be expressed as $-2F_i\sum dpq$, where $\sum dpq$ corresponds to

Table 4 Least square means for inbreeding depression according to traits, scaled on percentage of mean (β_m) and standard deviation (β_σ)

Trait category	Trait	β_m (SEM)	β_σ (SEM)
Reproduction	Age at first calving^{a}	−0.134** (0.044)	−0.727*** (0.100)
	First calving interval^{a}	−0.146** (0.044)	−0.665*** (0.100)
	Calving interval^{a}	−0.147** (0.044)	−0.620*** (0.100)
	Days open^{a}	−0.448*** (0.044)	−0.738*** (0.100)
	Gestation length^{a}	0.007^{NS} (0.044)	0.019^{NS} (0.100)
Weight/growth	Scrotal circumference	−0.227*** (0.051)	−1.810*** (0.116)
	Weaning weight (animal)	−0.237*** (0.044)	−1.136*** (0.101)
	Weaning weight (maternal)	−0.098* (0.044)	−0.448*** (0.101)
	Weight gain from weaning to yearling	−0.471*** (0.044)	−1.200*** (0.100)
	Yearling weight (550 days of age)	−0.311*** (0.044)	−1.414*** (0.100)

NS, not significantly different than zero.

^{a}Inverted sign.

*$p < 0.05$; **$p < 0.01$; ***$p < 0.001$.

the contribution of all loci to inbreeding depression in the respective trait, and *d* corresponds to the genotypic value of the heterozygote in relation to the mean of the homozygotes for each locus. As a consequence, the intensity at which inbreeding will affect a given trait will depend on directional dominance (the genes are mainly dominant in one direction) and also on allele frequency (Falconer & Mackay 1996). If, in general, *d* is positive, inbreeding depression will be harmful. This is the case of selection, in which fixation occurs more rapidly at loci with negative *d* compared to loci with positive *d* (Leroy 2014). According to Leroy (2014), the directional dominance within a trait is the result of how intensely this trait has been selected. Zebu breeds have generally been selected for traits related to meat or milk production over a period of about 80 years. It is true that attention has also been given to reproductive traits, but the selection intensity was generally higher for production traits. It is therefore indeed expected that inbreeding depression is generally more intense for traits related to production compared to those related to reproduction. On the other hand, according to Leroy (2014), in wild populations, natural selection acts most markedly on fitness traits, a fact that would explain the results obtained by DeRose & Roff (1999).

Comparison of the effects of individual and maternal F_i on WW permits to conclude that the former is greater than the latter ($p < 0.001$), in agreement with the findings of Leroy (2014). On the other hand, Carolino & Gama (2008) found similar direct and maternal effects of F_i on WW in Alentejana animals. Furthermore, when WW and PWG were compared, the effect of inbreeding (β_m) was found to be more marked at older ages ($p < 0.001$), a fact also reported by Leroy (2014).

The standardization of the statistical models used here for the different breeds provided an adequate basis for comparison to identify differences in the effect of inbreeding on the same trait between breeds. No effect of the breed was observed when β_m was analysed. On the other hand, there was a significant effect of the breed when β_σ was used. The least square means for this parameter were −1.212% (SEM = 0.135%), −0.679% (SEM = 0.133%), −0.655% (SEM = 0.082%), −0.955% (SEM = 0.092%) and −0.868% (SEM = 0.070%) for Brahman, Gir, Guzerá, Nelore and Tabapuã animals, respectively. This result confirms the theory that inbreeding depression is related to the allele frequencies of the genes that affect each trait (Falconer & Mackay 1996), which should be different for each breed studied here.

The present results obtained for Zebu cattle support the theory that inbreeding affects reproductive performance and physiological efficiency (Falconer & Mackay 1996), thus causing a decline in the performance of animals in practically all traits of economic importance.

According to Woolliams *et al.* (2015), many breeders/breeding programmes believe that the management of inbreeding can be achieved by establishing an *ad hoc* threshold for the F_i of the mating products, which is incorrect as a father/mother can have a major contribution to the population and produce considerable inbreeding in the future considering that many pedigree loops will trace back to it, thus increasing the future rate of inbreeding (ΔF) even if the parent itself has $F_i = 0$. Also according to these authors, the rate at which relationships and inbreeding coefficients change in a population is more important to the fitness of a population because ΔF determines effective population size. Santana *et al.* (2016) observed an overall increase in average coancestry over the last 10 years for all five populations studied here. An increase in coancestry will increase the average F_i of future generations as the average inbreeding in generation *t* equals the average coancestry between the selected sires and dams in generation $t-1$ (Woolliams *et al.* 2015).

Woolliams *et al.* (2015) provided a broad description of a method for the management of inbreeding, called optimum contribution selection (OCS), which is designed to maximize genetic gain for a given ΔF. None of the cattle breeding programmes in Brazil possesses a comprehensive and effective strategy to manage inbreeding. In this respect, OCS could be an alternative to be implemented. For the sustainability of breeding programmes, it would be important that special attention is given to the balance between genetic gain and genetic diversity in the different Zebu breeds to control inbreeding and its harmful effects.

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