

Genetic parameters estimation of growth in Polled Nellore cattle via random regression models

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Abstract

In genetic breeding programs, body weight is measured overtime, and is historically the main source of information from animals. Random Regression Models (RRM) have been frequently used in beef cattle evaluations, but can significantly contribute to genetic progress in all species of economic importance. To our knowledge, there are no scientific studies using RRM to evaluate Polled Nellore. We aimed to estimate genetic parameters by using RRM as a way to provide basis for guidelines development of growth of this breed. The models included direct genetic and maternal genetic, permanent environmental and maternal permanent environmental as random, contemporary groups as fixed and cow age at calving as covariate effects. The residual variances were modeled from homogeneous to six heterogeneous classes. The model of orders 4, 2, 2 and 2 for direct additive genetic, maternal additive genetic, maternal permanent environmental and permanent environmental had greater performance according to statistical criteria (smaller AIC and BIC values). Estimates of direct additive genetic increased over time (range 0-5,000 Kg²) and the heritability estimates were up to 0.73 along the growth curve. Maternal heritability estimates were low, with values close to zero. Genetic correlations between ages ranged from moderate (0.60) to high (0.97). Random regression models may be an alternative to describe the changes in body weight variances throughout lifetime.

Keywords: genetic correlation, heritability, longitudinal data, orthogonal polynomials

Introduction

In genetic breeding programs, body weight is measured overtime, and historically are the main source of information of animals. These traits are traditionally analyzed as different traits through pre-adjustment at standard ages (Albuquerque and Meyer 2001). However, this methodology can reduce precision in genetic evaluations due to the elimination of some sources of information (Bertipaglia et al 2012).

In this scenario, random regression models (RRM) have emerged as an alternative and does not require pre-adjustment. This methodology treats body weights as repeated measures and describes the variance components behavior throughout the growth curve. It may allow to estimate genetic parameters and breeding values more accurately to better identify growth stages of greater genetic variability for later selection (Baldi et al 2010).

Random regression has been frequently used on beef cattle but can significantly contribute to genetic progress in all species of economic importance. Some authors have reported that RRM showed to be suitable to describe growth variation changes as a function of age (Dias et al 2006; Baldi et al 2010; Sousa Júnior et al 2010; Boligon et al 2011).

The Polled Nellore cattle is an important breed that represents around 14% of the total zebu animals raised in Brazil. These animals have been raised apart from the traditional Nellore, and, therefore, considered as a distinct breed. Despite several studies using RRM for the traditional Nellore cattle (Dias et al 2006; Baldi et al 2010; Sousa Júnior et al 2010; Boligon et al 2011), to our knowledge, this is not the case for Polled Nellore. To us, by offering another alternative to improve breeding programs seems to be reasonable. The aims of this study were to estimate the types and orders of random effects of (co)variance functions at the description of the growth trajectory as well as to estimate covariance components and genetic parameters for Polled Nellore cattle by using random regression models as a way to provide basis for guidelines development of growth of this breed.

Materials and methods

Body weight records of Polled Nellore cattle were provided by the Brazilian Association of Zebu Breeders (ABCZ). These records were taken between 63 and 653 days old from animals raised in Northeast Brazil and born between 1975

and 2011. Up to 10 body weights were acquired from each animal (Table 1). The contemporary group (CG; $n=153$ levels) was defined by animals from the same herd, sex, feeding management, year of birth and date of weighting. The following assumptions were applied for data consistency: minimum of two records per animal and three animals per CG. At the end, a total of 10,839 observations from 1,924 animals originated from 244 sires and 1,619 dams were available (Figure 1). A total of 3,626 animals remained after pedigree pruning to build the numerator relationship matrix.

Table 1. Number and percentage of animals with records.

Data analysis	Number of animals	Percentage (%)
Animals with 3 records	7	0.4
Animals with 4 records	140	7.3
Animals with 5 records	540	28.1
Animals with 6 records	1,101	57.2
Animals with 7-10 records	136	7.0
Total	1,924	100

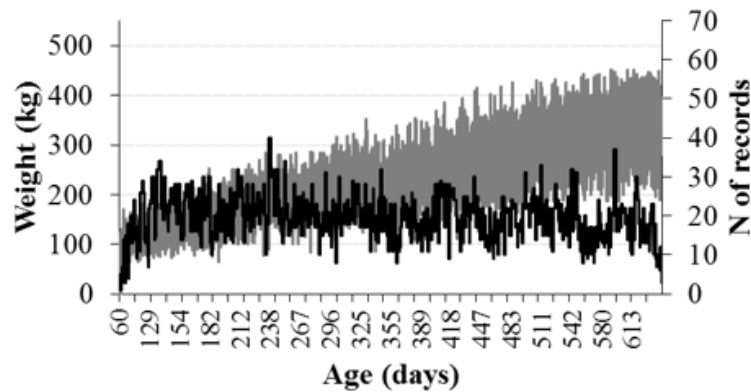


Figure 1. Number of records in black and body weights in gray of Polled Nellore animals.

The covariance components and genetic parameters were estimated via REML by using Wombat software (Meyer, 2007). The fixed regressions were tested for polynomials of third, fourth and fifth orders. These orders were chosen based on results from the traditional Nellore cattle (Dias et al 2006; Boligon et al 2011) since studies using Polled Nellore are scarce. RRM was fitted for each random effect, in which variables were described by Legendre polynomials from second to fourth orders. The contemporary groups were treated as fixed effect and the age of the cow at calving as covariate.

The residual variances were fitted in classes as follows: CL1 for homogenous; CL2 for 60-149 and 150-819 days; CL3 for 60-149, 150-299, and 300-819 days; CL4 for 60-149, 150-299, 300-499, and 500-819 days; CL5 for 60-149, 150-299, 300-419, 420-499, and 500-819 days; and CL6 for 60-149, 150-299, 300-419, 420-499, 500-649, and 650-819 days old. Here, CL m corresponds to heterogeneity variance modelling and m represents the number of classes. The covariance between additive genetic and maternal effects was assumed to be zero.

The models were compared via Akaike Information Criterion (AIC), and Schwarz' Bayesian Information Criterion (BIC).

The random regression model, in matrix notation can be described as follows:

$$y = X\beta + \Phi_1 d + \Phi_2 m + \Phi_3 mp + \Phi_4 p + e$$

where: y is the vector of observations, β is the vector of fixed effects, d , m , mp , p and e are vectors of direct additive genetic, maternal additive genetic, maternal permanent environmental, permanent environmental and residual random effects, respectively, and X , Φ_d , Φ_m , Φ_{mp} and Φ_p are incidence matrices.

The following assumptions were made:

$$E \begin{bmatrix} y \\ d \\ m \\ mp \\ p \\ e \end{bmatrix} = \begin{bmatrix} X\beta \\ 0 \\ 0 \\ 0 \\ 0 \\ 0 \end{bmatrix} \text{ and } V \begin{bmatrix} g \\ m \\ mp \\ p \\ e \end{bmatrix} = \begin{bmatrix} A \otimes k_d & 0 & 0 & 0 & 0 \\ 0 & A \otimes k_m & 0 & 0 & 0 \\ 0 & 0 & I_{Nm} \otimes k_{mp} & 0 & 0 \\ 0 & 0 & 0 & I_{Nd} \otimes k_p & 0 \\ 0 & 0 & 0 & 0 & R \otimes k_e \end{bmatrix},$$

where k_d , k_m , k_{mp} and k_p are, respectively, the direct additive genetic, maternal additive genetic, maternal permanent environmental and permanent environmental covariance matrices associated to the regression coefficients, A is the numerator relationship matrix; I_{Nd} is the identity matrix of dimension d (number of animals with records); I_{Nm} is the identity matrix of dimension m (number of cows with recorded calves); R is the diagonal matrix of residual variances, \otimes is the Kronecker product operator.

Results and discussion

The mean body weight was 228.78 ± 76.62 throughout the growth curve. This value is in the range reported in literature, e.g., by Amaral et al (2014), which reported an average of 168.78 and 307.25 Kg at 205 and 550 days, respectively in other Polled Nellore population.

The model Leg4222, i.e., of orders 4, 2, 2 and 2, respectively for direct additive genetic, maternal additive genetic, maternal permanent environmental and permanent environmental best fit due to AIC and BIC smaller values (Table 2). In general, models considering classes of residual variances best fit and indicated that residual variances were distinct throughout the growth curve (Table 3). Nevertheless, the number of classes of residual variance diverged between AIC and BIC criteria. According to AIC six classes were better whereas five seemed to be more appropriate for BIC (Table 2). Based on literature (Albuquerque and Meyer, 2001; Nobre et al 2003; Sakaguti et al 2003; Cyrillo et al 2004; Dias et al 2006) we assumed the model with six classes (Leg4222_6) as the best model to describe growth variations in this population. All of authors cited above suggested that residual variances are not constant and changes in residual variance behavior may be due to different treatments offered to animals during lifetime or even due to scale effect.

Table 2. Polynomial order for direct additive genetic, maternal additive genetic, permanent environmental and maternal permanent environmental effects, number of parameters (N_p), Akaike Information (AIC) and Schwarz Bayesian Information (BIC) criteria

Model	N_p	AIC	BIC
Leg2222_1	13	78,940.616	79,035.208
Leg3222_1	16	78,124.728	78,241.148
Leg3322_1	19	78,127.556	78,265.804
Leg4222_1	20	77,873.496	78,019.020
Leg4223_1	23	77,879.428	78,046.782
Leg4224_1	27	77,897.428	78,093.886
Leg4232_1	23	77,879.470	78,046.824
Leg4233_1	26	77,885.716	78,074.898
Leg4242_1	27	77,924.758	78,121.216
Leg4322_1	23	77,875.770	78,043.122
Leg4332_1	26	77,883.968	78,073.150
Leg4334_1	33	77,895.884	78,136.000
Leg4342_1	30	77,922.360	78,140.648
Leg4422_1	27	78,040.046	78,236.504
Leg4432_1	30	77,953.784	78,172.070
Leg4442_1	34	77,969.766	78,217.158
Leg4444_1	41	77,919.950	78,218.276
Leg4222_2	21	77,873.624	78,026.424
Leg4222_3	22	77,695.646	77,802.648
Leg4222_4	23	77,635.294	77,802.648
Leg4222_5	24	77,615.208	77,789.838
Leg4222_6	25	77,615.190	77,797.096

Leg $k_d k_p k_m k_{mp} r$, order of covariance function for direct additive genetic (k_d), permanent environmental (k_p), maternal additive genetic (k_m), maternal permanent environmental (k_{mp}) and classes of heterogeneous residual variance (r). Values in bold indicate best fit.

Estimates of direct additive genetic (A), maternal additive genetic (B), permanent environmental (C), maternal permanent environmental (D) and phenotypic (E) variances and standard errors (dashed line) under model Leg4222_6 are presented in Figure 2.

The estimates of direct additive genetic variance increased along the growth curve. This upward trend have been heavily described in literature for traditional Nellore (Albuquerque and Meyer 2001; Nobre et al 2003; Cyrillo et al 2004) and Tabapua (Dias et al 2006 and Sousa Júnior et al 2010) cattle. These estimates demonstrated genetic variability and plausible response to selection.

The maternal additive genetic variance were close to zero for the whole evaluated period (Figure 2). These results might be a consequence of the small number of offspring per dam, 1.19. In contrast, Nobre et al (2003) reported maternal additive genetic variances increasing from birth to adulthood. Dias et al (2006) observed that maternal additive genetic variance estimates increased up to 200 days old, decreased between 200 and 580 days and new increased after 580 days old. This trend reported by Dias et al (2006) has also been reported for different breeds (Mota et al 2013a).

The maternal permanent environmental variances were also small but slightly increased as the age increased (Figure 2). These values are lower than commonly reported in literature (Albuquerque and Meyer 2001; Cyrillo et al 2004; Dias et al 2006; Baldi et al 2010; Boligon et al 2010). These authors reported maximum estimates at weaning (up to 7 months) followed by gradual decrease after this period. Likewise, the estimates of permanent environmental variances were small but increased along the growth curve (Figure 2). Albuquerque e Meyer (2001) and Cyrillo et al (2004) reported similar trends in traditional Nellore cattle.

Phenotypic variance estimates showed gradual increased especially in adulthood (Figure 2). A sudden increased was also observed in the direct additive genetic variances after 543 days old and may explained such trend. Another explanation might come from the smaller number of records in this period which may cause unbiased estimates due to the phenomenon of Runge, (De Boor and Mathématicien 1978). Similar results were reported by Mota et al (2013b) and Bertipaglia et al (2012) in Simmental and Brahman beef cattle, respectively.

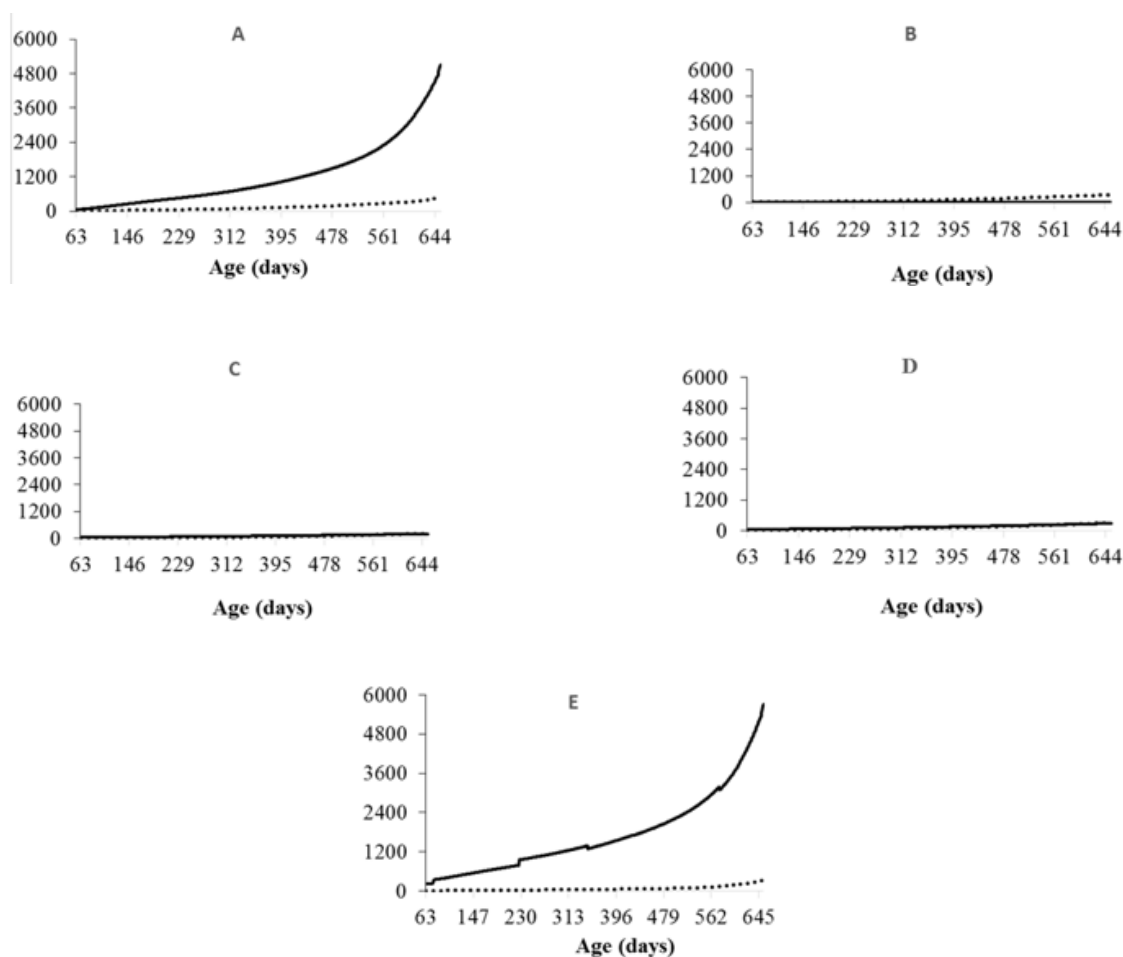


Figure 2. Estimates of direct additive genetic (A), maternal additive genetic (B), permanent environmental (C), maternal permanent environmental (D) and phenotypic (E) variances and respective standard errors (dashed line) under the best random regression model for different ages over time.

The direct heritability estimates displayed an increasing trend (Table 3). Our high values were similar than those reported by Lopes et al (2013). These authors observed values of 0.43, 0.61, 0.72 and 0.67 for 120, 240, 365 and 450 days old, respectively. Moderate to high direct heritability estimates were consequence of high direct additive genetic variance values. Pelicioni et al (2009) reported increasing heritability estimates up to 200 days old (from 0.03 to 0.52). On the other hand, several studies have been reported downward trend of direct heritability estimates up to weaning and subsequent increased until yearling (Albuquerque and Meyer 2001; Meyer 2001; Nobre et al 2003; Albuquerque e El Faro, 2008). The maternal heritability estimates were zero (Table 3). Boligon et al (2010) and Baldi et al (2010) reported maximum maternal heritability estimates in weaning, 0.16 and 0.11, respectively. In both studies the maternal heritabilities abruptly dropped after weaning and increased again from 400 days old. The estimates for maternal permanent environmental variances as a proportion of the phenotypic variances decreased from 100 days old (Table 3). In Tabapua cattle, Menezes et al (2013) reported gradual decreased after weaning, whereas Dias et al (2006) observed decrease from birth up to 70 days, an increased from 70-450 days and another decrease thereafter. In traditional Nellore, Albuquerque and Meyer (2001) reported constant estimates overtime. The estimates of proportion of residual variance increased from 100 to 205 days, decreased later on (Table 3). The decrease is possibly related to the smaller number of records in this period (Figure 1) as well as the lack of polynomial fit.

Table 3. Direct (h^2_d) and maternal (h^2_m) heritability estimates, and permanent environmental (p^2), maternal permanent environmental (mp^2) and residual (e^2) proportions of the phenotypic variance under the best random regression model for different ages over time.

Days	h^2_d	h^2_m	p^2	mp^2	e^2
205	0.42±0.05	0.00±	0.10±0.04	0.00±0.06	0.34±0.04
365	0.54±0.05	0.00±	0.08±0.04	0.00±0.08	0.29±0.04
450	0.65±0.07	0.00±	0.08±0.05	0.00±0.09	0.17±0.03
550	0.73±0.08	0.00±	0.07±0.06	0.00±0.09	0.11±0.02

The estimates of direct additive genetic, phenotypic, maternal additive genetic and maternal permanent environmental correlations for the model Leg4222_6 are presented in Tables 4 and 5. Standard ages (205, 365, 450 and 550 days) were selected for better illustration. The direct additive genetic correlations for weights at 205, 365, 450 and 550 were from moderate to high magnitude (range 0.60-0.97). It seemed that genetic effects from weaning to adulthood are controlled by the same group of genes and selection in earlier ages may change weights at advanced ages (Table 4). These results agreed with the literature in beef cattle (Sakaguti et al 2003; Nephawe 2004; Dias et al 2006; Baldi et al 2010; Sousa Júnior et al 2010; Mota et al 2013b). In general, the genetic correlations were higher between adjacent and smaller between non-adjacent ages. The phenotypic correlation estimates decreased as the age distance between ages increased (Table 4). Similar results were found by Albuquerque and Meyer (2001) and Cyrillo et al (2004) in traditional Nellore, and by Dias et al (2006) in Tabapua cattle.

Table 4. Direct additive genetic (abovediagonal) and phenotypic (below diagonal) correlations under the best random regression model for different ages over time

Days	205	365	450	550
205	-	0.91±0.02	0.80±0.03	0.60±0.05
365	0.57±0.05	-	0.97±0.01	0.85±0.02
450	0.53±0.05	0.78±0.03	-	0.95±0.01
550	0.43±0.07	0.70±0.04	0.81±0.03	-

The estimates of maternal additive genetic correlations were high (>0.99 ; Table 5). It corroborates with literature not only in traditional Nelore (Nobre et al 2003; Boligon et al 2010) but with other breeds such as Tabapua (Dias et al 2006; Sousa Júnior et al 2010; Menezes et al 2013), Canchim (Baldi et al 2010) and Simmental (Mota et al 2013a; Mota et al 2013b). Values close to unity were also observed for maternal permanent environmental correlations (Table 5). Several authors reported similar results in cattle (Cyrillo et al 2004; Dias et al 2006; Baldi et al 2010). More specifically, high correlation values were also found by Albuquerque e Meyer (2001) in traditional Nelore. These authors reported correlation values of 0.84, 0.85, and 0.95, respectively, between birth weight and weights at 240, 360 and 550 days old. In an old study, Boldman (1993) explained that in datasets with little available information, there is trend towards to values close to one not only for maternal permanent environmental but also maternal additive genetic effects. Medium to high values up to weaning demonstrated the importance of the permanent environmental effect at this point. It further indicated that if these factors affect the initial ages, it may reflect in advanced ages.

Table 5. Maternal additive genetic (above diagonal) and maternal permanent environmental (below diagonal) correlations under the best random regression model for different ages over time.

Days	205	365	450	550
205	-	1.00±0.19	0.99±0.33	0.99±0.56
365	1.00±0.06	-	1.00±0.09	0.99±0.57
450	1.00±0.12	1.00±0.02	-	0.99±0.25
550	0.99±0.20	1.00±0.05	1.00±0.01	-

Conclusion

- The random regression models of orders 4 for the direct genetic effect, 2 for the maternal genetic effect, 2 for the animal permanent environmental effect, and 2 for the maternal permanent environmental effect with 6 classes of residual variance were the most suitable to describe the changes in the body weight variances throughout lifetime.
- The estimates of this model demonstrated reasonable genetic variability and response to selection

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