

Heritability estimates and genetic correlations for body weight and scrotal circumference adjusted to 12 and 18 months of age for male Nellore cattle

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Heritability estimates and genetic correlations were obtained for body weight and scrotal circumference, adjusted, respectively, to 12 (BW12 and SC12) and 18 (BW18 and SC18) months of age, for 10 742 male Nellore cattle. The adjustments to SC12 and SC18 were made using a nonlinear logistic function, while BW12 and BW18 were obtained by linear adjustment. The contemporary groups (CGs) were defined from animals born on the same farm, in the same year and birth season. The mean heritability estimates obtained using the restricted maximum likelihood method in bi-trait analysis were 0.25, 0.25, 0.29 and 0.42 for BW12, BW18, SC12 and SC18, respectively. The genetic correlations were 0.30 ± 0.11 , 0.21 ± 0.13 , 0.21 ± 0.11 , -0.08 ± 0.15 , 0.16 ± 0.12 and 0.89 ± 0.04 between the traits BW12 and BW18; BW12 and SC12; BW12 and SC18; BW18 and SC12; BW18 and SC18; and SC12 and SC18. The heritability for SC18 was considerably greater than for SC12, suggesting that this should be included as a selection criterion. The genetic correlation between BW18 and SC12 was close to zero, indicating that these traits did not influence each other. The contrary occurred between SC12 and SC18, indicating that selection using one of these could alter the other. Because of the mean magnitudes of heritabilities in the various measurements of weight and scrotal perimeter, it is suggested that the practice of individual selection for these traits is possible.

Keywords: beef cattle, nonlinear model, genetic parameters, adjusted weights

Implications

Heritability estimates and genetic correlations were obtained for body weight and scrotal circumference at 12 and 18 months of age in Nellore cattle. All the measurements were obtained at different ages and it was necessary to adjust the data. Linear functions were used for the body weight adjust; however, nonlinear functions were more appropriate for the scrotal circumference adjust. The results contribute to the development of genetic improvement programs for Nellore cattle and can be applied to improving meat productivity in Brazil.

Introduction

Zebu breeds of cattle, particularly Nellore, present good adaptation to tropical environments and their adversities.

Thus, their use during the process of forming herds in Brazil was of fundamental importance in enabling beef production to attain importance in this country's economy. Therefore, it is essential to study the genetic and environmental factors that influence the development of these animals. Through this, greater support can be provided for animal genetic improvement programs.

The productive performance of the herds needs to be evaluated according to traits connected with the quantity and quality of the meat produced. Body weight (BW) measured at different ages is often used with the aim of identifying the most productive animals. BW measurements present heritability of medium to high magnitude and are highly correlated with each other, thus indicating that BW data obtained at young ages can be used as selection criteria for Zebu breeds (Garnero *et al.*, 2001; Mucari and Oliveira, 2003). These authors used weights at different ages that were adjusted by means of linear interpolation and, in this way, they corrected for weight measurements made at different ages.

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Scrotal circumference (SC) measurements can also be used as selection criteria in programs aiming to improve production efficiency, since they present medium to high heritability (Quirino and Bergmann, 1998; Gressler *et al.*, 2000; Pereira *et al.*, 2000; Silveira *et al.*, 2004) and favorable genetic associations with production traits (Moser *et al.*, 1996; Cyrillo *et al.*, 2001; Garnero *et al.*, 2001) and reproductive traits (Martin *et al.*, 1992; Gressler *et al.*, 2000; Gianlorenço *et al.*, 2003; Boligon *et al.*, 2007). Furthermore, because SC is an easily measured trait and can be measured at young ages (weaning, 365 days of age and 550 days of age), this makes it possible to identify animals that are genetically superior in relation to these traits.

Standardization of body measurements at certain ages is necessary to compare animals' performances, because they are weighed at different ages to facilitate husbandry. Adjustment of body measurements according to age is often done using linear models. However, it is known that the growth of cattle is described by a sigmoid curve. Thus, it is expected that nonlinear models would describe their body growth better (Laird, 1965). For beef cattle, in particular Zebu breeds, the standard ages of 205, 365 and 550 days are used.

Nonlinear functions were studied by Lôbo and Martins Filho (2002), who observed that sigmoid functions are more appropriate than linear regression equations, for adjusting the growth of beef cattle. Those authors observed that the use of linear or nonlinear models for adjusting body measurements at different ages could influence the selection process and the expected response to the selection.

The aim of the present study was to estimate heritabilities and genetic correlations for weights and scrotal circumferences adjusted to 12 and 18 months, for Nellore cattle.

Material and methods

Animals and management

Data were collected from 10742 Nellore animals, born between 1990 and 2003, belonging to 21 farms located in the state of São Paulo, Brazil. These farms were participating in the Nellore Brazil Program, coordinated by the National Association of Breeders and Researchers ('Associação Nacional de Criadores e Pesquisadores' - ANCP). The animals were raised under a pasture regime without supplemental feeding. The calves were weaned at 7 to 8 months of age. The reproductive management consisted of a breeding season lasting from 60 to 120 days using artificial insemination or controlled natural breeding. An index termed 'total genetic merit', which was developed by Nellore Brazil Program, was used to select genetically superior males and females. This index included breeding value estimates for the following weighted traits: maternal ability (0.20), pre-weaning gain (0.20), post-weaning gain (0.20), yearling gain (0.20) and scrotal circumference at 12 (0.10) and 18 months of age (0.10).

Measurements and adjustments of body weight and scrotal circumference for age

BWs were obtained every 3 months between birth and a maximum of 18 months and SCs were measured every 3 months between the ages of 200 and 1020 days. To measure the SC, a metal measuring tape graduated in millimeters was used, positioned at the medial position of the scrotal sac, at the point of the greatest dimension, wrapping around both testicles and the scrotal skin.

The body weights at 12 and 18 months (BW12 and BW18) were derived as the product of observed BW and a linear correction factor, i.e. the ratio between the expected BWs at 12 and 18 months and the expected BWs at each age. The expected BWs at each age were obtained by means of quadratic regression of BW according to age. Thus, the BW considered was the one closest to the BW at 12 or 18 months, within intervals of 11 to 13 months or 17 to 19 months, respectively.

Analyses using least-squares methods indicated that linear adjustments were not efficient for correcting the SCs. Thus, it was decided to use a nonlinear correction factor for adjusting the SC. The SCs at 12 and 18 months (SC12 and SC18) were obtained from the nonlinear logistic function used by Nelder (1961). This was found to be the best out of six nonlinear curves for SC growth that were tried out in relation to the present database: Brody, Richards, Von Bertalanffy, Logistic, Gompertz and modified Logistic form, respectively, Brody (1945), Richards (1959), Von Bertalanffy (1957), Nelder (1961), Laird (1965) and Quirino *et al.* (1999). The nonlinear logistic function was described as follows:

$$Y_t = A (1 + e^{-kt})^{-m} + \varepsilon,$$

where 'Y' is the SC in cm adjusted for age 't'; 'A', the asymptotic value of 'Y' when 't' tends towards infinity, interpreted as the SC of an adult animal; 'e', natural logarithm; 'k', maturation rate; 't', animal's age in days; 'm', a constant that defines the shape of the curve and ' ε ', the random error associated with each measurement.

Data editing and contemporary groups

The data included were limited to offspring whose parents and birth dates were known. The definition of contemporary group (CG) was the same for all traits and comprised animals belonging to the same farm that were born in the same year and birth season. Two birth seasons were defined: calves born from October to March (rainy season) and calves born from April to September (dry season). The exclusion criteria were sires with less than three offsprings in each variable, CG showing less than five observations per trait and animals that died during husbandry.

Statistical analysis

The variance and covariance components and the respective estimates of heritability and the genetic and environmental correlations were obtained using the restricted maximum likelihood method, in bi-trait animal models, using the multiple-trait derivative-free restricted maximum likelihood (MTDFREML) software described by Boldman *et al.* (1995). The relationship matrix included 42 734 animals. The mixed model used in the two-trait analysis was:

$$\begin{bmatrix} y_1 \\ y_2 \end{bmatrix} = \begin{bmatrix} X_1 & 0 \\ 0 & X_2 \end{bmatrix} \begin{bmatrix} b_1 \\ b_2 \end{bmatrix} + \begin{bmatrix} Z_1 & 0 \\ 0 & Z_2 \end{bmatrix} \begin{bmatrix} a_1 \\ a_2 \end{bmatrix} + \begin{bmatrix} e_1 \\ e_2 \end{bmatrix},$$

where y_1 and y_2 represented different traits. The fixed-effect vectors for trait 1 (b_1) and trait 2 (b_2) were CGs, and the effect of the age of the dam at calving was a second-degree linear covariable. These effects were significant (P < 0.05) for all traits studied. The vectors a_1 and a_2 were random additive genetic effects, and e_1 and e_2 were residual effects for traits 1 and 2, respectively. The incidence matrices X_1 and X_2 associated elements of b_1 and b_2 with the records in y_1 and y_2 . The incidence matrices Z_1 and Z_2 associated elements of a_1 and a_2 with the records in y_1 and y_2 . The expectation of y_1 was X_1b_1 , and the expectation of y_2 was X_2b_2 ; the variance—covariance structure of random effects of the two-trait animal model was as follows:

$$\operatorname{Var} \begin{bmatrix} a_1 \\ a_2 \\ e_1 \\ e_2 \end{bmatrix} = \begin{bmatrix} A\sigma_{a_1}^2 & A\sigma_{a_1a_2} & 0 & 0 \\ A\sigma_{a_2a_1} & A\sigma_{a_2}^2 & 0 & 0 \\ 0 & 0 & I\sigma_{e_1}^2 & I\sigma_{e_1e_2} \\ 0 & 0 & I\sigma_{e_1e_2} & I\sigma_{e_2}^2 \end{bmatrix},$$

where $\sigma_{a_1}^2$ and $\sigma_{a_2}^2$ were direct additive genetic variances, $\sigma_{e_1}^2$ and $\sigma_{e_2}^2$ were the residual variances for traits 1 and 2, respectively; $\sigma_{a_1a_2}$ was the direct genetic covariance between traits 1 and 2, and $\sigma_{e_1e_2}$ was their residual covariance.

Six data sets were generated, combining the four studied traits in pairs, in which only the animals with both of the measurements in the pair were retained. In this way, standard error values for the estimates were obtained. The final data set is described in Table 1.

Results

The general means observed and the respective standard deviations, coefficients of variation, total numbers of observations and maximum and minimum values for BW12, BW18, SC12 and SC18 are presented in Table 2.

The heritabilities estimates in bi-trait analysis for each of the traits (BW12, BW18, SC12 and SC18) with the others ranged from 0.13 \pm 0.03 to 0.32 \pm 0.06; from 0.23 \pm 0.05 to 0.27 \pm 0.05; from 0.27 \pm 0.05 to 0.31 \pm 0.05 and from 0.42 \pm 0.06 to 0.43 \pm 0.06, respectively. The low values of the standard errors provided greater confidence in these estimates. The heritability estimates imply that a considerable proportion of the expression of these traits was due to

Table 1 Total number of animals and numbers of sires, dams and animals in contemporary groups (CG) considered in bi-trait analyses of body weight (BW) and scrotal circumference (SC) adjusted for 12 (BW12 and SC12) and 18 (BW18 and SC18) months of age

Traits*	Number of animals	Sires	Dams	CG
BW12 and BW18	6609	288	4080	216
BW12 and SC12	3870	210	2723	136
BW18 and SC18	3908	212	2738	137
BW12 and SC18	3899	212	2733	137
BW18 and SC12	3870	212	2723	135
SC12 and SC18	3705	165	2621	132

^{*}Same structure data for both traits.

Table 2 Numbers of observations (n), means, standard deviations (s.d.), coefficients of variation (CV) and minimum (Min) and maximum (Max) values for body weights (BWs) and scrotal circumference (SC) adjusted for 12 (BW12 and SC12) and 18 (BW18 and SC18) months of age

Trait	n	$Mean \pm s.d.$	CV (%)	Min	Max
BW12 (kg)	8543	255.08 ± 31.75	12.44	153.05	407.65
BW18 (kg)	7888	341.46 ± 46.93	13.75	200.22	583.68
SC12 (cm)	7036	19.38 ± 2.19	11.28	10.70	26.33
SC18 (cm)	6978	25.73 ± 3.18	12.37	12.42	36.41

Table 3 Mean heritability estimates (diagonal), and estimates of genetic (above diagonal) and environmental (below diagonal) correlations obtained in bi-trait analyses for body weight (BW) and scrotal circumference (SC), adjusted for 12 (BW12 and SC12) and 18 (BW18 and SC18) months of age

Variable	BW12	BW18	SC12	SC18
BW12	0.25	0.30 ± 0.11	0.21 ± 0.13	0.21 ± 0.11
BW18	0.80 ± 0.02	0.25	-0.08 ± 0.15	0.16 ± 0.12
SC12	$\textbf{0.58} \pm \textbf{0.03}$	0.56 ± 0.04	0.29	0.89 ± 0.04
SC18	0.55 ± 0.04	0.63 ± 0.04	0.53 ± 0.03	0.42

the additive effect of the genes. This makes individual selection practices possible, taking these values as the criteria.

Table 3 presents the mean heritabilities estimated for each trait and the genetic and environmental correlations obtained through bi-trait analyses. The genetic and environmental correlations estimated for the traits studied were all favorable, with the exception of the genetic correlation between BW18 and SC12. The high environmental correlation indicated that both traits were influenced by the same environmental conditions and by the same genes with non-additive action.

Discussion

The means for BW12 obtained in the present study were greater than those found by Perotto *et al.* (2001) and Boligon *et al.* (2008), who found 185.56 ± 2.3 and $217.29 \, \text{kg}$,

respectively. For BW18, Boligon *et al.* (2008), Horimoto *et al.* (2007) and Siqueira *et al.* (2003) reported lower means, of 269.84 kg, 319.6 \pm 38.80 kg and 293 \pm 49 kg, respectively. However, the herds studied in the present work were participating in a genetic improvement program for which the suggested selection criteria included traits that favored BW12 and BW18. Thus, higher means were expected. On the other hand, some of these authors (Siqueira *et al.*, 2003; Boligon *et al.*, 2008) presented means that were for males and females, and lower means were expected. Furthermore, the production system in Brazil is extensive and dependent on environmental, nutritional (grazing) and management factors that could influence the mean values.

Dias *et al.* (2003) obtained means that were similar to those of the present study for SC18 (26.33 cm). Horimoto *et al.* (2007) estimated higher adjusted values for SC18 (27.7 cm) in a herd in which the selection criterion (SC) had the aim of improving early sexual maturity.

The mean heritability estimates in bi-trait analysis for BW12 and BW18 were 0.25. These estimates were lower than those found in the literature for BW12 in the Nellore breed (Quirino and Bergmann, 1998) and the Canchim breed (da Silva *et al.*, 2000). For BW18, the heritability estimates in the literature consulted ranged from 0.30 to 0.70 (Quirino and Bergmann, 1998; Garnero *et al.*, 2001; Siqueira *et al.*, 2003; Silveira *et al.*, 2004), in animals of Nellore breed.

In the present study, the higher heritability estimate found for SC at the age of 18 months was indicative of individual selection that was more efficient than the selection at 12 months. Thus, selection for SC18 would result in greater gains, because of the existence of genetic variability, probably because at the age of 18 months, a large proportion of the animals studied had already reached sexual maturity.

According to Dal-Farra et al. (1998), genetic selection for SC between the ages of 17 and 18 months seems to be most appropriate, since it enables identification of males that present early testicular growth, since the rate of growth gradually decreases when the animal reaches the age of puberty, which occurs at around 19.4 months, thereby characterizing earlier sexual maturity. Puberty has been estimated as the age of production of 50×10^6 sperm with 10% motility (Lunstra et al., 1978). Although puberty is related to weight in some species and to age in others, for cattle, body weight and age both are important in determining the age at puberty (Yelich et al., 1995). Brody (1945) concluded that puberty is the point at which selfaccelerating growth changes to self-inhibiting growth and that weight at puberty occurs at approximately 60% of mature weight in all species.

Similar heritability estimates for SC12 were found by da Silva *et al.* (2000), who found a heritability estimate of 0.30, for the Canchim breed.

The heritability estimates for SC18 in the present study are in agreement with the findings of Dias *et al.* (2003), who studied Nellore cattle and estimated a value of 0.42 ± 0.04 for SC18, taking BW18 and yearling age as covariables. However, Quirino and Bergmann (1998)

obtained high heritability for adjusted SC18 for Nellore cattle (0.70) when BW was included as a covariable, thereby resulting in reductions in the additive, environmental and phenotypic components of genetic variance. Silveira *et al.* (2004) obtained heritabilities of 0.39, for SC18, among animals of Nellore breed.

In general, BWs measured at different ages are highly associated genetically. However, the correlation obtained for BW12 and BW18 (0.30 \pm 0.11) was lower than that found by Santos et~al.~(2005) for the Nellore breed (0.97) and by Malhado et~al.~(2002) and Mucari and Oliveira (2003) for the Guzerá breed (0.65 and 0.62, respectively). Nonetheless, the high environmental correlation (0.80 \pm 0.02) indicated that not only were these traits influenced by additive action of the same genes but also there was a non-additive and/or environmental genetic association. Thus, selection for BW12 would result in better performance for BW18.

Even though the genetic correlations between BW12 and SC12, BW12 and SC18 and BW18 and SC18 were small, they were favorable and indicated that the traits evaluated were influenced by the same genes. The genetic correlation found between BW12 and SC12 was similar to what was estimated by Cucco (2008), an estimate of 0.15 in Brown Swiss beef cattle, and smaller than the finding of Quirino and Bergmann (1998) in Nellore cattle, for which the estimate was 0.47.

There are few studies correlating BW12 and SC18 in the Nellore breed. Cucco (2008) found a small genetic correlation between these traits (0.07), thus indicating that, contrary to our results, selection for BW12 would not result in genetic progression for SC18. For BW18 and SC18, the results from the present study show a smaller magnitude compared to that found by Garnero *et al.* (2001), Silveira *et al.* (2004) and Pereira *et al.* (2001), whose estimates were 0.40, 0.46 and 0.25, respectively.

Only the genetic association between BW18 and SC12 was unfavorable and practically zero, thus indicating that the genes involved in the expression of these traits are not the same. However, de Castro-Pereira *et al.* (2007) observed heritability estimate of 0.42 between BW18 and SC12, for Canchim cattle.

The genetic association between SC12 and SC18 was high and positive (0.89 \pm 0.04) and indicated that indirect selection of one trait by another is possible. Gressler *et al.* (2000) also obtained a high correlation between these traits (0.99).

Considering that selection for SC may improve the reproductive performance of the animals and that SC12 presented the lowest heritability estimate and unfavorable correlation with BW18, selection for SC18 would be more indicated, since it responds better to selection and may provide genetic gains in BW12 and BW18.

Conclusion

The heritability estimates for BWs and circumferences at 12 and 18 months indicated considerable additive genetic

variation for these traits. Thus, direct selection for SC18 is appropriate and may result in genetic progress towards increasing BWs at 12 and 18 months of age and SC measured at 12 months of age.

References

Boldman KG, Kriese LA, Van Vleck LD and Kachman SD 1995. A manual for use of MTDFREML. A set of programs to obtain estimates of variance and covariance. USDA-ARS, Clay Center, NE, USA.

Boligon AA, Rorato PRN and Albuquerque LG 2007. Correlações genéticas entre medidas de perímetro escrotal e características produtivas e reprodutivas de fêmeas da raça Nelore. Revista Brasileira de Zootecnia 36, 565–571.

Boligon AA, Albuquerque LG and Rorato PRN 2008. Associações genéticas entre pesos e características reprodutivas em rebanhos da raça Nelore. Revista Brasileira de Zootecnia 37, 596–601.

Brody S 1945. Bioenergetics and growth. Reinhold Publications Company, New York, NY, USA.

Cucco DC 2008. Estimativa de parâmetros genéticos para características de crescimento e perímetro escrotal na raça Pardo Suíço Corte. MSc, São Paulo University. Retrieved August 27, 2008, from http://www.teses.usp.br/teses/disponiveis/74/74131/tde-11032008-090556/

Cyrillo JNSG, Razook AG, Figueiredo LA, Bonilha Neto LM, Mercadante MEZ and Tonhati H 2001. Estimativas de tendências e parâmetros genéticos do peso padronizado aos 378 dias de idade, medidas corporais e perímetro escrotal de machos Nelore de Sertãozinho, SP. Revista Brasileira de Zootecnia 30. 56–65.

Dal-Farra RA, Fries LA and Lobato JFP 1998. Adjustment factors of scrotal circumference for age and yearling weight effects of young Nellore bulls. Revista Brasileira de Zootecnia 27, 1092–1096.

da Silva AM, de Alencar MM, de Freitas AR, Barbosa RT, Barbosa PF, Oliveira MCD, Correa LD, de Novaes AP and Tullio RR 2000. Heritabilities and genetic correlations for male body weight and scrotal circumference and female reproductive and growth traits, in Canchim cattle. Revista Brasileira de Zootecnia 29, 2223–2230.

de Castro-Pereira VM, de Alencar MM and Barbosa RT 2007. Estimates of genetic parameters and of direct and correlated responses to selection for growth and reproductive traits in a Canchim cattle herd. Revista Brasileira de Zootecnia 36, 1029–1036.

Dias LT, El Faro L and Albuquerque LG 2003. Estimativas de herdabilidade para perímetro escrotal de animais da raça Nelore. Revista Brasileira de Zootecnia 32, 1878–1882.

Garnero AV, Fernandes MB, Figueredo LFC and Lôbo RB 2001. Influência da incorporação de dados de progênies na classificação de touros da raça Nelore. Revista Brasileira de Zootecnia 30, 714–718.

Gianlorenço VK, Alencar MM, Toral FB, Mello SP, Freitas AR and Barbosa PF 2003. Herdabilidades e correlações genéticas de características de machos e fêmeas, em um rebanho bovino da raça Canchim. Revista Brasileira de Zootecnia 32, 1587–1593.

Gressler SL, Bergmann JAG, Pereira CS, Penna VM, Pereira JCC and Gressler MGM 2000. Estudo das associações genéticas entre perímetro escrotal e características reprodutivas de fêmeas Nelore. Revista Brasileira de Zootecnia 29, 427–437.

Horimoto ARVR, Ferraz JBS, Balieiro JCC and Eler JP 2007. Phenotypic and genetic correlations for body structure scores (frame) with productive traits and index for CEIP classification in Nellore beef cattle. Genetics and Molecular Research 6, 188–196.

Laird AK 1965. Dynamics of relative growth. Growth 29, 249-263.

Lôbo RNB and Martins Filho R 2002. Avaliação de métodos de padronização dos pesos corporais às idades de 205, 365 e 550 dias. Revista Brasileira de Zootecnia 31, 1695–1706.

Lunstra DD, Ford JJ and Echternkamp SE 1978. Puberty in beef bulls: hormone concentrations, growth, testicular development, sperm production and sexual aggressiveness in bulls of different breeds. Journal of Animal Science 46, 1054–1062

Malhado CHM, Souza JC, Silva LOC and Ferraz Filho PB 2002. Correlações genéticas, fenotípicas e de ambiente entre os pesos de várias idades em bovinos da raça Guzerá no estado de São Paulo. Archives of Veterinary Science 7, 71–75. Retrieved August 26, 2008, from http://ojs.c3sl.ufpr.br/ojs2/index.php/veterinary/article/viewFile/3971/3211

Martin LC, Brinks JS, Bourdon RM and Cundiff LV 1992. Genetic effects on beef heifer puberty and subsequent reproduction. Journal of Animal Science 70, 4006–4017.

Moser DW, Bertrand JK, Benyshek LL, McCann MA and Kiser TE 1996. Effects of selection for scrotal circumference in Limousin bulls on reproductive and growth traits of progeny. Journal of Animal Science 74, 2052–2057.

Mucari TB and Oliveira JA 2003. Análise genético-quantitativa de pesos aos 8, 12, 18 e 24 meses de idade em um rebanho da raça Guzerá. Revista Brasileira de Zootecnia 32, 1604–1613.

Nelder JA 1961. The fitting of a generalization of the logistic curve. Biometrics 17, 89–110.

Pereira E, Eler JP and Ferraz JBS 2000. Genetic correlation between scrotal circumference and some reproductive traits in Nellore cattle. Brazilian Journal of Animal Science 29, 1676–1683.

Pereira E, Eler JP and Ferraz JBS 2001. Genetic analysis of some reproductive traits and their relationship with weight traits in Nellore cattle. Arquivo Brasileiro de Medicina Veterinaria e Zootecnia 53, 720–727.

Perotto D, Cubas AC, Abrahao JJD and Mella SC 2001. Daily gain from weaning to yearling weight of purebred and crossbred Nellore cattle. Brazilian Journal of Animal Science 30, 730–735.

Quirino CR and Bergmann JAG 1998. Heritability of scrotal circumference adjusted and unadjusted for body weight in Nellore bulls using univariate and bivariate animal models. Theriogenology 49, 1389–1396.

Quirino CR, Bergmann JA, Vale Filho VR, Andrade VJ and Pereira JC 1999. Evaluation of four mathematical functions to describe scrotal circumference maturation in Nellore bulls. Theriogenology 52, 25–34.

Richards FJ 1959. A flexible growth function for empirical use. Journal of Experimental Botany 10, 290–300.

Santos PF, Malhado CHMM, Carneiro PLS, Martins Filho R, Azevedo DMMR, Cunha EE, Souza JC and Ferraz Filho PB 2005. Correlação genética, fenotípica e ambiental em características de crescimento de bovinos da raça Nelore variedade mocha. Archives of Veterinary Science 10, 55–60. Retrieved August 27, 2008, from http://ojs.c3sl.ufpr.br/ojs2/index.php/veterinary/article/view/4414/3487

Silveira JC, McManus C, Mascioli AS, Silva LOC, Silveira AC, Garcia JAS and Louvadini H 2004. Fatores ambientais e parâmetros genéticos para características produtivas e reprodutivas em um rebanho Nelore no estado do Mato Grosso do Sul. Revista Brasileira de Zootecnia 33, 1432–1444.

Siqueira RLPG, Oliveira JA, Lobo RB, Bezerra LAF and Tonhati H 2003. Análise da Variabilidade Genética Aditiva de Características de Crescimento na Raça Nelore. Revista Brasileira de Zootecnia 32, 99–105.

Von Bertalanffy L 1957. Quantitative laws in metabolism and growth. Quarterly Review of Biology 32, 217–231.

Yelich JV, Wettemann RP, Dolezal HG, Lusby KS, Bishop DK and Spicer LJ 1995. Effects of growth rate on carcass composition and lipid partitioning at puberty and growth-hormone, insulin-like growth-factor. 1. Insulin, and metabolites before puberty in beef heifers. Journal of Animal Science 73, 2390–2405.