



Genetic parameter estimates and response to selection for weight and testicular traits in Nelore cattle

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ABSTRACT. We estimated genetic parameters for various phases of body and testicular growth until 550 days of age in Nelore cattle, using Bayesian inference, including correlation values and error estimates. Weight and scrotal records of 54,182 Nelore animals originating from 18 farms participating in the Brazilian Nelore Breeding Program (PMGRN) were included. The following traits were measured: weight at standard ages of 120 (W120), 210 (W210), 365 (W365), 450 (W450), and 550 (W550) days; weight gain between 120/210 (WG1), 210/365 (WG2), 365/450 (WG3), 450/550 (WG4), 120/365 (WG5), 120/450 (WG6), 120/550 (WG7), 210/450 (WG8), 210/550 (WG9), and 365/550 (WG10)

days of age; scrotal circumference at 365 (SC365), 450 (SC450) and 550 (SC550) days of age, and testicular growth between 365/450 (TG1), 450/550 (TG2) and 365/550 (TG3) days of age. The model included contemporary group (current farm, year and two-month period of birth, sex, and management group) and age of dam at calving, divided into classes as fixed effects. The model also included random effects for direct additive, maternal additive and maternal permanent environmental, and residual effects. The direct heritability estimates ranged from 0.23 to 0.39, 0.13 to 0.39 and 0.32 to 0.56 for weights at standard ages, weight gains and testicular measures, respectively. The genetic correlations between weights (0.69 to 0.94) and scrotal circumferences (0.91 to 0.97) measured at standard ages were higher than those between weight gain and testicular growth (0.18 to 0.97 and 0.36 to 0.77, respectively). The weights at standard ages responded more effectively to selection, and also gave strong correlations with the other traits.

Key words: Beef cattle; Gibbs samples; Growth; Reproductive traits

INTRODUCTION

The new economic order, based on competition and a constant search for productive efficiency, has forced livestock producers to adopt new technologies. These changes in farm management are accompanied by genetic alterations of the herds promoted by the selection of animals. This process is supported by the choice of criteria compatible with the objective of the activity and by the accurate estimation of (co)variance components of the traits selected.

In beef cattle, weights and weight gains between certain ages have been adopted as selection criteria because they are easy to measure and interpret, the possibility of promoting substantial genetic gain, and high genetic correlations between these measures. In Brazil, genetic breeding programs include scrotal circumference as a reproductive criterion since, in addition to its easy measurement, this trait presents favorable genetic correlations with productive and reproductive traits in both females (Eler et al., 2004; Forni and Albuquerque, 2005) and males (Sarreiro et al., 2002; Kealey et al., 2006).

The estimation of (co)variance components for any criteria adopted permits the construction and application of selection indices and of mixed model equations, as well as the calculation of parameters such as heritability and genetic correlation, thus facilitating the planning of breeding programs and the interpretation of genetic mechanisms involved in the expression of different traits (Henderson, 1986). In view of this importance, various methods of estimation have been tested in quantitative genetic analyses to obtain accurate estimates and to facilitate the implementation of complex models. In this respect, Gianola and Fernando (1986) introduced the Bayesian approach in animal breeding and Wang et al. (1993) subsequently applied it to linear mixed models using the Gibbs algorithm.

The objective of the present study was to test linear mixed models in combined analyses by Bayesian inference to estimate genetic parameters for different phases of body and testicular growth until 550 days of age in Nelore cattle, to contribute to selection programs designed to improve these traits.

MATERIAL AND METHODS

Weight and scrotal records of Nelore animals originating from 18 farms participating in the Brazilian Nelore Breeding Program (PMGRN) were used. The following traits were studied: weight at standard ages of 120 (W120), 210 (W210), 365 (W365), 450 (W450), and 550 (W550) days; weight gain between 120/210 (WG1), 210/365 (WG2), 365/450 (WG3), 450/550 (WG4), 120/365 (WG5), 120/450 (WG6), 120/550 (WG7), 210/450 (WG8), 210/550 (WG9), and 365/550 (WG10) days of age; scrotal circumference at 365 (SC365), 450 (SC450) and 550 (SC550) days of age, and testicular growth between 365/450 (TG1), 450/550 (TG2) and 365/550 (TG3) days of age.

Exploratory analysis was performed using the Statistical Analysis System software (SAS[®] Institute, 2003) to evaluate the consistency of the data. The contemporary groups consisted of current farm, year and two-month period of birth, sex, and management group. Records that were 3.5 standard deviations above or below the mean of the group and contemporary groups containing progeny from a single sire or fewer than five animals were eliminated. The file contained data from 54,182 individuals (Table 1) and the number of animals in the relationship matrix was 82,692.

Table 1. Summary of data structure and descriptive statistics for weight at standard ages (W), weight gain (WG), scrotal circumference (SC), and testicular growth (TG) in Nelore cattle.

Traits	N	Mean	SD	Min.	Max.	NS	NM
W120 (kg)	50,956	127.60	19.07	57.00	199.00	1,090	21,576
W210 (kg)	47,772	185.64	27.88	78.00	312.00	1,097	20,723
W365 (kg)	39,588	238.83	40.14	101.00	452.00	1,064	18,439
W450 (kg)	36,540	278.84	47.66	118.00	559.00	1,023	17,402
W550 (kg)	23,146	319.82	53.69	142.00	606.00	808	13,158
WG1 (kg)	45,139	57.74	14.09	-2.00	130.00	1,061	19,936
WG2 (kg)	35,237	52.37	25.27	-41.00	183.00	988	16,925
WG3 (kg)	31,917	40.73	16.03	-37.00	128.00	979	15,805
WG4 (kg)	20,738	46.88	20.15	-23.00	133.00	765	12,084
WG5 (kg)	37,907	110.44	30.42	-4.00	290.00	1,008	17,795
WG6 (kg)	33,980	151.97	37.07	16.00	402.00	954	16,359
WG7 (kg)	21,260	195.22	44.05	58.00	444.00	750	12,152
WG8 (kg)	33,679	93.71	33.75	-46.00	279.00	953	16,326
WG9 (kg)	21,139	137.06	39.18	5.00	358.00	747	12,112
WG10 (kg)	21,774	85.43	28.44	-64.00	261.00	794	12,444
SC365 (cm)	12,428	20.26	2.02	12.10	30.30	713	8,665
SC450 (cm)	14,715	23.43	2.81	12.70	36.30	736	9,640
SC550 (cm)	7,896	26.51	3.22	13.50	38.60	533	6,013
TG1 (cm)	10,241	3.20	1.30	-1.50	8.90	652	7,403
TG2 (cm)	6,717	3.44	1.34	-1.40	9.10	486	5,216
TG3 (cm)	5,624	6.63	2.08	-1.90	17.50	485	4,528

N = number of records; SD = standard deviation; NS = number of sires; NM = number of mothers.

(Co)variance components were estimated by multi-trait analysis simultaneously including the following traits: W120, SC365, WG1, WG2, WG3, WG4, TG1, and TG2. The model included contemporary group and age of dam at calving divided into classes (for W120 and WG1) as fixed effects. The model also includes random effects for direct additive, maternal additive (for W120 and WG1) and maternal permanent environmental (for W120 and WG1), and residual. In view of contradictory results in the literature, the covariance between direct and maternal genetic effects was fixed at zero as done in other studies (Albuquerque and Meyer, 2001a).

The GIBBS2F90 program (Misztal, 2007) was used for analysis. A chain of 1,131,500 cycles was generated, with a burn-in period of 30,000 iterations and a sampling interval of 100. Genetic parameters for the other characteristics (W205, W365, W450, W550, WG5, WG6, WG7, WG8, WG9, WG10, SC450, SC550, and TG3) were estimated through the sum of variances in each vector

The matrix presentation of the complete model used for analysis is:

$$y = X\beta + Z_1a + Z_2m + Wc + e \quad (\text{Equation 1})$$

where y , β , a , m , c , and e are vectors of observations, fixed effects, direct additive genetic effects, maternal additive genetic effects, maternal permanent environmental effects, and residual effects, respectively, and X , Z_1 , Z_2 , and W are incidence matrices that relate β , a , m , and c to the observations. Uniform and Gaussian priors were assumed for fixed and random effects, respectively:

$$\begin{aligned} \beta &\propto \text{constante} \\ a | G_a &\sim MVN[0, (A \otimes G_a)] \\ m | G_m &\sim MVN[0, (A \otimes G_m)] \\ c | E_p &\sim MVN[0, (I_n \otimes E_p)] \\ e | R &\sim MVN[0, (I_n \otimes R)] \end{aligned} \quad (\text{Equation 2})$$

where A , G_a , G_m , E_p , R , and I_n are the relationship matrices, direct genetic, maternal genetic, maternal permanent environmental and residual covariances, and identity, respectively, and \otimes is the operator of the Kronecker product. For variance components, priors derived from inverse Wishart distributions, corresponding to the inverse chi-square distribution in univariate cases, were used (Van Tassell and Van Vleck, 1996). Thus:

$$\begin{aligned} G_a | S_a, v_a &\sim IW[S_a, v_a] \\ G_m | S_m, v_m &\sim IW[S_m, v_m] \\ E_p | S_p, v_p &\sim IW[S_p, v_p] \\ R | S_r, v_r &\sim IW[S_r, v_r] \end{aligned} \quad (\text{Equation 3})$$

where S_a and v_a , S_m and v_m , S_p and v_p , and S_r and v_r are *a priori* values and degrees of freedom for direct additive, maternal additive, maternal permanent environmental, and residual covariances, respectively.

The burn-in period and the sampling interval were established empirically and post-Gibbs analysis was performed using the Gibanal program (Van Kaam, 1997) to determine convergence and the number of effective samples. The population parameters were calculated in each vector, and the mean, median and mode of posterior distributions were estimated. In addition, the 95% high-density interval (HDI) was calculated since this parameter is more informative than confidence intervals in the case of asymmetric or multimodal distributions (Hyndman, 1996).

RESULTS AND DISCUSSION

Analysis of convergence, dependence between samples and reliability of the estimates

The results obtained with the Gibanal program showed that the burn-in period was sufficient to determine convergence of the chain. The effective sample size obtained for the parameters was relatively small (22 to 1614) when compared to the total number of vectors generated. In general, the correlation estimates presented the greatest dependence, with a smaller effective sample size being associated with correlations of maternal origin.

Therefore, the use of a model simultaneously including a large number of traits, although representing a more extensive source of information (Schaeffer, 1984), increases the dependence between samples due to the number of parameters involved. In the case of estimates related to maternal effects, the number of offspring per dam may have increased the dependence between these parameters, although other factors such as the number of dams with records also interfere with these estimates (Heydarpour et al., 2008). However, no minimum effective sample size on which to infer has been reported in the literature. The size obtained in the present study seemed to be sufficient to obtain measures of central tendency and variation.

With respect to the reliability of the estimates, heritabilities and variances presented a small HDI and a low standard deviation, findings indicating that the parameters were reliable. The correlation estimates presented low standard deviations, but exceptions were observed.

Genetic parameter estimates and response to selection

The direct heritability estimates for weights at standard ages were moderate to high (0.23 to 0.39) and were higher at older ages (Table 2). The magnitude of variation in these estimates was similar to that reported by Albuquerque and El Faro (2008), but the point estimates were slightly higher. The growing trend in the heritability estimates, as also demonstrated by Albuquerque and Meyer (2001b) using random regression, is due to the fact that direct additive variance increases at a higher rate than residual variance with increasing age as a result of the combined action of a large number of genes on weights measured at the ages studied, whereas random environmental effects tend to cancel each other over time.

With respect to weight gains, the direct heritability estimates ranged from 0.13 to 0.39 and tended to be higher for wider intervals (WG5 to WG9). Similar estimates have been reported in the literature. Paneto et al. (2002) obtained estimates ranging from 0.16 to 0.32 for total gains between standard ages. Krejcová et al. (2007), studying daily weight gains over nine periods by multi-trait and random regression analysis, reported heritabilities ranging from 0.045 to 0.29.

Considering the results presented, the selection based on WG6 or WG7 was found to be as effective as selection based on weights at standard ages, because a substantial part of the variation was due to the average effect of genes. However, it is important to consider the magnitude of direct additive variance, its relationship with other traits of interest and operational aspects, because it requires at least two measures in animal.

With respect to maternal effects, the heritability estimates were of low magnitude and were higher for weights at standard ages (0.11 and 0.10 for W120 and W210, respectively) when compared to weight gain (0.04 for WG1). Albuquerque and Meyer (2001b) reported higher maternal heritabilities

Table 2. Descriptive statistics of posterior distribution for variance components and genetic parameters for weight at standard age (W) and weight gains (WG).

Traits	Parameters	Mean	Mode	Median	SD	ES	HDI (95%)	
W120	σ_a^2	50.75	50.82	50.73	3.10	754	44.61	56.64
	σ_e^2	121.53	122.01	121.50	1.94	942	117.80	125.80
	σ_c^2	23.42	23.00	23.27	2.23	377	19.61	27.78
	σ_{pm}^2	25.72	25.75	25.71	1.84	210	22.25	29.32
	h_d^2	0.23	0.23	0.23	0.01	754	0.20	0.25
	h_m^2	0.11	0.11	0.11	0.01	377	0.09	0.12
	c^2	0.12	0.12	0.12	0.01	283	0.10	0.13
W210	σ_a^2	102.28	102.98	102.39	6.38	707	90.65	114.76
	σ_e^2	226.56	227.04	226.65	4.08	943	218.92	234.48
	σ_c^2	41.64	40.73	41.73	4.02	404	34.39	49.66
	σ_{pm}^2	54.64	53.41	54.59	3.48	453	48.11	61.41
	h_d^2	0.24	0.24	0.24	0.01	566	0.21	0.27
	h_m^2	0.10	0.10	0.10	0.01	404	0.08	0.12
	c^2	0.13	0.13	0.13	0.01	453	0.11	0.14
W365	σ_a^2	173.00	175.61	173.01	9.27	941	154.40	190.80
	σ_e^2	322.38	321.17	322.28	6.44	1,414	310.74	335.27
	h_d^2	0.35	0.34	0.35	0.02	941	0.32	0.38
W450	σ_a^2	234.88	236.54	234.76	12.11	1,614	211.82	258.45
	σ_e^2	409.15	413.70	409.49	8.33	1,414	392.12	424.36
	h_d^2	0.36	0.36	0.36	0.02	942	0.34	0.40
W550	σ_a^2	336.42	332.64	336.06	16.43	1,615	302.91	368.34
	σ_e^2	533.29	534.18	533.46	11.94	1,413	509.13	556.31
	h_d^2	0.39	0.39	0.39	0.02	1,413	0.35	0.42
WG1	σ_a^2	18.21	18.20	18.20	1.37	566	15.66	20.70
	σ_e^2	79.76	79.43	79.76	1.01	754	77.88	81.88
	σ_c^2	4.47	4.58	4.46	0.67	147	3.31	5.77
	σ_{pm}^2	5.88	5.89	5.87	0.68	101	4.51	7.16
	h_d^2	0.17	0.17	0.17	0.01	566	0.14	0.19
	h_m^2	0.04	0.04	0.04	0.01	147	0.03	0.05
	c^2	0.05	0.05	0.05	0.01	101	0.04	0.07
WG2	σ_a^2	40.54	39.57	40.52	2.77	565	34.52	45.40
	σ_e^2	170.58	170.81	170.55	2.41	471	165.70	175.20
	h_d^2	0.19	0.19	0.19	0.01	565	0.17	0.22
WG3	σ_a^2	16.56	16.50	16.53	1.53	377	13.79	19.52
	σ_e^2	115.51	115.29	115.50	1.44	707	112.90	118.50
	h_d^2	0.13	0.12	0.13	0.01	377	0.10	0.15
WG4	σ_a^2	25.96	25.56	25.82	2.63	323	20.63	30.30
	σ_e^2	152.87	152.80	152.80	2.35	566	148.20	157.60
	h_d^2	0.15	0.14	0.15	0.01	323	0.12	0.17
WG5	σ_a^2	77.83	77.43	77.71	4.35	566	69.55	86.56
	σ_e^2	215.81	216.97	215.81	3.40	942	208.90	222.58
	h_d^2	0.27	0.27	0.27	0.01	707	0.24	0.29
WG6	σ_a^2	126.39	126.53	126.47	6.69	943	113.99	139.83
	σ_e^2	299.10	299.05	299.10	5.34	1,414	288.79	309.60
	h_d^2	0.30	0.30	0.30	0.01	943	0.27	0.33
WG7	σ_a^2	205.48	204.93	205.36	10.53	1,131	185.48	227.37
	σ_e^2	403.41	402.53	403.27	8.56	1,414	386.85	420.05
	h_d^2	0.34	0.33	0.34	0.02	1,131	0.31	0.37
WG8	σ_a^2	82.45	80.99	82.28	4.97	754	72.70	91.93
	σ_e^2	263.94	262.55	263.88	4.17	1,131	255.40	271.67
	h_d^2	0.24	0.24	0.24	0.01	942	0.21	0.26
WG9	σ_a^2	139.63	139.13	139.47	7.97	942	123.76	155.16
	σ_e^2	347.49	346.56	347.26	6.63	942	334.64	361.34
	h_d^2	0.29	0.29	0.29	0.02	1,131	0.26	0.32
WG10	σ_a^2	53.34	52.58	53.27	4.15	538	45.30	61.76
	σ_e^2	247.14	248.05	247.07	3.94	754	240.06	255.67
	h_d^2	0.18	0.18	0.18	0.01	377	0.15	0.20

σ_a^2 = direct additive variance; σ_e^2 = residual variance; σ_m^2 = maternal additive variance; σ_{pm}^2 = maternal permanent environmental variance; h_d^2 = direct heritability; h_m^2 = maternal heritability; c^2 = maternal permanent environmental variance component as proportion of phenotypic variances; ES = number of effective samples; SD = standard deviation; HDI = high-density interval.

for weights at 120 (0.25) and 240 (0.20) days of age. In contrast to these authors who observed a decrease in the maternal effect with age, in the present study this effect was stable at 120 and 210 days. Therefore, in view of the similarity of maternal effects at these ages and the higher phenotypic variance observed at 210 days, a greater response to selection is expected for maternal ability at this age.

Regarding measures of testicular growth, the heritability estimates were high (0.32 to 0.56), except for TG2 (Table 3). As observed for the weight traits, greater response to selection can be achieved through selection based on the scrotal circumference at standard ages. For traits obtained at standard ages, the estimates were higher than those reported by Yokoo et al. (2007) (0.48, 0.53 and 0.42 for SC365, SC450 and SC550, respectively). Similar estimates for TG1 and TG2 were observed by Paneto et al. (2002) (0.24 and 0.18 for scrotal growth between 365/455 and 455/550 days of age).

Table 3. Descriptive statistics of posterior distribution for variance components and genetic parameters for scrotal circumference (SC) and testicular growth (TG).

Traits	Parameters	Mean	Mode	Median	SD	ES	HDI (95%)	
SC365	σ_a^2	1.52	1.52	1.52	0.09	629	1.34	1.70
	σ_e^2	1.41	1.41	1.41	0.07	754	1.27	1.54
	h_d^2	0.52	0.51	0.52	0.03	629	0.47	0.57
SC450	σ_a^2	2.98	3.01	2.99	0.19	629	2.61	3.34
	σ_e^2	2.36	2.29	2.36	0.14	628	2.12	2.63
	h_d^2	0.56	0.56	0.56	0.03	706	0.50	0.61
SC550	σ_a^2	3.82	3.72	3.81	0.26	470	3.33	4.32
	σ_e^2	3.06	3.10	3.07	0.19	377	2.67	3.43
	h_d^2	0.56	0.58	0.56	0.03	471	0.49	0.62
TG1	σ_a^2	0.44	0.45	0.44	0.04	313	0.36	0.53
	σ_e^2	0.90	0.91	0.90	0.04	376	0.84	0.98
	h_d^2	0.33	0.33	0.33	0.03	313	0.27	0.38
TG2	σ_a^2	0.26	0.25	0.25	0.05	140	0.18	0.36
	σ_e^2	1.14	1.15	1.14	0.05	147	1.06	1.23
	h_d^2	0.18	0.18	0.18	0.03	113	0.12	0.25
TG3	σ_a^2	0.95	0.96	0.95	0.12	202	0.72	1.16
	σ_e^2	2.06	2.10	2.07	0.10	180	1.87	2.24
	h_d^2	0.32	0.32	0.32	0.04	202	0.24	0.38

σ_a^2 = direct additive variance; σ_e^2 = residual variance; h_d^2 = direct heritability; SD = standard deviation; ES = number of effective samples; HDI = high-density interval.

The genetic correlations between weights (0.69 to 0.94) and scrotal circumferences (0.91 to 0.97) measured at standard ages were higher than those between weight gain and testicular growth (0.18 to 0.97 and 0.36 to 0.77, respectively) (Table 4). High correlations for weight gain and testicular growth were only observed between overlapping measures. Similar results have been reported by Albuquerque and Meyer (2001b) for weights at standard ages using random regression models and by Yokoo et al. (2007) between measures of scrotal circumference at 365, 450 and 550 days of age. The genetic correlations obtained for weight gains showed a magnitude similar to that reported by Krejcová et al. (2007), except for some negative correlations (-0.131 to 0.958).

For traits measured at standard ages (weight and scrotal circumference), an inverse relationship was observed between the genetic correlation estimate and chronological distance between the two measures. Similar results have been reported by Albuquerque and Meyer (2001b) using random regression models for weights. Weight gains presented higher correlations with weights adjusted for age at the upper limit of the interval that determined the weight gain.

Table 4. Estimates of *a posteriori* average and standard deviation (in parentheses) of the genetic (top right) and environmental (bottom left) correlations between the characteristics of weight and testicular development [scrotal circumference (SC) and testicular growth (TG)] in the Nelore cattle.

	W120	W210	W365	W450	W550	WG1	WG2	WG3	WG4	WG5	WG6
W120	-										
W210	0.81 (0.00)	0.94 (0.01)	0.78 (0.02)	0.73 (0.02)	0.69 (0.02)	0.55 (0.04)	0.12 (0.05)	0.24 (0.05)	0.29 (0.06)	0.35 (0.04)	0.36 (0.04)
W365	0.58 (0.01)	-	0.88 (0.01)	0.82 (0.01)	0.80 (0.02)	0.81 (0.02)	0.24 (0.05)	0.25 (0.05)	0.42 (0.05)	0.56 (0.03)	0.53 (0.03)
W450	0.52 (0.01)	0.70 (0.01)	-	0.97 (0.00)	0.94 (0.01)	0.80 (0.02)	0.66 (0.03)	0.43 (0.05)	0.47 (0.05)	0.86 (0.01)	0.83 (0.02)
W550	0.49 (0.01)	0.61 (0.01)	0.85 (0.00)	-	0.97 (0.00)	0.73 (0.03)	0.70 (0.02)	0.63 (0.04)	0.48 (0.06)	0.86 (0.01)	0.90 (0.01)
WG1	0.13 (0.01)	0.59 (0.01)	0.73 (0.01)	0.85 (0.00)	-	0.76 (0.03)	0.67 (0.02)	0.60 (0.04)	0.68 (0.04)	0.85 (0.01)	0.88 (0.01)
WG2	-0.14 (0.01)	0.69 (0.01)	0.47 (0.01)	0.39 (0.01)	0.39 (0.01)	-	0.36 (0.05)	0.18 (0.06)	0.52 (0.06)	0.74 (0.02)	0.65 (0.03)
WG3	0.01 (0.00)	-0.19 (0.01)	-0.06 (0.01)	-0.05 (0.01)	0.33 (0.01)	-0.15 (0.01)	-	0.50 (0.05)	0.31 (0.06)	0.89 (0.01)	0.88 (0.01)
WG4	0.07 (0.01)	-0.02 (0.01)	-0.07 (0.01)	0.47 (0.01)	0.37 (0.01)	-0.05 (0.01)	-0.08 (0.01)	-	0.27 (0.07)	0.44 (0.05)	0.71 (0.03)
WG5	-0.05 (0.01)	0.11 (0.01)	-0.02 (0.01)	-0.06 (0.01)	0.48 (0.01)	0.09 (0.01)	-0.15 (0.01)	-0.08 (0.01)	-	0.47 (0.05)	0.47 (0.05)
WG6	-0.03 (0.01)	0.25 (0.01)	0.79 (0.01)	0.65 (0.01)	0.53 (0.01)	0.48 (0.01)	0.80 (0.00)	-0.10 (0.01)	-0.08 (0.01)	-	0.95 (0.01)
WG7	0.02 (0.01)	0.20 (0.01)	0.62 (0.01)	0.84 (0.00)	0.67 (0.01)	0.37 (0.01)	0.63 (0.01)	0.54 (0.01)	-0.11 (0.01)	0.79 (0.00)	-
WG8	-0.10 (0.01)	0.24 (0.01)	0.53 (0.01)	0.69 (0.01)	0.88 (0.01)	0.38 (0.01)	0.45 (0.01)	0.41 (0.01)	0.52 (0.01)	0.63 (0.01)	0.79 (0.01)
WG9	-0.04 (0.01)	-0.17 (0.01)	0.41 (0.01)	0.68 (0.01)	0.50 (0.01)	-0.15 (0.01)	0.75 (0.00)	0.60 (0.01)	-0.17 (0.01)	0.58 (0.01)	0.86 (0.00)
WG10	0.07 (0.01)	-0.07 (0.01)	0.34 (0.01)	0.55 (0.01)	0.76 (0.01)	-0.07 (0.01)	0.56 (0.01)	0.47 (0.01)	0.51 (0.01)	0.45 (0.01)	0.67 (0.01)
SC365	0.32 (0.02)	0.07 (0.01)	-0.06 (0.01)	0.27 (0.01)	0.63 (0.01)	0.04 (0.01)	-0.17 (0.01)	0.62 (0.01)	0.73 (0.01)	-0.13 (0.01)	0.28 (0.01)
SC450	0.30 (0.02)	0.39 (0.02)	0.52 (0.02)	0.49 (0.02)	0.44 (0.02)	0.27 (0.02)	0.26 (0.02)	0.06 (0.02)	0.02 (0.02)	0.40 (0.02)	0.37 (0.02)
SC550	0.31 (0.02)	0.36 (0.02)	0.48 (0.02)	0.53 (0.02)	0.52 (0.02)	0.25 (0.02)	0.24 (0.02)	0.20 (0.02)	0.09 (0.03)	0.36 (0.02)	0.44 (0.02)
TG1	0.08 (0.02)	0.38 (0.03)	0.46 (0.03)	0.50 (0.02)	0.57 (0.03)	0.26 (0.02)	0.20 (0.02)	0.18 (0.02)	0.25 (0.03)	0.33 (0.02)	0.39 (0.03)
TG2	0.08 (0.02)	0.09 (0.02)	0.13 (0.02)	0.25 (0.02)	0.28 (0.02)	0.06 (0.02)	0.07 (0.02)	0.26 (0.02)	0.12 (0.02)	0.09 (0.02)	0.24 (0.02)
TG3	0.11 (0.02)	0.10 (0.02)	0.07 (0.02)	0.06 (0.02)	0.20 (0.02)	0.06 (0.02)	-0.02 (0.02)	-0.01 (0.02)	0.27 (0.02)	0.02 (0.02)	0.02 (0.02)
		0.13 (0.02)	0.14 (0.02)	0.21 (0.02)	0.33 (0.02)	0.09 (0.02)	0.03 (0.02)	0.17 (0.02)	0.28 (0.02)	0.08 (0.02)	0.17 (0.02)

Continued on next page

Table 4. Continued.

	WG7	WG8	WG9	WG10	SC365	SC450	SC550	TG1	TG2	TG3
W120	0.39 (0.04)	0.19 (0.04)	0.27 (0.04)	0.34 (0.05)	0.49 (0.04)	0.41 (0.04)	0.40 (0.04)	0.16 (0.06)	0.13 (0.09)	0.18 (0.06)
W210	0.56 (0.03)	0.27 (0.04)	0.39 (0.04)	0.43 (0.04)	0.56 (0.03)	0.49 (0.04)	0.48 (0.04)	0.24 (0.06)	0.17 (0.09)	0.25 (0.06)
W365	0.82 (0.02)	0.66 (0.03)	0.71 (0.03)	0.57 (0.04)	0.53 (0.03)	0.49 (0.03)	0.49 (0.04)	0.28 (0.05)	0.24 (0.08)	0.32 (0.06)
W450	0.88 (0.01)	0.77 (0.02)	0.80 (0.02)	0.68 (0.04)	0.44 (0.03)	0.41 (0.03)	0.42 (0.04)	0.25 (0.05)	0.22 (0.09)	0.28 (0.06)
W550	0.93 (0.01)	0.74 (0.02)	0.86 (0.01)	0.81 (0.02)	0.42 (0.04)	0.38 (0.04)	0.41 (0.04)	0.22 (0.05)	0.26 (0.08)	0.29 (0.06)
WG1	0.69 (0.03)	0.33 (0.05)	0.48 (0.05)	0.46 (0.05)	0.50 (0.04)	0.48 (0.04)	0.47 (0.05)	0.31 (0.06)	0.16 (0.10)	0.30 (0.07)
WG2	0.80 (0.02)	0.92 (0.01)	0.84 (0.02)	0.49 (0.05)	0.22 (0.05)	0.23 (0.04)	0.26 (0.05)	0.19 (0.06)	0.24 (0.09)	0.26 (0.07)
WG3	0.65 (0.04)	0.79 (0.03)	0.73 (0.03)	0.74 (0.03)	-0.07 (0.05)	-0.03 (0.05)	-0.02 (0.06)	0.04 (0.07)	0.02 (0.11)	0.02 (0.09)
WG4	0.72 (0.03)	0.34 (0.06)	0.69 (0.03)	0.84 (0.02)	0.18 (0.06)	0.15 (0.06)	0.21 (0.06)	0.05 (0.07)	0.32 (0.10)	0.20 (0.07)
WG5	0.91 (0.01)	0.82 (0.02)	0.84 (0.02)	0.58 (0.05)	0.40 (0.04)	0.39 (0.04)	0.41 (0.04)	0.29 (0.05)	0.25 (0.08)	0.33 (0.06)
WG6	0.95 (0.01)	0.93 (0.01)	0.92 (0.01)	0.72 (0.03)	0.29 (0.04)	0.30 (0.04)	0.32 (0.04)	0.24 (0.05)	0.20 (0.09)	0.27 (0.06)
WG7	-	0.85 (0.01)	0.97 (0.00)	0.86 (0.02)	0.29 (0.04)	0.29 (0.04)	0.32 (0.04)	0.20 (0.05)	0.27 (0.08)	0.28 (0.06)
WG8	0.64 (0.01)	-	0.91 (0.01)	0.68 (0.03)	0.12 (0.04)	0.14 (0.04)	0.17 (0.05)	0.16 (0.06)	0.17 (0.08)	0.20 (0.06)
WG9	0.90 (0.00)	0.76 (0.01)	-	0.88 (0.01)	0.17 (0.04)	0.18 (0.04)	0.22 (0.04)	0.14 (0.05)	0.27 (0.08)	0.24 (0.06)
WG10	0.69 (0.01)	0.27 (0.01)	0.72 (0.01)	-	0.09 (0.05)	0.09 (0.05)	0.13 (0.05)	0.06 (0.06)	0.22 (0.09)	0.16 (0.07)
SC365	0.33 (0.02)	0.25 (0.02)	0.23 (0.02)	0.06 (0.02)	-	-	0.91 (0.01)	0.63 (0.05)	0.26 (0.08)	0.57 (0.05)
SC450	0.43 (0.03)	0.33 (0.02)	0.34 (0.03)	0.21 (0.02)	0.78 (0.01)	0.80 (0.01)	0.97 (0.01)	0.83 (0.02)	0.32 (0.08)	0.74 (0.04)
SC550	0.49 (0.03)	0.28 (0.02)	0.41 (0.03)	0.31 (0.02)	0.58 (0.02)	0.64 (0.02)	-	0.83 (0.03)	0.54 (0.07)	0.85 (0.02)
TG1	0.28 (0.02)	0.22 (0.02)	0.27 (0.02)	0.27 (0.02)	0.02 (0.03)	0.02 (0.03)	-	-	0.36 (0.09)	0.87 (0.03)
TG2	0.18 (0.02)	-0.02 (0.02)	0.17 (0.02)	0.21 (0.02)	-0.19 (0.04)	-0.14 (0.04)	0.49 (0.03)	0.01 (0.03)	-	0.77 (0.05)
TG3	0.32 (0.02)	0.14 (0.02)	0.30 (0.02)	0.33 (0.02)	-0.12 (0.04)	0.32 (0.03)	0.74 (0.02)	0.67 (0.02)	0.75 (0.01)	-

W = weight at standard age; WG = weight gain.

The highest residual correlations (Table 4) were observed between traits measured at standard ages, whereas the magnitude of residual correlations between measures of weight gain and testicular growth was low and negative correlations were frequently observed between subsequent measurements. Negative and low residual correlations were also observed between weight gain and weights and between testicular growth and measures of scrotal circumference. This finding indicates that environments favoring some traits can be unfavorable for others. These negative and low residual correlations especially between chronologically close measures suggest that climatic changes that occur during the year are the main factors responsible, although the contemporary groups included this effect.

With respect to weight and scrotal circumference, the highest residual correlation was observed between adjacent measures, i.e., the more distant the two measurements, the more distinct the environmental conditions and the non-additive genetic effects that influenced them. Analyzing the correlations between weight gains and weights at standard ages, the highest correlation was found between weight gain and weight measured at its upper limit, as observed for genetic correlations.

The higher heritabilities for weight and scrotal circumference measured at standard ages when compared to weight gain and scrotal growth also seem to be the result of the lower residual correlations compared to genetic correlations between gains. This fact also explains the increase of heritabilities for weight and scrotal circumference with increasing age of the animals.

Since weight and scrotal circumference measured at standard ages are normally used in Brazil as the main selection criteria for Nelore cattle, the response to selection of these traits was evaluated using different criteria that could be adopted (Figures 1 and 2). The use of weights at standard ages as selection criteria showed that, except for W210, direct selection is the most effective approach to increase weight at a certain age. Selection for weight at a certain age shows a similar efficiency to increase weights at previous ages as direct selection for these traits. WG1, WG6 and WG7 were found to be the most effective selection criteria among the weight gain traits. Among the testicular traits, SC365 was the most effective selection criterion to increase weights in the next generation.

When the objective was to increase scrotal circumference at different ages, the best selection criteria were W365 and WG5 among weight traits and TG1 among testicular traits since these traits showed the highest increases irrespective of age. With respect to scrotal circumference at a standard age, SC450 was found to be an attractive criterion since the gains obtained by indirect selection at other ages were similar to those obtained by direct selection.

Considerations regarding the choice of selection criteria for Nelore cattle

First, weights at standard ages are the best criteria since they respond more effectively to selection, providing also substantial indirect gains in other traits. W550 was found to be the most effective selection criterion among the weight traits studied. However, the choice of the selection criterion should take into account the importance of the traits for the breeder and the cost of maintenance of the animals until the age of recording.

The estimated genetic correlations between weight gain and weight at a standard age suggest the alternative use of the former as a selection criterion since they provoke a smaller increase in birth weight and mature weight. In addition, other studies have demonstrated favorable associations between these measures and other traits of economic interest (Arthur et al., 2001). Further studies investigating weight gain as a selection criterion for Nelore cattle are necessary.

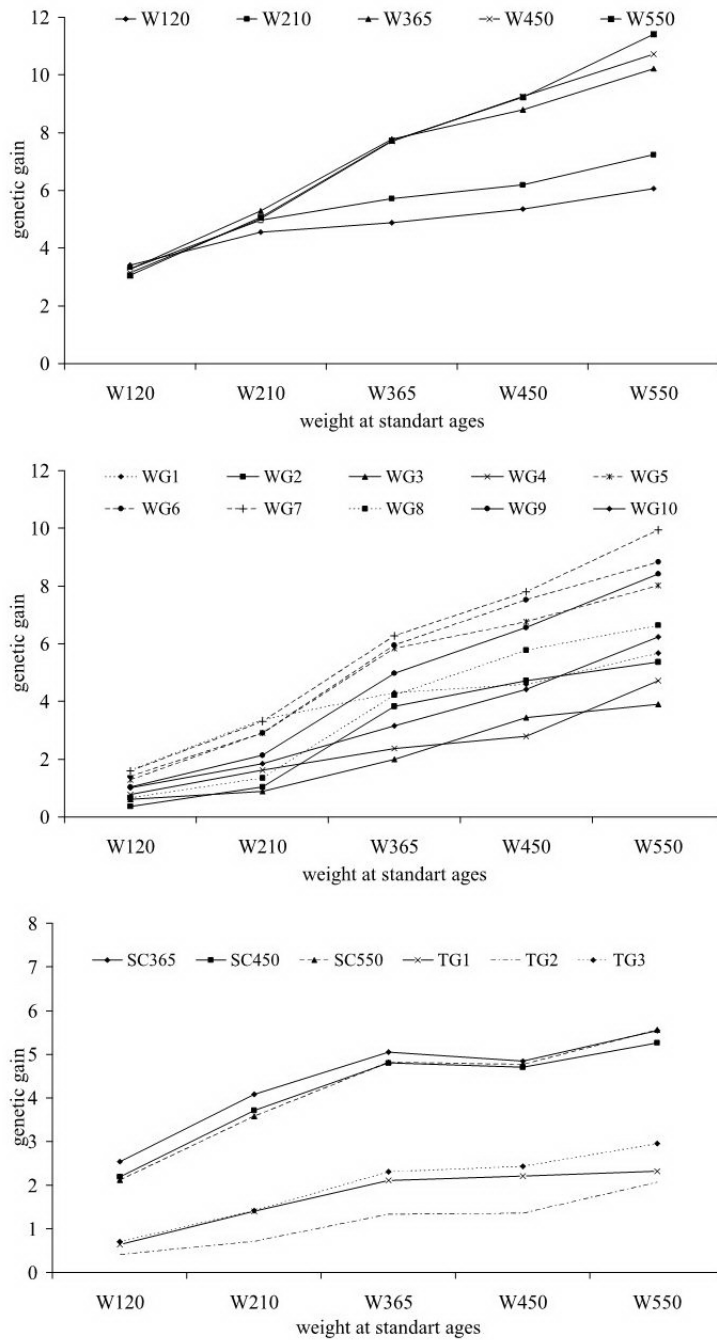


Figure 1. Expected response to selection for weights at standard ages, when the selection is done through: **A.** weights at standard ages (W, in kg), **B.** weight gain (WG, in kg), and **C.** scrotal circumference (SC) and testicular growth (TG), both in cm.

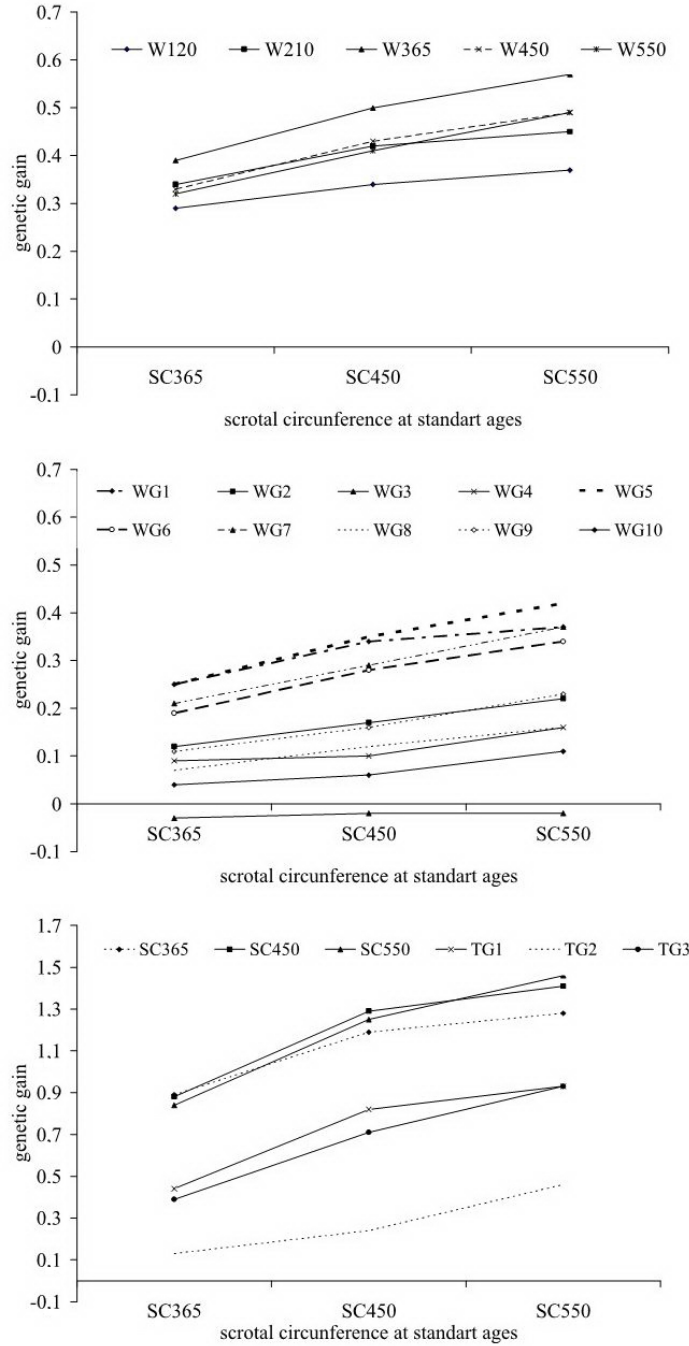


Figure 2. Expected response to selection for scrotal circumference, when the selection is done through: **A.** weights at standard ages (W, in kg), **B.** weight gain (WG, in kg), and **C.** scrotal circumference (SC) and testicular growth (TG), both in cm.

With respect to testicular traits, SC365 was found to be the best selection criterion since its heritability was similar to that of SC450 and SC550, in addition to presenting a higher genetic correlation with weights at standard ages. In this respect, the fact that this trait manifests at a younger age permits a reduction in the generation interval. According to Toelle and Robison (1985), early testicular traits are a reflex of body development, whereas late traits are influenced by the hormonal system. This statement is supported by the higher genetic correlations between weights and SC365 observed in this study, with higher testicular activity being observed after this age in Zebu animals. As a consequence, measures obtained after 365 days of age may present a higher correlation with female reproductive traits.

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